BIOLOGY OF THE REPTILIA

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Preface

The literature on reptilian physiology proves to be remarkably scattered. Reptiles have not only been studied to determine the pattern of their physiology; as many or more studies have resulted from their use as subjects for pharmacological or physiological assay. The last two decades have seen a particular burgeoning of such studies. In parallel, summaries of parts of this literature have become as ubiquitous and are as scattered as the original records.

The present volume is the first physiological one in the series. We here attempt to present the initial part of an overall summary oriented toward reptiles as a group rather than toward such single topics as metabolic rate, themoregulation, or water balance. The editors are pleased to have been able to enlist authors, who in each case had contributed signally to our understanding of the topics they now summarize. As in the chapters of previous volumes, we have not objected to bias as long as alternative viewpoints are clearly referenced.

The reports fully document that the physiological studies thus far carried out involve only a first level analysis of a series of fascinating topics. To interest others in such approaches to reptiles, and to facilitate the entry into the field of herpetologists now avoiding physiological topics, and of physiologists who have not previously concerned themselves with reptiles, we have added two general chapters. The first, by the editors, represents a brief summary of reptilian physiological adaptations and their uses to the physiologist. It is hoped that this account will serve as an introduction to the more sophisticated treatments offered by the accounts that follow it.

We have also included a discussion by Dr Harry McDonald of techniques for use in reptilian physiology. This account summarizes the techniques previously reported in the literature and presents some value judgements on their adequacy as well as cautions to be observed in applying them.

The editors would like to dedicate this volume to our friend James Templeton, whose untimely death occurred while he was preparing an account for this series.

Drs G. A. Bartholomew, A. F. Bennett, P. J. Bentley, S. D. Bradshaw, E. C. Crawford, Jr., W. H. Dantzler, P. Dejours, D. B. Dill, W. A. Dunson, G. E. H. Foxon, E. T. B. Francis, J. E. Heath, H. Heatwole, M. R. Hughes, V. H. Hutchison, D. C. Jackson, K. Johansen, P. F. A. Maderson, R. L.

Malvin, J. E. Minnich, R. K. Mullen, K. Nagy, H. Rahn, D. W. Rennie, B. Schmidt-Nielsen, V. H. Shoemaker, G. J. W. Webb, and F. N. White reviewed individual manuscripts and Drs G. Zug and H. Wermuth critically read the entire set of manuscripts for current usage and accuracy of the Latin names employed. I thank my co-editor for his patience in handling editorial chores. The index was compiled and typed by Mrs Frances Scott and Linda Hilton. National Science Foundation grant GN-815 provided for some financial assistance, and the Department of Zoology of The University of Michigan paid part of the considerable bills for postage and copying.

February, 1976 Carl Gans

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CHAPTER 1

Reptilian Physiology: An Overview

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I. Why Study Reptiles?

The physiologist is fundamentally concerned with the workings of organisms. The basic questions are: How do organisms maintain themselves? How do their tissues and cells function to effect their component activities and integrate these with those of the organism as a whole? Towards this end, the physiologist dissects both process and structure. Traditionally this has led to such questions as: How is the pH of the blood maintained at a particular level? How is an impulse propagated along an axon or a neuronal membrane? How does a cell membrane contribute to the maintenance of the internal condition of its cell?

Many such questions have an immediate medical implication; thus Claude Bernard referred to his physiology as a kind of "médecine experimentale". Since man was the organism ultimately addressed, the experiment proceeded on those organisms most likely to yield comparable results and provide the advantages of low cost and ease of experimentation. This approach led to the use of frogs, dogs, cats, rats, and mice; the study of reptiles did not have much of a place here.

A second approach to physiology followed upon the discovery that particular principles might be most amenable to analysis in tissues in particular animals. Thus the glomeruli of frog and *Necturus* appeared to provide ideal sites to study ultrafiltration processes, and the giant axon of the squid allowed an approach to membrane phenomena. The "simple" nervous systems of invertebrates have now been suggested as containing the potential for understanding of the fundamental process of neural integration. A corollary of this "principles" approach has been the use of particular tissues to assay the pharmacological properties of a variety of compounds. The "turtle heart preparation" (see, for example, Wedd and Blair, 1945) represents an obvious example of a reptilian system utilized in this way.

A new approach to physiology seeks to define the mechanisms animals employ in functioning successfully in their respective environments. This "ecological physiology" deals with the adaptive meaning and energetic implications of particular specializations, rather than approaching each physiological topic from an anthropocentric viewpoint or studying systems in isolation from the animal. It identifies the physiological differences between diverse forms and attempts to explain each of these in terms of the basic organization and the characteristic environment of the particular species. What is the functional importance of the fact that some moths are endothermic? How have marine iguanas adjusted to their seemingly inhospitable environment? Such questions lead to more basic ones of ecological physiology. Not only do they let us characterize organismic diversity from a mechanistic standpoint, but they permit us to recognize and quantify the web of selective advantages that established and now maintains it.

Reptiles represent an ideal group for which such questions may be asked. They, rather than the Recent amphibians, represent the forms closest to those that successfully made the transition from an amphibious to a terrestrial existence. Moreover, they show the results of a series of independent adaptive radiations. Turtles, lizards, and snakes, but not rhynchocephalians, amphisbaenians, and crocodilians, have successfully invaded the vast majority of terrestrial, freshwater, and even some marine environments of the temperate and tropical zones. The reptilian success in doing so is linked with the development of multiple processes for dealing with the terrestrial environment.

