GANS BELLAIRS PARSONS

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# BIOLOGY OF THE REPTILIA

Edited by

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VOLUME 1

### MORPHOLOGY A

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### Preface

Reptiles may be defined as those amniotes that have neither feathers nor hair, yet such a characterization by exclusions is not particularly satisfactory. It points by implication to the lack of obvious similarities among the surviving members of this once flourishing group. Recent reptiles represent at least three distinct lines whose separation antedates the origin of birds and mammals.

Until fairly recently the surviving reptiles were accorded relatively little attention. There were many individual papers, but few summaries. Textbook references often indicated an assumption that the reptilian condition represented the midway point between "the frog" and either "the pigeon" or "the rat". Others implied that there was a single reptilian condition, characterized perhaps by the situation in one particular lizard or turtle. Knowledge of the paleontological record had also led to the view that Recent reptiles represented but the pitiful surviving species of a once flourishing group.

Two of the three surviving groups, the crocodiles and turtles, seem to have passed their evolutionary peak; only a relatively limited number of forms remain. Some lepidosaurians, members of the third group, seem also on the way to extinction. Yet certain other lepidosaurians (some lizards and snakes) represent extremely successful lines that have invaded a variety of niches and are still engaged in adaptive radiations.

The lack of research emphasis has been particularly unfortunate because the reptiles are after all the group that "invented" many of the innovations that led to birds and mammals, which in this context are little more than modified reptiles. Recent reptiles retain many of these modifications in various early stages. Their study can yield important clues to the understanding of endothermy, water conservation, and osmoregulation. Remnants of the earliest stages of such terrestrial adaptions as columnar rather than cantilevered limbs, a "head joint", an articulated vertebral column, and a bipedal progression pattern can also be seen in this group.

The last twenty years have shown the benefits to be derived from their study and a direct consequence has been an almost exponential increase in the number of articles and papers dealing with these animals. Not only have these studies increased in absolute numbers, but there has been a continuous extension of their scope. The center of emphasis has consequently shifted,

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in a relatively short time, from problems of classification and faunistics to problems of physiology, behavior, population dynamics, and biochemistry. Raw materials are being accumulated for a better understanding of the patterns of reptilian evolution.

Yet the results of past lack of concern are still noticeable. It is difficult to determine what is and what is not known. Facts are widely scattered across the literature, and there is often uncertainty whether a specific observation should be interpreted as applying only to one individual species or more

broadly to a genus, family, or higher category.

There is no single summary of the kind that Noble provided in his "Biology of the Amphibia". Specialization of scientists has become more restrictive with each passing year; simultaneously the questions asked by new investigators have become more searching. This places a premium on the expertise required to do reptilian studies; experimenters still tend to skip reptiles when selecting experimental animals for problems. Needed now are both discussions of particular organs, systems, and processes in reptiles, as well as background information on the condition in other groups of vertebrates.

It was a recognition of these difficulties that led Angus d'A. Bellairs, Ernest E. Williams and me to meet during 1961 to plan a series of volumes that would fill this gap. The subsequent discussions forced us to make some value judgments. The process of selection of topics and of authors, furthermore, disclosed a number of fundamental problems. The following statements deal with some of these; their presentation here is intended to characterize the aims and perhaps the limitations of the present project.

1. The BIOLOGY OF THE REPTILIA is addressed to and designed for specialists who need a summary on the status of our knowledge in a particular system or process in reptiles. It is hence intended for people who have at least some minimal background in the areas concerned. Our aim is to facilitate future work rather than place a tombstone upon past

knowledge.

- 2. The emphasis in the series is on Recent reptiles since, for instance, the osteology of fossils has been well summarized by others. The classification proposed in A. S. Romer's "Osteology of the Reptilia" with departures noted in the individual chapters has been used as a basis for these volumes. It is hoped that the data uncovered and investigations undertaken by the contributors should permit a reevaluation of current views so that summary statements of major aspects of reptilian biology may be placed into a last volume.
- 3. The level of detail required makes it unlikely that one, two, or even half a dozen authors could provide the entire series. Subdivision had to be greater so that each chapter is furnished by a specialist, preferably by one

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who is currently engaged in active research on the chapter's topic.

4. The kind of presentation needed often required information that was not currently available. Major gaps in our knowledge have become evident; these persisted after the facts scattered throughout the literature had been assembled by the contributors.

The survey of the literature often had to serve as a basis for a research project designed to fill the gaps disclosed by the survey. These original investigations demanded a major commitment of time and energy. They further complicated our search for authors and forced modification of the initial and overly optimistic time schedule. They also restricted the area that any one specialist could usefully cover.

