Thermoregulation in Extant Reptiles: Patterns, Constraints, and Evolutionary Implications

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Abstract: ***The Class Reptilia have traditionally been classified as ectothermic vertebrates; however, accumulating evidence demonstrates that thermoregulation in extant reptiles is physiologically, ecologically and evolutionarily heterogeneous. Although the taxon Reptilia is paraphyletic under cladistic taxonomy, the term remains useful when referring to extant non-avian, non-mammalian sauropsids, including Testudines, Crocodylia, Rhynchocephalia, and Squamata. This review synthesizes current knowledge on reptilian thermoregulation, emphasizing ectothermy, heterothermy, mesothermy, and inertial homeothermy (gigantothermy). We examine the roles of body size, metabolic rate, habitat, phylogenetic inertia, and evolutionary constraints in shaping thermal strategies. Special attention is given to exceptional cases such as leatherback sea turtles and tuatara, as well as implications for extinct reptilian lineages, including Dinosauria and marine reptiles. We argue that most extant reptiles are better characterized as obligate ectothermic heterotherms rather than simple ectotherms and discuss how ongoing anthropogenic climate change may challenge their thermal ecology and evolutionary resilience.***

Keywords: Thermoregulation, Ectothermy, Mesothermy, Gigantothermy, Heterothermy, Reptilia, Phylogenetic inertia

1. Introduction

Although Reptilia does not represent a monophyletic clade in modern cladistic taxonomy, the term remains widely used to collectively describe extant non-avian Sauropsids excluding Mammalia and Aves. Living reptiles comprise four major lineages: Testudines (turtles, terrapins, and tortoises), Crocodylia, Rhynchocephalia (represented by the tuatara, *Sphenodon* spp.), and Squamata (Sauria/lizards, Amphisbaenians, and Ophidia/snakes).

Reptiles are traditionally described as ectotherms, relying primarily on environmental heat sources to regulate body temperature. Behavioral mechanisms such as heliothermy (absorption of solar radiation) and thigmothermy (heat exchange with substrates) dominate their thermoregulatory strategies. In contrast, birds and mammals are endotherms, generating metabolic heat through elevated basal metabolic rates (BMR) supported by oxidative phosphorylation and continuous food intake.

However, this binary classification oversimplifies reptilian thermal biology. Increasing evidence suggests a continuum of thermoregulatory strategies in reptiles, including mesothermy, heterothermy, and inertial homeothermy (gigantothermy). This review explores these diverse modes of thermoregulation, their ecological and evolutionary determinants, and their implications for both extant and extinct reptilian lineages.

Ectothermy, Metabolism, and Body Size

Most ectothermic reptiles exhibit relatively low metabolic rates, allowing reduced energetic demands and infrequent feeding compared to endotherms. This strategy promotes efficient trophic resource utilization and contributes to the ecological persistence of reptiles across diverse environments.

Body size plays a critical role in reptilian thermoregulation. Large-bodied reptiles experience reduced heat loss due to a lower surface-area-to-volume ratio, whereas smaller reptiles lose heat rapidly. Consequently, body size strongly influences thermal stability, activity patterns, and geographic distribution.

These observations have led to the hypothesis that while endothermy in birds and mammals represents a key evolutionary innovation, ectothermy in reptiles may reflect phylogenetic inertia. Mesothermy, where metabolic heat production partially contributes to body temperature regulation, appears to have evolved independently in certain reptilian taxa through physiological and behavioral modifications.

Heterothermy and Thermal Diversity in Reptiles

Reptiles exhibit substantial heterogeneity in thermal physiology, driven by adaptive radiation into diverse climatic zones. Most species cannot maintain a constant body temperature independent of environmental conditions and instead regulate temperature behaviourally and temporally.

Thus, overall reptilian thermal physiology may be largely described as obligatory ectothermic heterothermy, characterized by fluctuating body temperatures within species-specific preferred ranges. These thermal preferences reflect evolutionary constraints, phylogenetic history and ecological specialization.

Mesothermy and Inertial Homeothermy

Marine Reptiles and Mesothermy

A notable exception to classical ectothermy is observed in the leatherback sea turtle (*Dermochelys coriacea*), which maintains body temperatures approximately 10–18 °C above ambient seawater. This capacity is facilitated by large body size, reduced heat loss, counter current heat exchange, and thick subepidermal adipose tissue. These traits support a mesothermic condition rather than true endothermy.

