International Journal of Molecular Zoology 2024, Vol.14, No.2, 84-96
http://animalscipublisher.com/index.php/ijmz

Review Article **Open Access**

Genomic Insights into the Adaptation of Reptiles to Extreme Environments

Xinghao Li, Hongbo Liang, Jia Xuan
Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
Corresponding email: jia.xuan@jicat.org

International Journal of Molecular Zoology, 2024, Vol.14, No.2 doi: 10.5376/ijmz.2024.14.0010
Received: 27 Jan., 2024
Accepted: 08 Mar., 2024
Published: 29 Mar., 2024

Preferred citation for this article:
Li X.H., Liang H.B., and Xuan J., 2024, Genomic insights into the adaptation of reptiles to extreme environments, International Journal of Molecular Zoology, 14(2): 84-96 (doi: 10.5376/ijmz.2024.14.0010)

Abstract Reptiles exhibit a remarkable diversity in habitats, ranging from arid deserts to high altitudes and marine environments. Understanding the genomic adaptations that enable reptiles to thrive in such varied conditions is essential for comprehending their evolutionary success. This study aims to elucidate the genetic mechanisms underpinning thermoregulation, arid environment survival, high-altitude adaptation, and marine life in reptiles. This study examined genetic mechanisms of heat and cold tolerance, water conservation strategies, oxygen transport efficiency, and saltwater tolerance through comprehensive genomic analyses. A detailed case study on desert-dwelling reptiles, including the Gila monster and various desert snakes and lizards, provides insights into their unique adaptations. Advanced genomic tools and techniques, such as next-generation sequencing and bioinformatics, have facilitated these discoveries. Our findings highlight emerging trends and challenges in reptilian genomics, with significant implications for conservation and evolutionary biology. Future research should focus on integrating functional genomics and gene editing to further explore these adaptive mechanisms and their applications in conservation efforts.

Keywords Reptilian genomics; Thermoregulation; Arid environment adaptation; High-altitude adaptation; Marine environment adaptation

1 Introduction

Reptiles, a diverse group of ectothermic vertebrates, have successfully colonized a wide range of habitats, from lush tropical forests to arid deserts. This adaptability is evident in the morphological, physiological, and behavioral traits that enable them to thrive in such varied environments. For instance, the lizard species *Liolaemus fuscus* has shown significant adaptations to the extreme conditions of the Atacama Desert, including lower evaporative water loss and morphological changes such as smaller body size and larger eyeballs (Araya-Donoso et al., 2021). Similarly, the South African sand lizards (Meroles) exhibit rapid speciation and morphological evolution as they adapt to desert conditions, particularly aeolian sand habitats. These examples underscore the remarkable ability of reptiles to adapt to extreme environments, making them an excellent model for studying evolutionary processes (Field et al., 2022).

Understanding the genomic basis of these adaptations is crucial, especially in the context of climate change and environmental fluctuations. Genomic studies can reveal the specific genes and pathways involved in adaptation, providing insights into the mechanisms that enable reptiles to survive and thrive in extreme conditions. For example, functional genomics approaches have identified a set of genes in lacertid lizards that are involved in physiological and morphological adaptations to climate, highlighting the role of a comparatively small set of genes in environmental adaptation (Valero et al., 2021). Additionally, chromosome-level genome assemblies, such as that of the desert horned lizard *Phrynosoma platyrhinos*, have provided insights into chromosomal rearrangements and the dynamic karyotypic evolution across reptiles (Koochekian et al., 2022). These genomic insights are not only important for understanding the evolutionary history of reptiles but also for informing conservation strategies, as many reptile populations are in decline due to habitat loss and climate change (Nordstrom et al., 2022).

This study investigates the genomic adaptations that enable reptiles to survive in extreme environments. By integrating genomic, physiological, and morphological data, this study identifies the specific genetic changes associated with adaptation to harsh conditions. This study will focus on several key questions: What are the genomic signatures of adaptation in reptiles inhabiting extreme environments? How do these genomic adaptations correlate with physiological and morphological traits? What are the evolutionary processes driving these adaptations, and how do they contribute to speciation? By addressing these questions, this study seeks to provide a comprehensive understanding of the mechanisms underlying reptilian adaptation to extreme environments, contributing to the broader field of evolutionary biology and offering valuable insights for conservation efforts.

2 Genomic Basis of Thermoregulation

2.1 Genetic mechanisms of heat tolerance

The genetic mechanisms underlying heat tolerance in reptiles have been extensively studied, revealing significant insights into how these organisms adapt to high-temperature environments. For instance, research on three sympatric species of Cuban *Anolis lizards* (*Anolis allogus*, *A. homolechis*, and *A. sagrei*) identified differentially expressed genes (DEGs) that are crucial for heat adaptation. In particular, the warm-adapted *A. homolechis* showed upregulation of ribosomal protein genes, suggesting that enhanced protein synthesis is a key physiological mechanism for coping with higher temperatures (Akashi et al., 2016). Additionally, a study on the *Sceloporus undulatus* complex demonstrated that effective thermoregulation can limit local adaptation of thermal tolerance, indicating that behavioral plasticity might hinder the evolutionary shift towards greater heat tolerance (Buckley et al., 2015). Furthermore, the evolutionary potential of heat tolerance in *Drosophila subobscura* was found to be influenced by the methodology used in thermal tolerance assays, with static assays providing higher heritability estimates than slow ramping assays (Castañeda et al., 2019).

2.2 Genomic adaptations to cold environments

Reptiles inhabiting cold environments have developed various genomic adaptations to survive low temperatures. For example, terrestrially hibernating reptiles like the hatchling painted turtles (*Chrysemys picta marginata*) exhibit freeze tolerance, which involves the upregulation of genes encoding proteins for iron binding, antioxidant defense, and serine protease inhibitors. These adaptations help counteract the effects of ischemia caused by plasma freezing (Storey, 2006). Similarly, a study on the tuatara (*Sphenodon punctatus*) demonstrated that these cold-adapted reptiles can modify their thermoregulatory behavior in response to different thermal environments, maintaining higher body temperatures even in low-quality habitats (Besson and Cree, 2010). Moreover, research on the invasive brown anole (*Anolis sagrei*) revealed that limited recombination in certain genomic regions might constrain the adaptation to colder climates, highlighting the role of genetic constraints in evolutionary stasis (Bock et al., 2023).

2.3 Evolutionary significance of thermoregulatory genes

The evolutionary significance of thermoregulatory genes is evident from their recurrent involvement in adaptation to various thermal environments. A comparative genomics study on lacertid lizards and other vertebrates identified a set of 200 genes with signatures of positive diversifying selection, many of which are involved in physiological and morphological adaptations to climate. These genes form a tightly connected interactome, enriched in functions related to climate adaptation and organismal stress response, indicating a high degree of functional similarity and posttranslational modifications across different species (Figure 1) (Valero et al., 2019; Valero et al., 2021). Additionally, the study on tropical *Anolis lizards* showed that cold tolerance evolves faster than heat tolerance due to the differential exposure to selection pressures, emphasizing the role of thermoregulatory genes in shaping evolutionary trajectories (Muñoz et al., 2014). The identification of candidate genes involved in high elevation adaptation in *Phrynocephalus lizards* further underscores the importance of coordinated changes in multiple genes for thermoregulation and overall fitness in extreme environments (Yang et al., 2014).