- 5. Some of the topics discussed will we hope be of interest to anatomists, physiologists, and behaviorists who are not herpetologists. The chapters have hence been grouped to place organ systems or associated topics into immediate juxtaposition; thus each volume should have a place independent of the series as a whole. Yet the amount of work that needed to be done on specific topics and the time that authors could commit varied widely. In order to avoid drastic delays that would penalize the prompt, we have accepted a more pragmatic approach to the composition of volumes. Their size has been reduced by limiting the number of included chapters. The arrangement of topics has also been interpreted more loosely, both in terms of inclusion and of separation.
- 6. A knowledge of comparative anatomy forms the basis of comparative physiology; both of these areas are essential to the comparative study of ecology and behavior. Relatively few broad, yet detailed, studies of reptilian morphology are now available. The present series hence begins with a series of morphological topics. The information depicted in these is intended as a basis for the discussions in the subsequent, functionally oriented chapters.
- 7. The series has been subdivided into (i) morphological, (ii) embryological and physiological, and (iii) ecological and behavioral portions. These divisions overlap. Thus morphology may be discussed at the gross, microscopic, and fine structural levels each of which contact a different aspect of physiology and is often studied by a different specialist.

Where a system such as the visual or acoustic is well enough known to justify a separate treatment of morphology and physiology, it is so treated. Where the amount of available information is sufficiently limited or no one is currently working in one or the other division morphology and physiology have been combined into a single chapter, particularly when a specialist appeared both capable and willing to deal with both. This explains the treatment of certain aspects in the morphological sections and also some of the omissions there.

We have at the same time discouraged the inclusion of superficial "func-

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tional" comments or off-hand descriptions of morphology in the functional sections. Morphology and function deserve equivalent treatment; only this will permit these volumes to serve as a reference as well as a stimulant.

8. It was obviously impossible to elicit broad surveys on every facet on which the BIOLOGY OF THE REPTILIA is intended to report. Unevenness of treatment is inherent in the levels of our knowledge; it cannot be avoided. Considerable energy has, however, been expended to achieve statements that indicate the extent of the available information and that define the nature of the gaps remaining after each author has combined the results of his own work with gleanings from the literature. The chapter size has been expanded, where necessary, to permit the inclusion of new information and illustrations, as well as of any new syntheses that an author could derive from the data.

The editors have not insisted on an absence of bias but have encouraged the presentation of diverse viewpoints. Whenever possible, chapters espousing a particular approach also refer to discussions of opposing opinions. The editors have sometimes had to inform authors of their disagreement with points raised in discussion or interpretation; they have not insisted that changes be made. It is hoped that the inherent diversity of views will prove germinal in inducing additional study.

The present volume starts with a statement of the pre-history of the major groups of Recent reptiles and continues to deal with bone as a tissue, and with such osseous elements as epiphyses and sesamoids, the turtle shell, the vertebral column and ribs, and the reptilian dentition. The second and third volumes will deal with the morphology of the sense and endocrine organs and of blood. It is hoped that the later volumes on morphological topics will appear in parallel with the first volumes on physiology and behavior.

Finally it is my pleasure to be able to acknowledge the very substantial help received from many sources. The co-editors provided major assistance and Dr. E. E. Williams participated in the planning of the early sections. Numerous friends and colleagues cooperated by reviewing the individual papers; some of the most useful comments were offered by authors reviewing each other's contributions. Miss A. G. C. Grandison was kind enough to review the proofs for mis-spelling of Latin names. The staff of Academic Press proved to be exceptionally patient during the period when we were trying to formulate policy. National Science Foundation Grant GB-3881 provided some assistance for editorial work. Finally, I should like to express my appreciation to Mrs. Gloria Griffin and to my wife who handled the extensive correspondence and manuscript preparation that proved to be necessary.

October, 1968 Carl Gans

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SUBJECT INDEX .. ..

#### CHAPTER 1

# Origin of Reptiles

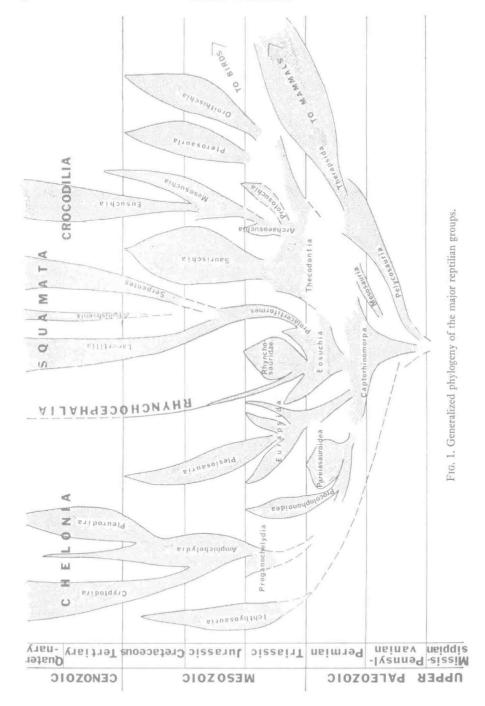
ROBERT L. CARROLL
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### L. Introduction

Living reptiles can be thought of as relicts of the great Mesozoic differentiation of this group. Of the sixteen orders recognized by Romer (1956), only four survive today. These living orders can all be traced back to the Triassic. Prior to that period, their origin and relationships are subject to varying degrees of speculation. More primitive forms, still unquestionably reptiles, are known from as early as the base of the Pennsylvanian. Prior to that time, neither reptiles nor any appropriate ancestors are known. The exact origin of the group among the amphibians, and the conditions under which essentially aquatic amphibians evolved toward primarily terrestrial reptiles, remain in doubt. These problems will be considered in this chapter, together with brief mention of the fossil record of the living groups.

