Biology of the Reptilia

Volume 14, Development A

Edited by

Carl Gans, Frank Billett & Paul F.A. Maderson

BIOLOGY OF THE REPTILIA

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Ann Arbor, Michigan

VOLUME 14
DEVELOPMENT A

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Preface

The last decade has seen a renewed interest in the area of vertebrate development, not only in relation to the molecular mechanisms controlling it, but also in terms of such classical areas as neoteny, organogenesis, and regeneration, of the parallel shift of structure and function during ontogeny, as well as of comparative and evolutionary approaches. Also, the viewpoints of morphology and ecology are becoming increasingly important in the approach to the study of development. The nature of possible developmental constraints, their reality, and their range is again being discussed.

The tremendous diversity of reptilian size, growth, body shape, and proportions, as well as of the temperature regimes to which reptiles are exposed and of the environments they occupy, have made them obvious but as yet poorly exploited candidates for such expanded developmental studies. Volumes 14 and 15 begin to characterize the developmental patterns exhibited by members of this group, again summarizing what is known and explicitly, or by implication, pointing to the major gaps that remain. It is with considerable gratification that we note the collaboration of a distinguished and international group of colleagues in this venture.

This is the first attempt to summarize the state of our knowledge of developmental pattern in this diverse group of organisms. To meet the needs of the audience, we have incorporated two approaches. For each group of reptiles, we have provided a chapter of variable length that summarizes developmental studies and the topics on which these have been carried out in reptiles. These chapters should provide a guide and a review of the level of work that has thus far proceeded, for instance, with turtles or with *Sphenodon*. The chapters also include data on the reproductive biology of the group, at least guiding the specialist in development to the requisite literature on those ecological and behavioral topics pertinent to this. Also, we have included a separate series of chapters dealing with special topics on which substantial work has been done among the Reptilia or for which reptilian work is particularly pertinent.

The two-volume set (Volumes 14 and 15) are arranged in a mixed pattern. Volume 14 includes the special chapters pertinent for turtles in general, for marine turtles, for crocodilians, and for *Sphenodon*. It also includes chapters on oogenesis, on the development of the skin, of the immune system, and of the pituitary. Finally, we have attempted to provide an introductory chapter that places the remaining material into perspective and provides such ancillary information as sources of Normal Tables and serial sections, and techniques of sampling and preservation. Volume 15 emphasizes the accounts of the Squamata (lizards and snakes). In view of the extreme diversity encompassed by this group, the general chapter is much shorter, and the subject has been divided into a variety of subcategories. A special chapter documents the diversity of reptilian reproductive patterns, introducing the developmental biologist to the range of conditions exhibited by these animals. Other and more general chapters treat topics such as caudal autotomy and regeneration, limb development and reduction, and the development of the reproductive system. The last two chapters include some data not only on the lepidosaurians, but also on turtles and crocodilians. Finally, we are very pleased to have been able to include up-to-date treatments of reptilian parthenogenesis, placentation, and viviparity, topics that are particularly pertinent to the embryology of squamates.

I am indebted to Frank Billett and Paul F. A. Maderson, whose discerning efforts allowed us to bring Volumes 14 and 15 to completion and to my wife for substantial editorial aid. Individual accounts were reviewed by A. d'A. Bellairs, Ruth Bellairs, C. J. Cole, D. Crews, B. Doneen, M. Ewert, M. W. J. Ferguson, H. Fox, P. R. Gould, R. Jurd, W. King, J. Lang, P. F. A. Maderson, M. J. Manning, J. D. Miller, M. Miller, Vr. Muthukaruppan, P. D. Nieuwkoop, R. A. Nussbaum, G. Packard, T. S. Parsons, D. Robertson, D. Starck, G. Underwood, Y. L. Werner, M. Whitear, A. E. Wild, J. Wright, C. Wylie, and G. Zug. We again thank George Zug for his careful efforts at updating the taxonomic terminology. As in previous volumes of this series, we list animals only by their current names. Ms. S. Konchal and Ms. K. Vernon typed some of the manuscript. Mr. J. Goode modified some of the illustrations. The British Council supported a trip by Dr. Billett to Ann Arbor. We appreciate the support of our institutions toward the substantial cost of copying and postage. Finally, in this, the first volume to be published under the aegis of John Wiley & Sons, Inc., I would like to express my personal appreciation to Miss Diana Beavan, formerly

with Academic Press, London, whose personal interest, professional expertise, and commitment greatly aided authors and editors in the successful production of the last six volumes.