Ontogenetically, leatherback hatchlings and juveniles remain ectothermic, with mesothermy emerging gradually as body size increases a phenomenon that may be described as ontogenetic heterothermy.

Gigantothermy in Large Reptiles

Inertial homeothermy, or gigantothermy, refers to thermal buffering achieved through large body mass rather than metabolic heat production. Large crocodilians such as *Crocodylus porosus* maintain relatively stable body temperatures through basking and aquatic thermoregulation. Behavioural responses such as gaping or submergence prevent overheating.

Similarly, large varanid lizards (*Varanus komodoensis*, *V. salvator*) may exhibit partial thermal inertia, particularly in insular settings where gigantism has evolved in the islands (insular gigantism). Despite high activity levels and elevated glycolytic output leading to lactic acid accumulation, these species remain fundamentally ectothermic.

Preferred Body Temperature and Seasonal Dormancy

Rather than single optimal body temperature (Topt) reptiles are better described by a preferred body temperature (Tpref) typically ranging from 20–38 °C across species.

Seasonal dormancy strategies further reflect thermal adaptation:

Brumation occurs during cold periods.

Aestivation occurs during extreme heat or aridity.

Lizards generally exhibit the highest Tpref (28–38 °C), possibly driven by ecological competition and sympatric speciation. Many agamids and geckonids have successfully adapted to urban environments, where anthropogenic heat islands provide thermal advantages.

Thermal Ecology of Snakes, Turtles, and Crocodilians

As compared to lizards, snakes typically exhibit narrower thermal optima (26–33 °C) compared to lizards, potentially reflecting their later evolutionary origin and ecological constraints following the Cretaceous–Paleogene mass extinction. Large pythons are frequently observed basking during cooler periods, suggesting partial benefits of thermal inertia.

Freshwater turtles, terrapins, and terrestrial tortoises generally maintain lower optimal temperatures (25–33 °C), influenced by aquatic heat loss, limited insulation, and dietary constraints. Island gigantism in taxa such as *Chelonoidis* and *Aldabrachelys* is best explained by island biogeography theory rather than Cope's rule. Adult crocodilians, despite ectothermy, exhibit remarkable thermal stability through gigantothermic buffering, maintaining preferred body temperatures of approximately 30–34 °C.

The Tuatara: An Extreme Case of Thermal Conservatism

The tuatara (*Sphenodon* spp.) represents the lowest reported thermal optimum among extant reptiles, with preferred temperatures of 16–21 °C. This reflects extreme phylogenetic conservatism, ecological specialization and evolutionary constraint, making tuatara a textbook example of phylogenetic inertia in thermal biology as well as evolutionary relict.

Implications for Extinct Reptiles

Thermoregulation in extinct reptiles, particularly Dinosaurs, remains controversial. Bone histology, growth rates, and lines of arrested growth (LAGs) suggest lineage-specific metabolic strategies and possible ontogenetic shifts in thermal physiology. Early Archosauromorphs were likely ectothermic, with gradual transitions toward warm blooded mesothermy following the Permo–Triassic mass extinction (252 Ma) may be largely explained through Turnover Pulse Hypothesis (TPH). The Triassic radiation of archosaurs coincided with climatic instability, postural evolution (Avemetatarsalian gait) and increased locomotor efficiency. The Pycnofibers in pterosaurs and filamentous early feathers in Dinosaurs likely played roles in thermal insulations as well as sexual display. Marine reptiles such as Ichthyosaurs, Sauropterygians and Mosasaurs may have evolved elevated metabolic rates to maintain thermal performance in Mesozoic oceans.

Anthropocene Challenges and Conservation Implications

In the Anthropocene, reptiles face unprecedented challenges due to habitat destruction, fragmentation, pollution, and climate change. As key ecological components of food webs, their persistence depends on physiological plasticity, life-history adjustments, and adaptive responses to rapid environmental change.

Not Darwinian but much rapidly adaptive natural selection remains the ultimate mechanism may shape their future survival, but the rate of anthropogenic change may exceed the evolutionary response for many species. as evolutionary responses are considered much slower as compared to the speed of environmental change.

2. Conclusions

Thermoregulation in extant reptiles represents a complex continuum rather than a simple ectothermic condition. Body size, phylogeny, habitat and evolutionary history interact to produce diverse thermal strategies. Recognizing reptiles as obligate ectothermic heterotherms provides a better framework for understanding their physiology, evolution and conservation in a rapidly changing world.

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