Although the vast number of totally extinct Mesozoic groups—dinosaurs, marine and flying reptiles—will not be discussed here, their general relationship with other reptiles can be seen in the phylogeny given in Fig. 1. Some minor Paleozoic groups—araeoscelids and mesosaurs—are also omitted from consideration since they have no direct bearing on the ancestry of living reptiles.

The major reptile groups have been defined primarily on the basis of the anatomy of the skull, with particular emphasis on the nature of the openings in the temporal region to accommodate the jaw musculature. Crocodiles have both dorsal and lateral temporal openings, as does *Sphenodon*. The lizards have a dorsal temporal opening. The openings for jaw musculature in a turtle are on the occipital rather than the dorsal or lateral surface, and so turtles are considered to lack true temporal openings. Although the nature of the temporal region is useful in defining the living groups, it is not a sufficient criterion to determine their interrelationships, nor to establish affinities with fossil groups.



There is apparently a high selective value in having some sort of temporal opening, but the particular position and number of these openings is of lesser importance. It is quite possible for a similar configuration to be achieved independently in distantly related lines of primitive reptiles, and for closely related groups to develop temporal openings in different positions.

Romer (1956) groups the reptiles in six subclasses:

ANAPSIDA. Turtles and the primitive stem reptiles.

LEPIDOSAURIA. Squamates, rhynchocephalians, and their Permian and Triassic ancestors, the eosuchians.

ARCHOSAURIA. Crocodiles, two orders of dinosaurs, flying reptiles, and the basal stock from which these groups arose, the thecodonts.

ICHTHYOPTERYGIA. Ichthyosaurs.

EURYAPSIDA. Plesiosaurs and their relatives.

SYNAPSIDA. The mammal-like reptiles.

Only the first three subclasses are represented in the living fauna and these in greatly reduced numbers and diversity.

### II. The Ancestry of Living Reptiles

Except for the rhynchocephalians, the living orders have a fairly good fossil record throughout the Cenozoic and Late Mesozoic, and, except for the turtles, their immediate ancestry among more primitive reptiles can be established with confidence (Fig. 2).

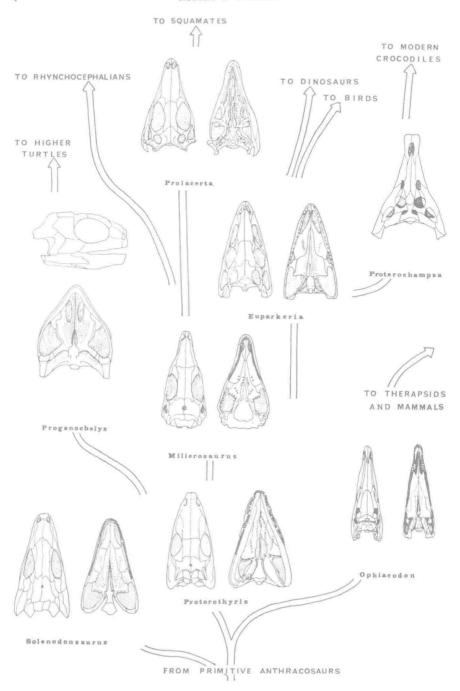
#### A. LEPIDOSAURIA

## 1. Rhynchocephalia

Aside from the turtles, whose ancestry is unclear, *Sphenodon*, the New Zealand tuatara, the only surviving member of the order Rhynchocephalia, is considered the most primitive of living reptiles. The family Sphenodontidae has a longer fossil record than any other group within the class. The structure of the palate shows *Sphenodon* to be little advanced over Permian reptiles. The marginal dentition is modified, however, with the teeth fused to the top of the jaw.

Sphenodon resembles lizards in general body shape and size, but differs in possessing two well-defined temporal openings and in having a rigidly fixed quadrate. There are also a number of basic differences in the soft anatomy which set these two groups apart (cf. Bogert, 1953).

No fossils of this family are known later than the Jurassic, suggesting that the rhynchocephalians have been restricted in numbers and distribution since the Late Mesozoic. Forms very similar to the living genus, although slightly more primitive, are known from the Upper Jurassic of both Europe



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