the biology of the amphibia

by G. Kingsley Noble

an unabridged republication of the standard
work on the natural history and biology of frogs, toads, and salamanders

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Dover Publications, Inc. New York 10, N. Y.

PRINTED IN THE UNITED STATES OF AMERICA

This new Dover edition is an unabridged republication of the first edition with a new biographical note on the author.

BIOGRAPHICAL NOTE

Gladwyn Kingsley Noble was born September 20, 1894 in Yonkers, New York, the son of Gilbert Clifford Noble and Elizabeth Adams. From earliest boyhood he displayed a marked interest in the world of nature and long before graduating from the Yonkers High School he had made up his mind to become a naturalist.

Majoring in zoology at Harvard, he received his A.B. in 1916 and his A.M. in 1918. Much of his time in Cambridge was spent at the Museum of Comparative Zoology working as assistant to the late Thomas Barbour. His early enthusiasm was for birds, and his first scientific paper, published when he was nineteen, dealt with the depredations of cats among the nesting gull colonies of Muskeget Island. It was chiefly as a bird student and collector that he was sent to Guadeloupe at the end of his freshman year and to Newfoundland the following summer. In 1916 a third Harvard expedition took him as general zoologist to the Marinan Valley in northwestern Peru. Dr. Barbour encouraged his field activity, gave him a thorough grounding in taxonomy, published several herpetological papers with him, and undoubtedly was responsible for stimulating his interest in reptiles and amphibians. His first paper on frogs was largely taxonomic but gave promise of depth and versatility in its histological drawings and data.

The young scientist's career was interrupted early in 1918 when he obtained a commission as ensign and was sent to Washington to serve in the Office of the Chief of Naval Operations. At the close of the war he came to the American Museum of Natural History as assistant curator in the department of herpetology. At the same time he began working for his doctor's degree at Columbia University with Dr. William K. Gregory as his faculty adviser and later his deeply esteemed friend. His thesis, entitled "The Phylogeny of the Salientia," was published in 1922 and was soon recognized as a major herpetological contribution. In it he reclassified frogs and toads on the basis of such fundamental characteristics as vertebral articulation and thigh musculature. Subsequent papers also reflected his intense training at Columbia in morphology, phylogeny, and palaeontology.

In 1921 he married Miss Ruth Crosby, a member of the museum educational staff, and many of his later field trips were taken with her and with their two sons. Much as he delighted in field work, he never had a keen desire to explore the far corners of the world, feeling that for him the mysteries of laboratory and countryside offered adventure enough. Short excursions were frequently made to study or collect forms in which he was particularly interested, such as the aquatic lizards of Cuba, the giant tree frogs and iguanas of Santo Domingo. He loved the pine barrens and cedar swamps of south Jersey with their Anderson's tree toads, carpenter frogs, and fence lizards; the heron and gull colonies of Long Island, Nantucket, and the Jersey coast; the cave creatures of the Ozark mountains; the fish life of the Florida reefs and the Marineland Aquarium. Intimate contact with these creatures brought him to the realization that life history, like structure and physiology, could indicate evolutionary relationships. A number of ontogenic papers were published and later summarized in "The Relation of Life History to Phylogeny within the Amphibia," read before the British Association for the Advancement of Science in 1925.

That summer and fall were spent in England and Europe visiting universities, museums, zoological gardens, and aquaria—studying not only the collections of animals but also techniques of storing, cataloguing, and exhibition.

During his comparatively short career he published about 180 papers. From 1916 to 1932 four-fifths of these were on amphibians. His interest in life history lead inevitably to a closer study of courtship and social behavior, and of the effects upon them of the endocrine glands, especially in salamanders. He learned that much of this behavior, so difficult to spot in the field, could be induced artificially in the laboratory. Reptiles and amphibians proved to be excellent subjects for experimental work because of their basic position in the evolutionary scale and because they were easy and economical to rear in the laboratory. A long series of studies were made on the physiology and behavior of various frogs, salamanders, snakes, and lizards. Many of the results were woven into this book originally published in 1931.

Henry Fairfield Osborn, long president of the museum, had followed these researches with consistent enthusiasm, and in 1928 the trustees voted funds to establish a separate department of experimental biology—a department which is still producing regularly and which is undoubtedly Dr. Noble's greatest memorial.

The last twelve years of his life were devoted chiefly to problems of physiology and behavior; characteristically, he prepared himself to meet them by taking courses in endocrinology, neurology, and psychology. To some extent reptiles and amphibians gave way to fish and once more to birds. Fish had the advantage of more frequent breeding cycles, and bird reactions were perhaps more spectacular.