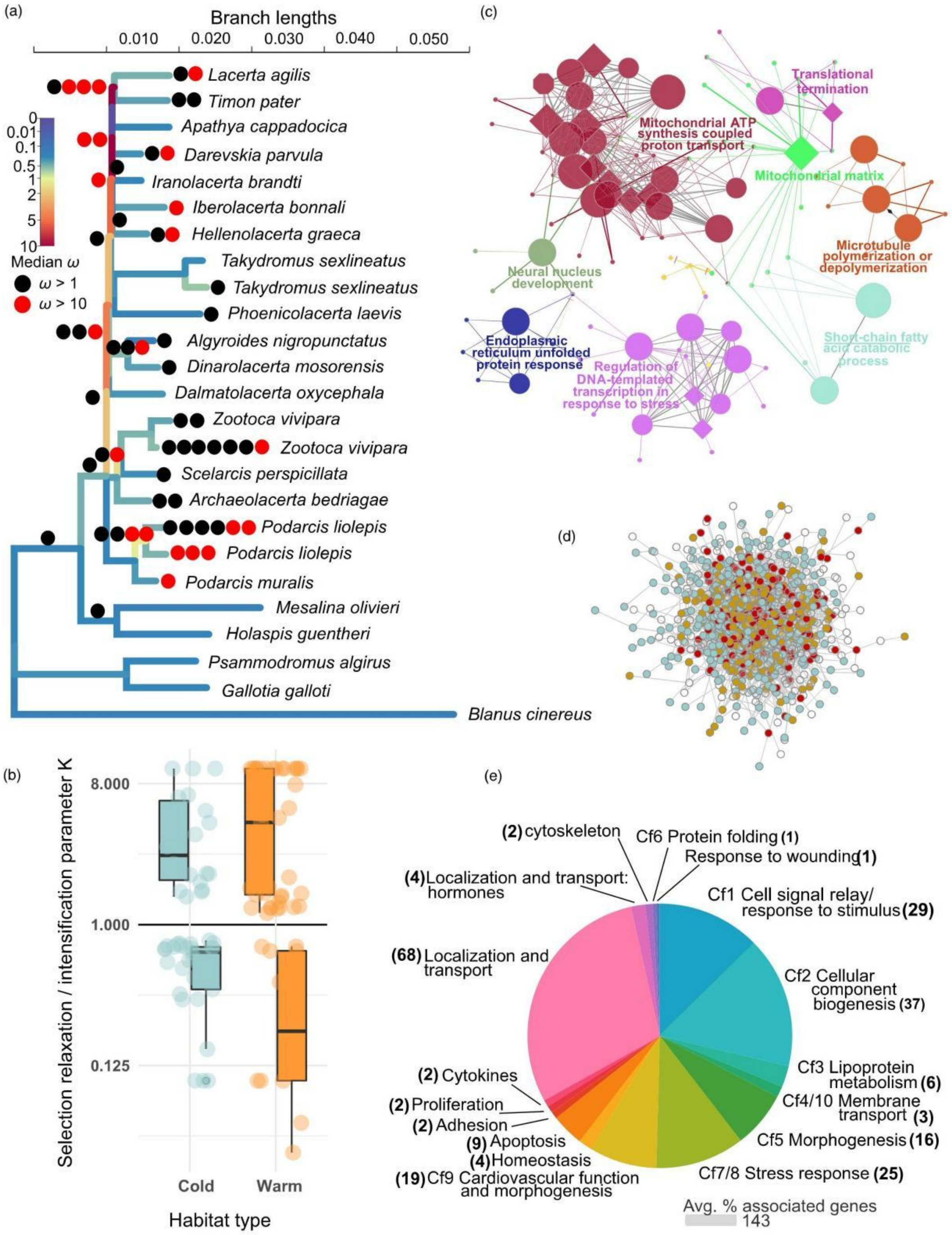

Figure 1 Phylogenetic and functional properties of lacertid and vertebrate pEAGs (Adopted from Valero et al., 2019)

Image caption: (a) Visualization of median selection coefficient (ω) on an RNAseq maximum likelihood phylogram of 24 lacertid species for 200 genes under episodic positive diversifying selection. Genes with $10 > \omega > 1$ and $\omega > 10$ are shown along the branches as circles. (b) Box and jitter plots showing genes with significant evidence for relaxation ($K \leq 1$) and intensification ($K \geq 1$) of selective pressure among cold- and warm-adapted clades. (c) Network of significantly enriched functions for these genes in Lacertidae (circles-biological process; diamond—molecular function; octagon—cellular component; and size of circles-number of genes per category). (d) Functional genomic network containing 902 pEAGs across endotherm and ectotherm vertebrates (blue-genes that adapted to environmental parameters more than once in different species; ochre-genes that are stress responsive; and maroon-genes that adapted in more than one species and are additionally stress responsive). (e) Graph of functional categories of significantly over-represented ClueGo Gene Ontology groups, for the 902 pEAGs, categorized by candidate functions (Cf) and additional functions. Numbers in labels refer to numbers of Gene Ontology terms within each category (Adopted from Valero et al., 2019)

3 Adaptations to Arid Environments

3.1 Genomic strategies for water conservation

Reptiles inhabiting arid environments have evolved various genomic strategies to conserve water. For instance, the study on the Arabian camel (*Camelus dromedarius*) revealed that the suppression of cholesterol biosynthesis facilitates water retention in the kidney by indirectly enhancing AQP2-mediated water reabsorption (Figure 2) (Alvira-Iraizoz et al., 2021). Similarly, the kangaroo rat (*Dipodomys spectabilis*) exhibits ultra-efficient kidney function and osmoregulation, with specific genes such as Slc12a1 and Slc12a3 playing crucial roles in physiological water conservation (Marra et al., 2012). These findings highlight the importance of specific genomic adaptations that enable reptiles and other desert-dwelling animals to maintain hydration in extreme conditions.

3.2 Genetic basis of drought resistance

The genetic basis of drought resistance in reptiles involves a complex interplay of multiple genes and regulatory regions. In the lizard species *Liolaemus fuscus*, genomic analyses identified 110 fixed and 30 outlier loci associated with cellular membrane and development, which are crucial for adapting to the arid Atacama Desert (Araya-Donoso et al., 2021). Additionally, a study on lacertid lizards identified 200 genes with signatures of positive diversifying selection, many of which are involved in physiological and morphological adaptations to climate, including drought resistance (Valero et al., 2021). These genetic adaptations are essential for reptiles to survive and thrive in environments with limited water availability.