The chapters of this and of the following volumes document these views of ecological physiology by a detailed dissection of the adaptive processes for a series of major systems. The present introduction briefly identifies some of the relevant physiological and behavioral capacities in the process and considers some of the peculiar demands imposed by the environment. In neither instance is the list complete; we describe well-known or suggestive cases in order to stimulate the formulation of additional questions. Toward this aim we have also included a brief discussion of problems in comparative analysis. The natural world is full of marvelous and fascinating phenomena, but understanding of mechanisms may be more rapidly acquired when topics are systematically approached by comparisons that facilitate interpretation of the data.

II. Interpretation of Structure and Function

Ecological physiology rests upon the axiom that organisms are adapted to their particular environments, to the niche they occupy within the particular biotope. The mere recognition that reptiles occupy very diverse habitats (Heatwole, this series) should then let one expect diverse adaptations. Consequently one should not expect to discover "the reptilian system" of thermoregulation, ion metabolism, or integumentary permeability by examining one reptile, or even one member of each reptilian order, chosen at random from a supply house catalog.

Some physiological characteristics are common to all or most reptiles. However, the process of natural selection, which has produced the diversity of organisms populating the earth, permits a great potential for change at any stage. Environmental changes may leave new resources open to exploitation; increased reproductive success of those able to utilize those new resources provides the potential for departures from, and modifications of, each aspect of the organism. Uniformity of functional capacities and underlying structural features in related lines may not be assumed; it must be subjected to test.

The pervasiveness of the adaptive process makes it highly probable that physiological parameters will show significant differences even among closely related species. Therefore reproducibility of results requires that as much attention be paid to specification of the identification, geographical sources, and seasonal status of the experimental animals as to the purity of reagents. It is important to keep in mind that the identifications furnished by dealers are nothing more than a preliminary indication of what might have been shipped. Precautions such as those outlined by Gans and Parsons (1970) are essential.

In many cases the eco-physiologist is interested in the adaptations of those organisms specific to a particular habitat. For instance, one may ask which of the integumentary differences between two species are due to the adaptation of each to its respective environment and which reflect the fact that the particular organisms derive from genetically distinct stocks. Such a set of questions cannot be answered by comparing, for instance, one aquatic and one terrestrial species; thus comparison of the aquatic snake *Natrix sipedon* with the desert viper *Echis carinatus* would lead to quite different conclusions than comparison of *Natrix* with a species of *Pituophis* or of *Tantilla*. Inclusion of several to many species in multifactorial comparisons provides a better chance of separating aquatic adaptations from those associated with such things as the size of the average individual or with food type.

When species are chosen at random from among the members of the class or order, one has only a limited chance of identifying structural or physiological peculiarities common to sub-groups for phylogenetic rather than immediately functional reasons (cf. Gans, 1966). A random selection of invertebrates might lead one into a futile search for an immediate functional basis for the type and molecular weight of the respiratory pigment or the type of phosphagen; we know that both of these kinds of compounds are conservative, show major group-specific differences, and only rarely differ substantiallyon the specific or even generic level.

In some cases fine resolutions of structural or physiological characteristics may not be desirable or economic for a particular project. When fine discrimination of such characteristics is sought, one may best compare populations within a widely distributed species or a series of related species scanning for similarities and differences across members of a single or some closely parallel adaptive radiations. If the taxonomy of the group is adequately understood (one may be at a disadvantage if the group has not been reviewed for a century), one may then find multiple taxa adapted to such circumstances as terrestriality, estuarine conditions, or feeding on arthropods, in different combinations.

Even when, for example, several species are clearly adapted to a particular food type or thermal regime one must still expect that the adaptations will differ in detail. Selection often results in compromise rather than perfection and any development that permits a species to meet the multiple demands of a particular niche is by definition adaptive. The genetic pattern of the population first subjected to such selection will determine the nature of the initial variability and, with this, the possible ways in which the process or structure can form.

Thermoregulation in the heat may involve evasion (ground squirrel) or evaporative cooling (horse). Such methods are responses to the thermal loads imposed by the environment or produced by the animal. Each represents a distinct solution to the problem appropriate to the size, functional characteristics, and general biology of the species. As selection at any time can only affect the frequencies of the variants already present in the population, it is the variability of the genetically determined physiological pattern, in magnitude and direction, that will determine the solution actually adopted by an animal. Different evolutionary solutions may involve different costs with respect to time, energy, and materials, and thereby limit the capacity of the species to occupy or persist in particular environments. Thus evaporative cooling may be a useful response to hot weather in habitats where surface water is readily accessible, but may keep small animals from entering hot environments where this fluid is less readily available. Radiant and convective cooling seems insufficient for large animals confined to environments where ready access to effective heat sinks is lacking on hot days.

III. Some Reptilian Physiological and Behavioral Capacities

A. General

One of the concerns of comparative physiology is the analysis of the various means by which different animals meet common functional problems. Information on reptilian physiological and related behavioral capacities has grown considerably in the past two decades. In addition to providing some fundamental insights concerning physiological processes of vertebrates, this