CARL GANS

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CHAPTER

1

Why Study Reptilian Development?

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I. INTRODUCTION

The study of animal development has its own history, one which has proceeded with extraordinary rapidity in the last two centuries. From ancient times through the eighteenth century, "embryology" involved the documentation of the phenomenon of the gradual emergence of a recognizable living organism from a fertilized egg (Fig. 1); analysis of these data was influenced by prevailing religious and philosophical trends (Needham, 1959). By the end of the seventeenth century, microscopic techniques became available, and their use laid the foundation for an association among embryology, comparative anatomy, and later, paleontology. This was directed toward phylogenetic analysis, which dominated zoology throughout the nineteenth century (Goodrich, 1930; Gould, 1977; Bonner, 1982; Goodwin et al., 1983). During the latter half of the nineteenth century, the works of Huxley, Owen, Agassiz, and others established the patterns of interrelationships among vertebrate groups, which are still broadly accepted today. Simultaneously, the pioneering concepts of von Baer were increasingly overshadowed by the pervasive dominance of Haeckelian thinking (Gould, 1977). Had it not been for the impetus of Haeckel and his disciples, reptiles, both embryos and adults, might have remained forever in the low esteem accorded them by Linnaeus (1766), who did not distinguish them from amphibians: "These foul and loathsome animals are distinguished by a heart with a single ventricle and a single auricle, doubtful lungs and a double penis. Most are abhorrent because of their cold body, pale color, cartilaginous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habitation and terrible venom; and so their Creator has not exerted his powers (to make) many of them." (Translation after Smith, 1951, pp. 8–9.) Instead, the study of the developmental anatomy of reptiles reached its zenith between 1850 and 1920.

In the 1880s, Roux founded the experimental science of *Entwicklungsmechanik* and thus changed the direction of embryological research by asking the question: "How does an embryo develop"? Subsequently, it became recognized that this original question is but a more specific expression of an even more fundamental one: "How does any cell (or population of cells) acquire the information necessary to attain and maintain its differentiated state"? Contemporary Developmental Biology not only analyzes the embryo, but also treats the nature of cellular control mechanisms from the moment of fertilization through the death of the individual. Hatching, birth, or metamorphosis are now but arbitrary points in a temporal continuum. Consequently, "embryonic mechanisms" may be recognized in phenomena such as tissue and organ homeostasis, wound healing, regeneration, growth, aging, and eventual death. This set of concepts has important practical consequences in investigating developmental phenomena in reptiles.