3.3 Evolution of kidney function in reptiles

The evolution of kidney function in reptiles is a key adaptation to arid environments. Comparative genomic analysis of camelids, including the Bactrian camel and dromedary, revealed unique osmoregulation and osmoprotection mechanisms that facilitate water reservation under desert conditions (Wu et al., 2014). In kangaroo rats, the identification of overexpressed genes in the kidney, such as Slc12a1 and Slc12a3, underscores the evolutionary significance of kidney function in water conservation (Marra et al., 2012). These studies demonstrate that the evolution of specialized kidney functions is a critical factor in the adaptation of reptiles and other desert-dwelling animals to extreme arid environments (Tigano et al., 2019; Tigano et al., 2020).

By integrating genomic, physiological, and morphological data, researchers can gain a comprehensive understanding of the adaptations that enable reptiles to survive in some of the harshest environments on Earth. These insights not only advance our knowledge of evolutionary biology but also have potential applications in conservation and climate change resilience strategies.

4 Adaptations to High Altitude

4.1 Genetic changes in oxygen transport

High-altitude environments impose significant challenges due to low oxygen availability. Reptiles, such as the toad-headed agamas (Genus Phrynocephalus), have shown genetic adaptations that enhance oxygen transport. Comparative transcriptome analysis between high-elevation *P. vlangalii* and low-elevation *P. przewalskii* revealed positively selected genes (PSGs) like ADAM17 and HSP90B1, which are likely involved in hypoxia response (Yang et al., 2014). Additionally, the rock agama (*Laudakia sacra*) from the Qinghai-Tibet Plateau exhibits mutations in genes such as HIF1A and TIE2, which are crucial for hypoxia adaptation (Figure 3) (Yan et al., 2022). These genetic changes facilitate improved oxygen transport and utilization, enabling survival in hypoxic conditions (Storz, 2021).

4.2 Evolution of respiratory adaptations

Respiratory adaptations are critical for reptiles living at high altitudes. Studies on various high-altitude species, including the plateau zokor (*Myospalax baileyi*), have identified accelerated evolution in genes related to respiratory gaseous exchange and blood vessel development (Shao et al., 2015). These adaptations are essential for maintaining efficient respiratory function under low oxygen conditions. Furthermore, the rock agama (*Laudakia sacra*) has shown genomic adaptations in genes related to cardiovascular remodeling and erythropoiesis, which are vital for enhancing respiratory efficiency in hypoxic environments (Storz and Cheviron, 2020; Yan et al., 2022).

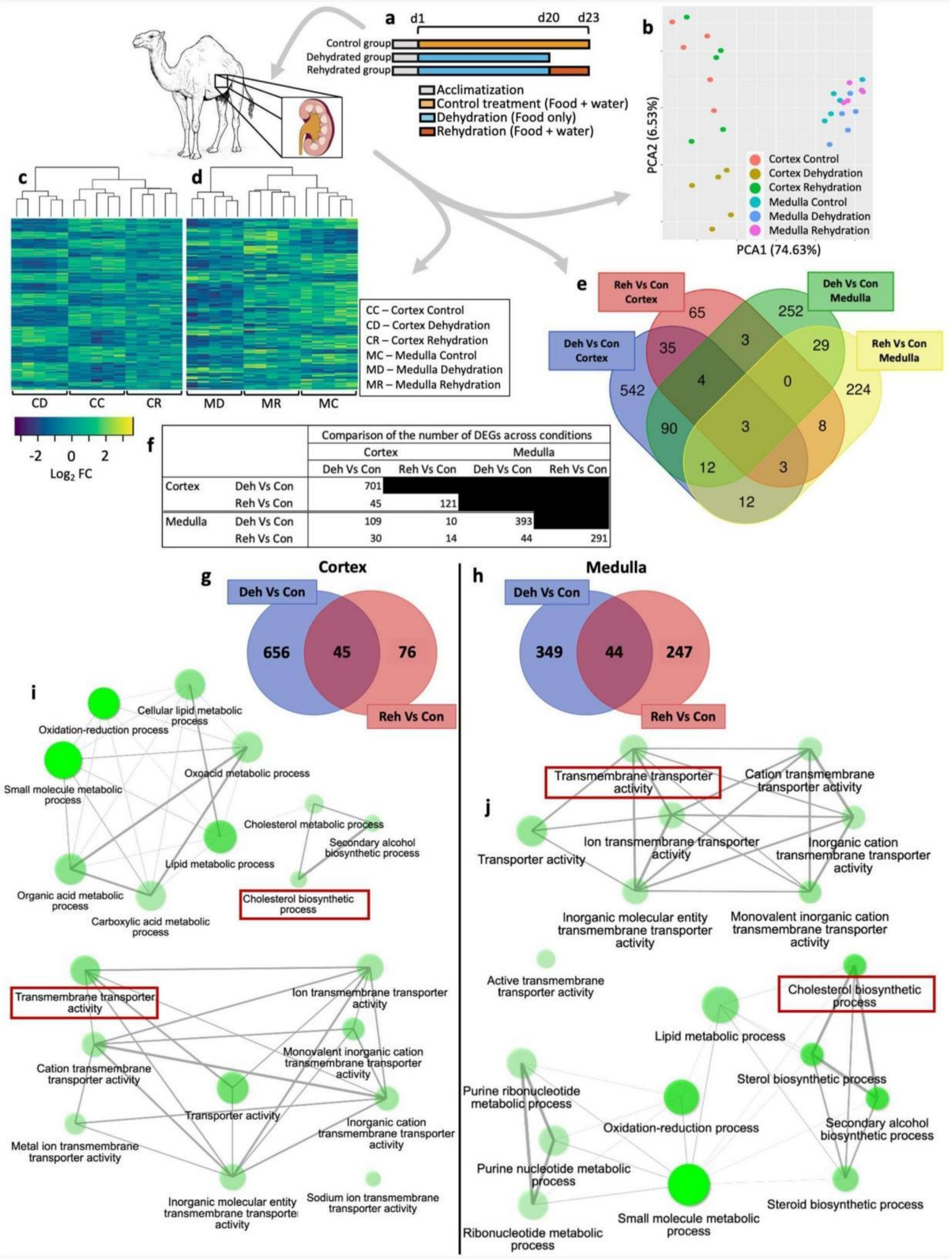

Figure 2 Experimental design and analysis of the transcriptomes of the one-humped Arabian camel kidney during severe dehydration and acute rehydration (Adopted from Alvira-Iraizoz et al., 2021)