At various times, Dr. Noble was a lecturer in biology at Columbia University, a visiting professor at the University of Chicago and at New York University. On several occasions he was offered university posts of distinction and responsibility; although he enjoyed a university environment, he decided not to change. He had a sincere devotion to the museum and a tremendous desire to see it develop—not as a storehouse—but as a dynamic educational force which would interpret the fundamental principles of life. He felt, too, that his own particular type of research could best be carried on in the museum. Always he remained a naturalist at heart, fully recognizing the importance of the more technical "ologies" but accepting them only as tools to the deeper understanding of birds, frogs, and men.

1954 R. C. N.

PREFACE

With the increasing use of both frogs and salamanders in experimental biology, the need has arisen for a general textbook which summarizes the relations of Amphibia to one another and to their environments. The salamanders, for example, are commonly believed to be more primitive than frogs, although this is true for only certain features of their anatomy. Again, Necturus, which is now frequently employed in university courses of zoölogy, is often described as a very primitive type, without further reference to its systematic position among the Caudata. There is no book written in English since Gadow's volume in the "Cambridge Natural History" (1901) which attempts to combine both the natural history and the biology of Amphibia in a single volume. Holmes's splendid book on "The Biology of the Frog" has accomplished this task for Rana, and in extending the field to all the Amphibia, I have been influenced by this work in the selection of material.

Although the present volume was written primarily to introduce the student to the biology of both frogs and salamanders, technicalities have been avoided wherever possible and much has been included which should be of interest to the field naturalist or traveler. The systematic names employed are those in current use by naturalists and not the more familiar ones of the experimental laboratory. The difference between these two nomenclatures is not sufficiently great, however, to cause confusion.

The sections dealing with the physiology of Amphibia are necessarily greatly abridged, but reference has been made wherever possible to the more comprehensive papers and summaries where a historical treatment of the subject may be found. Unfortunately, the extensive account of the Amphibia by Professor Franz Werner in Kükenthal's "Handbuch der Zoologie" appeared after my manuscript had gone to press and no reference is made to this authoritative work in the following pages.

In the preparation of the text I have received help from many sources. My thanks are due first to Professor Henry Fairfield

Osborn for his enthusiastic interest and for the many facilities I have enjoyed at the American Museum where the work was carried forward. I have received considerable bibliographical assistance from Dr. Cora S. Winkin and Mr. Ludwig Hirning, who have also collated various parts of the text. Dr. Winkin has contributed original notes to the chapters dealing with the nervous system and with metabolism. Professor Frank H. Pike has kindly read the chapters on the nervous system and on respiration. Dr. Thomas Barbour has loaned for study valuable material preserved in the Museum of Comparative Zoölogy. The drawings are the work of Mrs. E. L. Beutenmuller and many are based on original material in the American Museum. I am especially appreciative of the aid given throughout the course of the work by my research assistant, Miss Gertrude Evans.

G. K. N.

THE AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK, N. Y.,
April, 1931.

ACKNOWLEDGMENTS

Many of the figures used in the text have previously appeared in my papers published in the *Bulletin* and in *Novitates* of the American Museum as well as in the *Annals* of the New York Academy of Science. I am indebted to the authorities of the Museum and to the Academy for the privilege of republishing them. Many others have been taken from various scientific journals and books and I wish to express my obligation to the publishers and the authors for the opportunity of redrawing these figures for the present work. Acknowledgment of this courtesy is made to the following sources:

Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique for Fig. 68 from *Bull. Acad. Roy. Belg. Cl. Sci.*

Akademische Verlagsgesellschaft, for Fig. 100 from *Zool. Anz.*, Figs. 65, 92, 92*D* from *Morph. Jahrb.*, Figs. 118, 119 from *Zeitschr. Wiss. Zool.*

American Microscopical Society for Figs. 103*A*, 103*B*, 114*B*, 138 from *Trans. Amer. Micr. Soc.*, Figs. 78*A*, 78*B*, 115 from *Proc. Amer. Micr. Soc.*

Bergmann-Verlagsbuchhandlung, J. F., for Figs. 117, 122 from *Anat. Hefte.*

Bonnier, Albert, for Fig. 114*A* from *Acta Zoologica.*

Cambridge University Press and The Macmillan Company for Fig. 130 from Coghill, "Anatomy and the Problem of Behaviour."

Crowell Company, Thomas Y., for Fig. 126 from Papez, "Comparative Neurology."