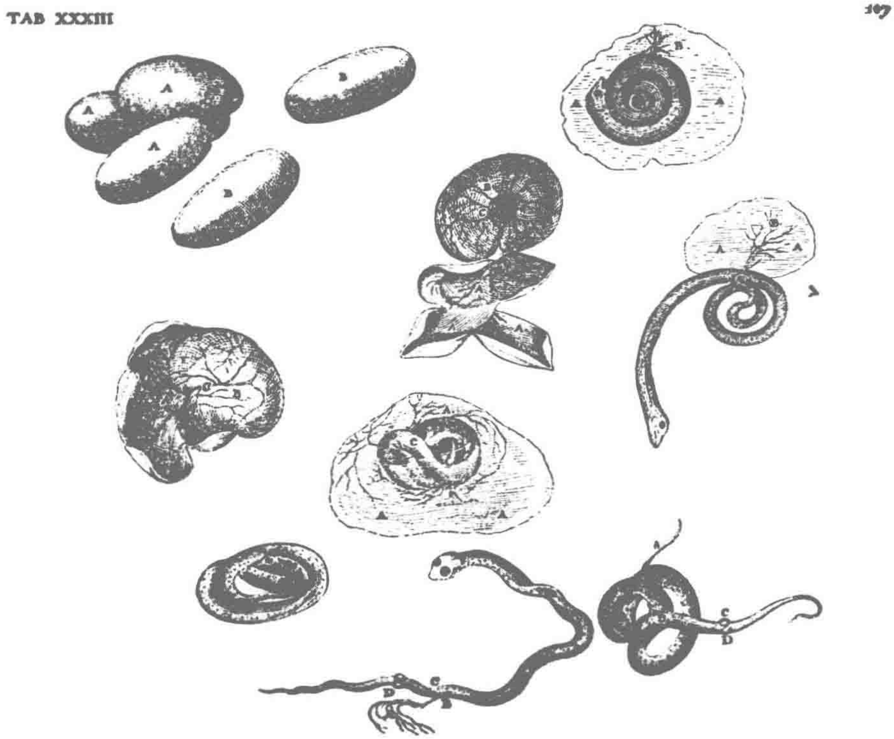

Fig. 1. Drawings of a developing snake, as illustrated by Fabricius, 1684. The individual figure shows: 1. five eggs of a snake which Fabricius refers to as *Carbo*, and which may be a species of *Natrix*; 2–7, the late embryo (approximately equivalent to stage 30 for *Vipera aspis*, Hubert and Dufaure, 1968), extra-embryonic membranes (A) are depicted attached to the embryo via umbilical vessels (B); 8–9, some detail of the embryo, the hemipenes (D) is clearly shown. (From Adelmann, 1942).

As the *Entwicklungsmechanik* of the late nineteenth century underwent the transition through Experimental Embryology to Developmental Biology, reptiles seemed to become less and less important. The reptilian embryo had enjoyed the center stage of research interest during the "phyletic era" of embryologic investigation. However, the practical problems of obtaining living embryos were much greater for reptiles than for other taxa; consequently, reptilian embryos (and by extension most potentially interesting developmental phenomena in reptiles) were increasingly ignored. Because textbooks are derivative, the paucity of original literature led to reptilian topics becoming excluded except for occasional references to tail regeneration and viviparity. This vicious circle of decreasing interest was reinforced by activities, or lack thereof, in many other disciplines.

The pattern of vertebrate evolution established in the late nineteenth century had left extant amphibians and reptiles in an ambiguous position.

Once it was realized that they were but the remnants of major radiations in the Paleozoic and Mesozoic eras, original research on the two classes centered more and more on paleontology, and emergent data increasingly emphasized that the position of living forms was separate from the "mainline of vertebrate evolution," i.e., that leading to the mammals. During the first half of the twentieth century, research, which was conducted initially on mammalian subjects, produced techniques that permitted the emergence of comparative disciplines such as endocrinology, neurology, serology, immunology, and molecular biology. Developed first by researchers with medical backgrounds, these disciplines were assumed by zoologists who found themselves in an invidious position; although these scholars knew that extant amphibians and reptiles were specialized in their own rights, comparisons between "a mammal," "a bird," "a reptile," "an amphibian," and "a fish" soon began to appear in the literature. Only in the last 25 years have sufficient data accumulated for specific topics in specific taxa for these irrational "fallacies of intermediacy" to have become modulated, at least to some degree. Unhappily, developmental phenomena in reptiles are only now beginning to be evaluated in an appropriate fashion. Why should this be so?

Many of the first experiments in *Entwicklungsmechanik* were conducted on amphibian eggs by Roux and others in the 1880s (Oppenheimer, 1955a, b, 1957). The Europeans continued to concentrate on such material in spite of many technical difficulties and personal hardships (see Brachet, 1977:113); Hans Spemann received the Nobel Prize in 1935 for his work on primary induction in amphibians. In North America, marine invertebrates and amphibians were the primary subject of embryological investigations until the 1930s, through the stimulus of a group of outstanding scholars working at the Marine Biological Laboratory at Woods Hole (e.g., E. B. Wilson, E. G. Conklin, T. H. Morgan, F. R. Lillie) and through the profound influence of Ross Harrison at Yale University. For unknown reasons, European and North American embryologists ignored reptiles, even in regions in which reptilian material was available, such as in the southwest United States and in the southern continents, e.g., Australia, South Africa, and South America. The widely quoted morphological studies of viviparity in Australian scincids by Boyd and Weekes in the 1930s (see Yaron, and Shine, Vol. 15, Chapters 7 and 8), a little-known report of grafting of lacertid embryonic tissues onto chick chorioallantoic membranes (Nakao, 1939) and some experiments on caudal regeneration in lizards (Bellairs and Bryant, Vol. 15, Chapter 5), have been the sole exceptions to a general absence of interest in developmental phenomena in reptiles. Faced with a plenitude of data from other vertebrates, most developmental biologists probably assume that there is little of general interest to be gained from the study of reptiles; it is our hope that these volumes will vitiate such assumptions.

It would be both wrong and misleading to deduce from the above that