Image caption: a Experimental protocol for each experimental group. b PCA plot displaying the clustering of the samples based on their expression profiles where all expressed genes are included. c, d Heatmaps including all differentially expressed genes (DEGs) identified in the cortex (c) and medulla (d) across conditions show clear clustering of differentially expressed genes by condition. e Venn plot displaying the overlap of differentially expressed genes identified in dehydration and rehydration compared to control in cortex and medulla. f Absolute number of DEGs displayed in panels (e), (g) and (h). g, h Venn plots showing the distribution of DEGs during dehydration and rehydration compared to controls in the kidney cortex (g) and medulla (h) of the camel. Number of genes differentially expressed solely in dehydration compared to control (blue), in rehydration compared to control (light red) and those differentially co-regulated in both conditions (dark red) are shown. (i), j Gene Ontology (GO) networks displaying a subset of the most significantly enriched ($p < 0.05$) biological processes and molecular functions in the kidney cortex (i) and medulla (j) during dehydration. Two nodes are connected if they share 20% or more genes and thicker edges represent more overlapped genes, darker nodes are more significantly enriched gene sets and bigger nodes represent larger gene sets (Adopted from Alvira-Iraizoz et al., 2021)

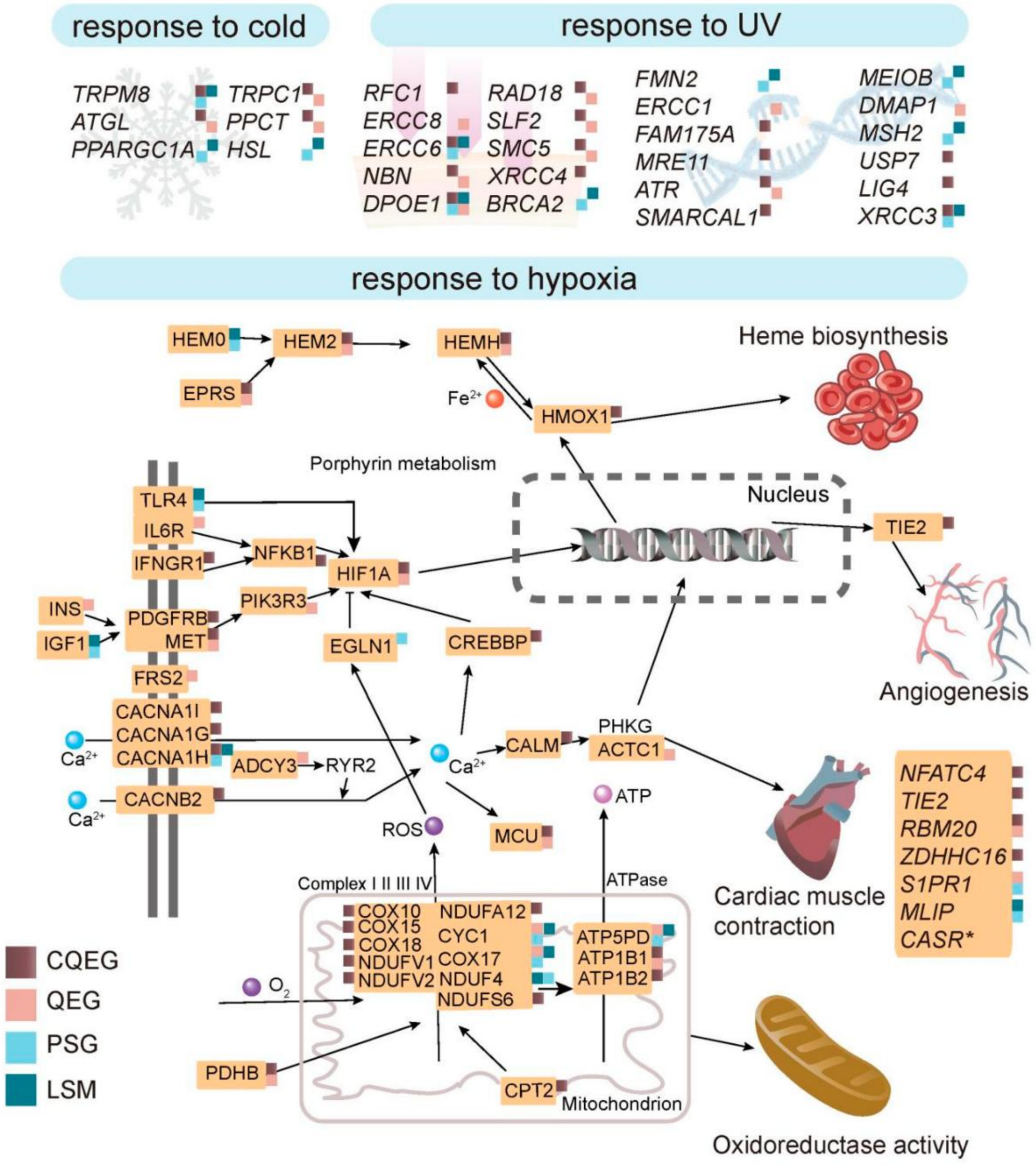

Figure 3 Genes and pathways associated with plateau animal adaptation to hypoxia, cold temperature, and high UV radiation (Adopted from Yan et al., 2022)

Image caption: Hypoxia-activated pathways that regulate erythropoiesis, cardiovascular development, and oxidative phosphorylation in plateau animals are depicted in detail. Different categories of genes, i.e., CQEGs, QEGs, PSGs, and genes with *L. sacra*-specific mutations (LSM) are indicated by squares with different colors. Expanded CASR in *L. sacra* is marked with an "*" (Adopted from Yan et al., 2022)

4.3 Genomic responses to hypoxia

Genomic responses to hypoxia involve a complex interplay of multiple genes and pathways. In high-altitude reptiles, such as the toad-headed agamas, functional analyses have identified numerous PSGs involved in gene expression and metabolism, which are crucial for hypoxia adaptation (Yang et al., 2014). Comparative genomic studies across different high-altitude species have revealed convergent evolution in genes related to hypoxia response, such as the hypoxia-inducible factor (HIF) pathway (Pamenter et al., 2020; Lyu et al., 2022). These genomic adaptations enable reptiles to cope with the chronic lack of oxygen by modulating physiological and biochemical pathways to maintain homeostasis (Beckman et al., 2021).

5 Adaptations to Marine Environments

5.1 Genomic adaptations to saltwater tolerance

Marine reptiles have developed various genomic adaptations to tolerate high salinity environments. Studies on different species have identified key genes and genomic regions that play crucial roles in osmoregulation and ion transport. For instance, research on nine-spined sticklebacks (*Pungitius pungitius*) has highlighted the importance of genes such as growth hormone receptor 2 and DEAD box polypeptide 56 in adapting to different salinity levels (Shikano et al., 2010). Similarly, the Atlantic cod (*Gadus morhua*) has shown genomic divergence in regions associated with osmoregulation, which are crucial for survival in varying salinity conditions (Berg et al., 2015). In threespine sticklebacks (*Gasterosteus aculeatus*), specific quantitative trait loci (QTL) and candidate genes have been identified that contribute to salinity tolerance through mechanisms like ATP synthesis and hormonal signaling (Kusakabe et al., 2017). Additionally, the Alewife (*Alosa pseudoharengus*) has demonstrated parallel evolution in the expression of osmoregulatory genes, particularly those regulating gill ion exchange, which facilitates adaptation to freshwater and saltwater environments (Velotta et al., 2017).

5.2 Evolution of diving capabilities

The evolution of diving capabilities in marine reptiles involves significant genomic changes that enhance their ability to withstand prolonged periods underwater. In cetaceans, for example, the loss of certain genes has been linked to improved diving adaptations. Genes such as F12 and KLKB1, which are associated with thrombus formation, and MAP3K19, related to oxidative stress-induced lung inflammation, were inactivated in ancestral cetaceans, reducing the risks associated with deep diving (Huelsmann et al., 2019). Additionally, genes involved in vasoconstriction and pulmonary surfactant composition, such as SLC6A18 and SEC14L3, respectively, have also been lost, further supporting diving adaptations (Huelsmann et al., 2019). These genomic changes highlight the complex evolutionary processes that enable marine reptiles to thrive in aquatic environments.

5.3 Genetic basis of osmoregulation

Osmoregulation is a critical function for marine reptiles, allowing them to maintain ionic balance in varying salinity conditions. *Decapod crustaceans*, for example, have been studied extensively to understand the genetic mechanisms underlying osmoregulation. Research has identified 32 candidate genes involved in processes such as ion transportation, active ion exchange, and regulation of cell volume, which are essential for osmoregulation (Rahi et al., 2018). In Atlantic salmon (*Salmo salar*), genetic variation in osmoregulatory genes has been observed between landlocked and anadromous populations, indicating adaptive responses to freshwater environments (Yuan et al., 2021; Harder and Christie, 2022). These findings underscore the importance of specific genes and genomic regions in facilitating osmoregulation and adaptation to different osmotic niches in marine reptiles.

6 Case Study: Desert-Dwelling Reptiles

6.1 Genomic insights from the Gila monster

The Gila monster (*Heloderma suspectum*) is a venomous lizard native to the southwestern United States and northwestern Mexico. Its adaptation to desert environments has been a subject of interest due to its unique physiological and genomic traits. Studies have shown that the Gila monster's genome contains specific adaptations that allow it to thrive in arid conditions, such as genes related to water retention and temperature regulation. These adaptations are crucial for survival in extreme environments where water is scarce and temperatures can be extreme (Araya-Donoso et al., 2021; Koochekian et al., 2022).

6.2 Comparative genomics of desert snakes

Desert snakes, such as the sidewinder (*Crotalus cerastes*) and the horned viper (*Cerastes cerastes*), exhibit remarkable adaptations to their harsh environments. Comparative genomic studies have revealed that these snakes have evolved specific genetic traits that enhance their ability to conserve water and regulate body temperature. For instance, genes involved in kidney function and skin permeability have undergone positive selection, allowing these snakes to minimize water loss and survive in arid conditions. Additionally, the evolution of venom composition in these snakes is linked to their adaptation to desert prey, which often includes small mammals and other reptiles (Yang et al., 2014; Tollis et al., 2018; Valero et al., 2021).

6.3 Adaptive evolution in desert lizards

Desert lizards, such as the sand lizards (Meroles) and the horned lizards (Phrynosoma), have developed a range of morphological, physiological, and genomic adaptations to cope with extreme desert environments. For example, the sand lizards exhibit rapid speciation and morphological evolution, with adaptations such as elongated limbs and specialized scales that facilitate movement on loose sand. Genomic studies have identified genes associated with water retention, heat tolerance, and metabolic efficiency, which are crucial for survival in arid habitats (Laurent et al., 2016; Westfall et al., 2020). Furthermore, the horned lizards have shown chromosomal rearrangements that may contribute to their ability to adapt to desert conditions, highlighting the dynamic nature of their genomic evolution (Melville et al., 2006; Koochekian et al., 2022).

These case studies illustrate the diverse strategies employed by desert-dwelling reptiles to adapt to extreme environments. By integrating genomic, physiological, and morphological data, researchers can gain a comprehensive understanding of the mechanisms underlying these adaptations, providing valuable insights into the evolutionary processes that shape biodiversity in harsh habitats.

7 Genomic Tools and Techniques

7.1 Advances in sequencing technologies

Recent advancements in sequencing technologies have significantly enhanced our understanding of reptile genomics, particularly in the context of adaptation to extreme environments. High-throughput sequencing methods, such as Illumina sequencing, have enabled the generation of vast amounts of genomic data. For instance, in a study on high elevation adaptation in toad-headed agamas, more than 100 million sequence reads were generated for each species using Illumina sequencing, leading to the identification of candidate genes linked to high elevation adaptation (Yang et al., 2014). Additionally, the use of PacBio HiFi long-read and Hi-C sequencing has facilitated the generation of highly contiguous reference genomes, as demonstrated in the genomic studies of the Christmas Island blue-tailed skink and Lister's gecko (Dodge et al., 2023). These technologies have provided insights into genetic diversity and evolutionary histories, which are crucial for conservation efforts (Das et al., 2020).

7.2 Bioinformatics approaches in reptile genomics

Bioinformatics tools and approaches play a pivotal role in analyzing and interpreting the vast amounts of genomic data generated by advanced sequencing technologies. Comparative genomics and meta-analyses have been employed to identify genes under selection and their functional roles in adaptation. For example, a meta-analysis of 1100 genes from various vertebrate species revealed a tightly connected interactome enriched in functions related to climate adaptation and stress response (Valero et al., 2019; Valero et al., 2021). Furthermore, redundancy analyses integrating genomic, physiological, and morphological data have been used to detect adaptations in desert lizards, highlighting the importance of combining multiple data types to understand local adaptation and speciation (Araya-Donoso et al., 2021). Synteny analysis, which compares chromosomal structures across species, has also been utilized to study chromosomal rearrangements and their evolutionary implications in reptiles (Westfall et al., 2020; Koochekian et al., 2022).

7.3 Functional genomics and gene editing

Functional genomics and gene editing techniques are essential for validating the roles of candidate genes identified through sequencing and bioinformatics analyses. Functional genomics approaches, such as transcriptome analysis, have been used to identify genes involved in physiological and morphological adaptations to extreme environments. For instance, transcriptome analysis of lacertid lizards identified 200 genes with signatures of positive diversifying selection, which were linked to climate adaptation (Valero et al., 2021). Gene editing technologies, such as CRISPR-Cas9, offer the potential to experimentally manipulate specific genes to study their functions in adaptation processes. Although gene editing in reptiles is still in its early stages, the development of high-quality genomic resources, such as the chromosome-level genome assemblies for the desert horned lizard and the eastern fence lizard, provides a foundation for future functional studies (Westfall et al., 2020; Koochekian et al., 2022).

In summary, the integration of advanced sequencing technologies, bioinformatics approaches, and functional genomics techniques has greatly enhanced our understanding of the genetic basis of adaptation in reptiles to extreme environments. These tools and techniques not only facilitate the identification of candidate genes and pathways involved in adaptation but also provide valuable resources for conservation and evolutionary studies.

8 Future Directions and Challenges

8.1 Emerging trends in reptilian genomics

Recent advancements in genomic technologies have significantly enhanced our understanding of reptilian adaptation to extreme environments. Functional and comparative genomics have revealed that specific subsets of genes are repeatedly selected for adaptation to various abiotic stresses, such as temperature and altitude, across different vertebrate species (Valero et al., 2019; Valero et al., 2021). The use of high-throughput sequencing technologies has facilitated the identification of genes involved in physiological and morphological adaptations, providing insights into the genetic basis of these adaptations (Wang and Guo, 2019; Yang et al., 2014). Additionally, environmental DNA (eDNA) techniques are emerging as valuable tools for detecting elusive and cryptic reptile species, thereby aiding in conservation efforts (Nordstrom et al., 2022).

8.2 Challenges in genomic research of reptiles

Despite these advancements, several challenges persist in the genomic research of reptiles. One major challenge is the complexity of adaptation genetics, where many traits are polygenic and influenced by minor differences in regulatory networks and epigenetic variations that are not easily detectable through conventional genomic methods (Harrisson et al., 2014). Furthermore, the development of genomic tools in wild species is often hindered by computational and sampling constraints, making it difficult to obtain comprehensive genomic data (Steiner et al., 2013). Another significant challenge is the limited application of eDNA techniques to terrestrial reptiles, which restricts the ability to gather data on species with high diversity and those inhabiting remote regions (Nordstrom et al., 2022).

8.3 Conservation implications of genomic studies

Genomic studies have profound implications for the conservation of reptile species. By identifying loci associated with inbreeding depression, disease susceptibility, and adaptive variation, genomic analyses can inform management strategies for both wild and captive populations (Steiner et al., 2013; Shaffer et al., 2015; Dodge et al., 2023). For instance, the genomic characterization of extinct-in-the-wild species, such as the Christmas Island blue-tailed skink and Lister's gecko, has provided critical insights into their evolutionary histories and genetic diversity, which are essential for successful reintroduction and management programs (Dodge et al., 2023). Moreover, understanding the genetic basis of adaptation to extreme environments can help predict how reptiles might respond to future environmental changes, thereby aiding in the development of conservation strategies that enhance their evolutionary potential (Harrisson et al., 2014; Valero et al., 2019; Valero et al., 2021).

In conclusion, while significant progress has been made in reptilian genomics, addressing the existing challenges and leveraging emerging trends will be crucial for advancing our understanding of reptile adaptation and improving conservation outcomes.

9 Concluding Remarks

The study of reptilian adaptation to extreme environments has revealed significant insights into the genetic and physiological mechanisms underlying these adaptations. High elevation adaptation in *Phrynocephalus lizards* identified 143 positively selected genes (PSGs) and several functional categories linked to hypoxia response and DNA repair. Similarly, lacertid lizards showed genomic signatures of adaptation to various abiotic environments, with a notable enrichment in genes related to stress response and physiological adaptations. In ants, high-altitude adaptation involved strong positive selection and relaxation of purifying selection, highlighting the role of heat-shock proteins and glycolytic enzymes. The Amur ide fish demonstrated genomic adaptations to extreme alkalinity, including expansions in genes related to ion homeostasis and stress response. Additionally, the green anole lizard exhibited rapid phenotypic and genomic shifts in response to extreme cold events, emphasizing the role of natural selection in shaping adaptive traits.

These findings underscore the complexity and diversity of genetic mechanisms driving adaptation to extreme environments. The recurrent identification of specific genes and pathways across different species suggests a degree of evolutionary constraint and convergence in the genomic basis of adaptation. This convergence indicates that certain genetic solutions are repeatedly favored in response to similar environmental pressures, providing a clearer understanding of the predictability and repeatability of evolutionary processes. Moreover, the rapid adaptation observed in some species, such as the green anole lizard, highlights the potential for swift evolutionary responses to environmental changes, which is particularly relevant in the context of ongoing climate change.

Future research should focus on functional validation of the identified candidate genes and pathways to confirm their roles in adaptation. Comparative studies across a broader range of species and environments will help elucidate the generality of the observed patterns and identify additional adaptive mechanisms. Integrating genomic data with ecological and physiological studies will provide a more comprehensive understanding of how organisms cope with extreme conditions. Additionally, investigating the interplay between genetic adaptation and phenotypic plasticity will shed light on the relative contributions of these processes to survival in extreme environments. Finally, exploring the potential for rapid evolutionary responses in other taxa will be crucial for predicting the impacts of climate change on biodiversity and ecosystem function.

Acknowledgements

The authors express the gratitude to the anonymous peer reviewers for their feedback and suggestions on this manuscript.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Akashi H., Díaz A., Shigenobu S., Makino T., and Kawata M., 2016, Differentially expressed genes associated with adaptation to different thermal environments in three sympatric Cuban *Anolis* lizards, Molecular Ecology, 25(10): 2273-2285.
https://doi.org/10.1111/mec.13625
PMid:27027506

Alvira-Iraizoz F., Gillard B., Lin P., Paterson A., Pauža A., Ali M., Alabsi A., Burger P., Hamadi N., Adem A., Murphy D., and Greenwood M., 2021, Multiomic analysis of the Arabian camel (*Camelus dromedarius*) kidney reveals a role for cholesterol in water conservation, Communications Biology, 4(1): 779.
https://doi.org/10.1038/s42003-021-02327-3
PMid:34163009 PMCid:PMC8222267

Araya-Donoso R., Juan E., Tamburrino Í., Lamborot M., Veloso C., and Véliz D., 2021, Integrating genetics, physiology, and morphology to study desert adaptation in a lizard species, Journal of Animal Ecology, 91(6): 1148-1162.
https://doi.org/10.1111/1365-2656.13546
PMid:34048024

Beckman E., Martins F., Suzuki T., Bi K., Keeble S., Good J., Chavez A., Ballinger M., Agwamba K., and Nachman M., 2021, The genomic basis of high-elevation adaptation in wild house mice (*Mus musculus domesticus*) from South America, Genetics, 220(2): iyab226.
https://doi.org/10.1093/genetics/iyab226
PMid:34897431 PMCid:PMC9097263

Berg P., Jentoft S., Star B., Ring K., Knutsen H., Lien S., Jakobsen K., and André C., 2015, Adaptation to low salinity promotes genomic divergence in Atlantic cod (*Gadus morhua* L.), Genome Biology and Evolution, 7(6): 1644-1663.
https://doi.org/10.1093/gbe/evv093
PMid:25994933 PMCid:PMC4494048

Besson A., and Cree A., 2010, A cold-adapted reptile becomes a more effective thermoregulator in a thermally challenging environment, Oecologia, 163: 571-581.
https://doi.org/10.1007/s00442-010-1571-y
PMid:20140685

Bock D., Baeckens S., Kolbe J., and Losos J., 2023, When adaptation is slowed down: genomic analysis of evolutionary stasis in thermal tolerance during biological invasion in a novel climate, Molecular Ecology, 33(10): e17075.
https://doi.org/10.1111/mec.17075
PMid:37489260

Buckley L., Ehrenberger J., and Angilletta M., 2015, Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change, Functional Ecology, 29(8): 1038-1047.
https://doi.org/10.1111/1365-2435.12406

Castañeda L., Romero-Soriano V., Mesas A., Roff D., and Santos M., 2019, Evolutionary potential of thermal preference and heat tolerance in *Drosophila subobscura*, Journal of Evolutionary Biology, 32(8): 818-824.
https://doi.org/10.1111/jeb.13483
PMid:31038253

Das D., Singh S., Bierstedt J., Erickson A., Galli G., Crossley D., and Rhen T., 2020, Draft genome of the common snapping turtle, *Chelydra serpentina*, a model for phenotypic plasticity in reptiles, G3 (Bethesda, Md.), 10(12): 4299-4314.
https://doi.org/10.1534/g3.120.401440
PMid:32998935 PMCid:PMC7718744

Dodge T., Farquharson K., Ford C., Cavanagh L., Schubert K., Schumer M., Belov K., and Hogg C., 2023, Genomes of two Extinct-in-the-Wild reptiles from Christmas Island reveal distinct evolutionary histories and conservation insights, Molecular Ecology Resources, 00: 1-17.
https://doi.org/10.1111/1755-0998.13780
PMid:36872490

Field E., Hartzheim A., Terry J., Dawson G., Haydt N., and Neuman-Lee L., 2022, Reptilian innate immunology and ecoimmunology: what do we know and where are we going? Integrative and Comparative Biology, 62(6): 1557-1571.
https://doi.org/10.1093/icb/icac116
PMid:35833292

Harder A., and Christie M., 2022, Genomic signatures of adaptation to novel environments: hatchery and life history-associated loci in landlocked and anadromous Atlantic salmon (*Salmo salar*), Canadian Journal of Fisheries and Aquatic Sciences, 79(5): 761-770.
https://doi.org/10.1139/cjfas-2021-0066

Harrisson K., Pavlova A., Telonis-Scott M., and Sunnucks P., 2014, Using genomics to characterize evolutionary potential for conservation of wild populations, Evolutionary Applications, 7(9): 1008-1025.
https://doi.org/10.1111/eva.12149
PMid:25553064 PMCid:PMC4231592

Huelsmann M., Hecker N., Springer M., Gatesy J., Sharma V., and Hiller M., 2019, Genes lost during the transition from land to water in cetaceans highlight genomic changes associated with aquatic adaptations, Science Advances, 5(9): eaaw6671.
https://doi.org/10.1126/sciadv.aaw6671
PMid:31579821 PMCid:PMC6760925

Koochekian N., Ascanio A., Farleigh K., Card D., Schield D., Castoe T., and Jezkova T., 2022, A chromosome-level genome assembly and annotation of the desert horned lizard, *Phrynosoma platyrhinos*, provides insight into chromosomal rearrangements among reptiles, GigaScience, 11: giab098.
https://doi.org/10.1093/gigascience/giab098
PMid:35134927 PMCid:PMC8848323

Kusakabe M., Ishikawa A., Ravinet M., Yoshida K., Makino T., Toyoda A., Fujiyama A., and Kitano J., 2017, Genetic basis for variation in salinity tolerance between stickleback ecotypes, Molecular Ecology, 26(1): 304-319.
https://doi.org/10.1111/mec.13875
PMid:27706866

Laurent S., Pfeifer S., Settles M., Hunter S., Hardwick K., Ormond L., Sousa V., Jensen J., and Rosenblum E., 2016, The population genomics of rapid adaptation: disentangling signatures of selection and demography in white sands lizards, Molecular Ecology, 25(1): 306-323.
https://doi.org/10.1111/mec.13385
PMid:26363411

Lyu T., Zhou S., Fang J., Wang L., Shi L., Dong Y., and Zhang H., 2022, Convergent Genomic Signatures of High-Altitude Adaptation among Six Independently Evolved Mammals, Animals, 12(24): 3572.
https://doi.org/10.3390/ani12243572
PMid:36552492 PMCid:PMC9774524

Marra N., Eo S., Hale M., Waser P., and Dewoody J., 2012, A priori and a posteriori approaches for finding genes of evolutionary interest in non-model species: osmoregulatory genes in the kidney transcriptome of the desert rodent *Dipodomys spectabilis* (banner-tailed kangaroo rat), Comparative biochemistry and Physiology Part D: Genomics & Proteomics, 7(4): 328-339.
https://doi.org/10.1016/j.cbd.2012.07.001
PMid:22841684

Melville J., Harmon L., and Losos J., 2006, Intercontinental community convergence of ecology and morphology in desert lizards, Proceedings of the Royal Society B: Biological Sciences, 273(1586): 557-563.
https://doi.org/10.1098/rspb.2005.3328
PMid:16537126 PMCid:PMC1560059

Muñoz M., Stimola M., Algar A., Conover A., Rodriguez A., Landestoy M., Bakken G., and Losos J., 2014, Evolutionary stasis and lability in thermal physiology in a group of tropical lizards, Proceedings of the Royal Society B: Biological Sciences, 281(1778): 20132433.
https://doi.org/10.1098/rspb.2013.2433
PMid:24430845 PMCid:PMC3906933

Nordstrom B., Mitchell N., Byrne M., and Jarman S., 2022, A review of applications of environmental DNA for reptile conservation and management, Ecology and Evolution, 12(6): e8995.
https://doi.org/10.1002/ece3.8995
PMid:35784065 PMCid:PMC9168342

Pamenter M., Hall J., Tanabe Y., and Simonson T., 2020, Cross-species insights into genomic adaptations to hypoxia, Frontiers in Genetics, 11: 743.
https://doi.org/10.3389/fgene.2020.00743
PMid:32849780 PMCid:PMC7387696

Rahi M., Moshtaghi A., Mather P., and Hurwood D., 2018, Osmoregulation in *Decapod crustaceans*: physiological and genomic perspectives, Hydrobiologia, 825: 177-188.
https://doi.org/10.1007/s10750-018-3690-0

Shaffer H., Gidiş M., McCartney-Melstad E., Neal K., Oyamaguchi H., Tellez M., and Toffelmier E., 2015, Conservation genetics and genomics of amphibians and reptiles, Annual Review of Animal Biosciences, 3(ch_1): 113-138.
https://doi.org/10.1146/annurev-animal-022114-110920
PMid:25580719

Shao Y., Li J., Ge R., Zhong L., Irwin D., Murphy R., and Zhang Y., 2015, Genetic adaptations of the plateau zokor in high-elevation burrows, Scientific Reports, 5(1): 17262.
https://doi.org/10.1038/srep17262
PMid:26602147 PMCid:PMC4658562

Shikano T., Ramadevi J., and Merilä J., 2010, Identification of local- and habitat-dependent selection: scanning functionally important genes in nine-spined sticklebacks (*Pungitius pungitius*), Molecular Biology and Evolution, 27(12): 2775-2789.
https://doi.org/10.1093/molbev/msq167
PMid:20591843

Steiner C., Putnam A., Hoeck P., and Ryder O., 2013, Conservation genomics of threatened animal species, Annual Review of Animal Biosciences, 1(1): 261-281.
https://doi.org/10.1146/annurev-animal-031412-103636
PMid:25387020

Storey K., 2006, Reptile freeze tolerance: metabolism and gene expression, Cryobiology, 52(1): 1-16.
https://doi.org/10.1016/j.cryobiol.2005.09.005
PMid:16321368

Storz J., 2021, High-altitude adaptation: mechanistic insights from integrated genomics and physiology, Molecular Biology and Evolution, 38(7): 2677-2691.
https://doi.org/10.1093/molbev/msab064
PMid:33751123 PMCid:PMC8233491

Storz J., and Cheviron Z., 2020, Physiological genomics of adaptation to high-altitude hypoxia, Annual Review of Animal Biosciences, 9(1): 149-171.
https://doi.org/10.1146/annurev-animal-072820-102736
PMid:33228375 PMCid:PMC8287974

Tigano A., Colella J., and MacManes M., 2019, Comparative and population genomics approaches reveal the basis of adaptation to deserts in a small rodent, Molecular Ecology, 29(7): 1300-1314.
https://doi.org/10.1111/mec.15401
PMid:32130752 PMCid:PMC7204510

Tollis M., Hutchins E., Stapley J., Rupp S., Eckalbar W., Maayan I., Lasku E., Infante C., Dennis S., Robertson J., May C., Crusoe M., Bermingham E., DeNardo D., Hsieh S., Kulathinal R., McMillan W., Menke D., Pratt S., Rawls J., Sanjur O., Wilson-Rawls J., Sayres M., Fisher R., and Kusumi K., 2018, Comparative genomics reveals accelerated evolution in conserved pathways during the diversification of anole lizards, Genome Biology and Evolution, 10(2): 489-506.
https://doi.org/10.1093/gbe/evy013
PMid:29360978 PMCid:PMC5798147

Valero K., Garcia-Porta J., Irisarri I., Feugere L., Bates A., Kirchhof S., Glavaš O., Pafilis P., Samuel S., Müller J., Vences M., Turner A., Beltran-Alvarez P., and Storey K., 2021, Functional genomics of abiotic environmental adaptation in lacertid lizards and other vertebrates, Journal of Animal Ecology, 91(6): 1163-1179.
https://doi.org/10.1111/1365-2656.13617
PMid:34695234

Valero K., Garcia-Porta J., Irisarri I., Feugere L., Bates A., Kirchhof S., Glavaš O., Pafilis P., Samuel S., Müller J., Vences M., Turner A., Beltran-Alvarez P., and Storey K., 2019, Abiotic environmental adaptation in vertebrates is characterized by functional genomic constraint, bioRxiv, 2019: 726240.
https://doi.org/10.1101/726240

Velotta J., Wegrzyn J., Ginzburg S., Kang L., Czesny S., O'Neill R., McCormick S., Michalak P., and Schultz E., 2017, Transcriptomic imprints of adaptation to fresh water: parallel evolution of osmoregulatory gene expression in the Alewife, Molecular Ecology, 26(3): 831-848.
https://doi.org/10.1111/mec.13983
PMid:28012221

Wang Y., and Guo B., 2019, Adaption to extreme environments: a perspective from fish genomics, Reviews in Fish Biology and Fisheries, 29: 735-747.
https://doi.org/10.1007/s11160-019-09577-9

Westfall A., Telemeco R., Grizante M., Waits D., Clark A., Simpson D., Klabacka R., Sullivan A., Perry G., Sears M., Cox C., Cox R., Gifford M., John-Alder H., Langkilde T., Angilletta M., Leaché A., Tollis M., Kusumi K., and Schwartz T., 2020, A chromosome-level genome assembly for the eastern fence lizard (*Sceloporus undulatus*), a reptile model for physiological and evolutionary ecology, GigaScience, 10(10): giab066.
https://doi.org/10.1101/2020.06.06.138248

Wu H., Guang X., Al-Fageeh M., Cao J., Pan S., Zhou H., Zhang L., Abutarboush M., Xing Y., Xie Z., Alshanqeeti A., Zhang Y., Yao Q., Al-Shomrani B., Zhang D., Li J., Manee M., Yang Z., Yang L., Liu Y., Zhang J., Altammami M., Wang S., Yu L., Zhang W., Liu S., Ba L., Liu C., Yang X., Meng F., Wang S., Li L., Li E., Li X., Wu K., Zhang S., Wang J., Yin Y., Yang H., Al-Swailem A., and Wang J., 2014, Camelid genomes reveal evolution and adaptation to desert environments, Nature Communications, 5(1): 5188.
https://doi.org/10.1038/ncomms6188
PMid:25333821

Yan C., Zhang Z., Lv Y., Wang Z., Jiang K., and Li J., 2022, Genome of *Laudakia sacra* provides new insights into high-altitude adaptation of ectotherms, International Journal of Molecular Sciences, 23(17): 10081.
https://doi.org/10.3390/ijms231710081
PMid:36077479 PMCid:PMC9456099

Yang W., Qi Y., and Fu J., 2014, Exploring the genetic basis of adaptation to high elevations in reptiles: a comparative transcriptome analysis of two toad-headed agamas (*genus Phrynocephalus*), PLoS ONE, 9(11): e112218.
https://doi.org/10.1371/journal.pone.0112218
PMid:25386640 PMCid:PMC4227734

Yuan Y., Zhang Y., Zhang P., Liu C., Wang J., Gao H., Hoelzel A., Seim I., Lv M., Lin M., Dong L., Gao H., Yang Z., Caruso F., Lin W., Fonseca R., Wang D., Wang X., Rasmussen M., Liu M., Zheng J., Zhao L., Campos P., Kang H., Iversen M., Song Y., Guo X., Guo J., Qin Y., Pan S., Xu Q., Meng L., A Y., Liu S., Lee S., Liu X., Xu X., Yang H., Fan G., Wang K., and Li S., 2021, Comparative genomics provides insights into the aquatic adaptations of mammals, Proceedings of the National Academy of Sciences of the United States of America, 118(37): e2106080118.
https://doi.org/10.1073/pnas.2106080118
PMid:34503999 PMCid:PMC8449357