Deutsche geologische Gesellschaft for Fig. 3*B* from *Zeitschr. Deutsch. Geol. Gesellschaft.*

Essex Institute, The, for Fig. 82 from *Bull. Essex Inst.*

Fisher, Gustav, for Figs. 60, 64, 72 from *Anat. Anz.*, Figs. 6*B*, 6*C* from *Biol. Unters.*, Fig. 97 from Hertwig's "Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere," Fig. 125 from *Jena. Zeitschr. Naturw.* Fig. 9 from Keibel's "Normentafeln zur Entwicklungsgeschichte der Wirbeltiere," Fig. 128*C* from Kuhlenbeck "Vorlesungen über das Zentralnervensystem der Wirbeltiere," Fig. 123 from *Zool. Jahrb., Abt. Allg. Zool. Physiol. Tiere,* Figs. 111, 128*A*, 129 from *Zool. Jahrb., Abt. Anat.*

Folia Anatomica Japonica, Editors of the, for Figs. 84*A*, 84*B*, 84*C*, 84*E*, 128*B* from *Folia Anat. Japonica.*

Hokkaido Imperial University for Fig. 133 from *Jour. College Agr.*

Hollandsche Maatschappij der Wetenschappen and F. J. J. Buytendyk for Fig. 134 from *Arch. Neerland. de Physiol. de l'Homme et des Animaux.*

Marine Biological Laboratory for Figs. 7*A*, 52, 103*C* from *Biol. Bull.*

New York Zoological Society for Fig. 133*F* from *Zool. Soc. Bull.*

Royal Society, The, for Figs. 1, 2, 83 from *Phil. Trans. Roy. Soc. London*, Figs. 56*A*, 56*B* from *Proc. Roy. Soc. London.*

Smithsonian Institution for Figs. 77, 139 from *U. S. Nat. Mus. Bull.*

Springer, Julius, for Figs. 3*A*, 10 from "Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon" (Sarasins), Figs. 13, 55 from *Arch. Mikr. Anat.*, Fig. 8 from *Zeitschr. Zell. Gewebel.*

Taylor and Francis for Figs. 4, 85 from *Ann. Mag. Nat. Hist.*

Thieme, Georg, for Figs. 79, 106, 132 from *Biol. Zentralbl.*

University of California Press for Fig. 137 from *Univ. Calif. Pub. Zool.*

University of Chicago Press for Fig. 16 from *Physiol. Zool.*

University of Wisconsin for Fig. 71 from *Bull. Univ. Wis.*

University Press Cambridge for Figs. 12, 112 from *Brit. Jour. Exp. Biol.*

Wegner, Julius E. G., for Fig. 133*D* from *Blätt. Aquar.-Terrar.-Kde.*

Wistar Institute of Anatomy and Biology for Fig. 109 from *Anat. Rec.*, Fig. 108 from *Amer. Anat. Mem.*, Figs. 69, 70, 75 from *Amer. Jour. Anat.* Figs. 113, 116, 120, 124, 127 from *Jour. Comp. Neurol.*, Figs. 15, 101, 107 from *Jour. Exp. Zool.*, Figs. 6*D*, 10*A*, 14, 93, 98, 102, 105, 121 from *Jour. Morph.*

Zoological Society of London and Dr. O. M. B. Bulman for Fig. 5 from *Proc. Zool. Soc.*

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CHAPTER I

THE ORIGIN OF THE AMPHIBIA

There are many backboned animals which lead an amphibious life. The crocodile and the seals live at times in water and again on land. The name "Amphibia," first used by Linnaeus for a rather odd assemblage of more or less aquatic vertebrates, referred to this amphibious habit of the members of the group. Today the name is restricted to that class of vertebrates which is intermediate between fishes and reptiles. The group includes the frogs, salamanders, caecilians, and many fossil creatures, frequently of large size and bizarre form.

The living Amphibia are cold-blooded vertebrates possessing limbs instead of paired fins like the fish and having a soft, moist skin lacking the protective hair or feathers of higher vertebrates. Salamanders are often confused with lizards, which they resemble superficially. The latter have a dry, scaly skin similar to that of other reptiles. Minute scales are present between the transverse body rings of caecilians but these are rarely seen without making a dissection. Amphibia may, therefore, be defined as cold-blooded vertebrates having a smooth or rough skin rich in glands which keep it moist; if scales are present, they are hidden in the skin.

The development of Amphibia, also, serves to distinguish them from reptiles, birds, or mammals. The eggs are usually laid in the water and the larvae pass through an aquatic stage before metamorphosing into the adult. Many frogs and salamanders lay large-yolked eggs on land and the young never enter the water. These terrestrial eggs lack the calcareous shell of reptiles and birds. Further, the embryo as it develops is never surrounded by the protective amnion or equipped with a respiratory allantois as in the case of higher vertebrates. Modern Amphibia differ from reptiles in many details of their skeletal anatomy, but some Carboniferous and Permian Amphibia, especially the Rachitomi, were so similar to contemporary reptiles that it is impossible to draw a sharp line of distinction between them. Palaeontological discoveries have also done much to fill in the gap between Amphibia and fishes but even here all the intermediate stages have not yet been found. Modern Amphibia have arisen from a group of more or less aquatic tetrapods which flourished from at least early Carboniferous to Triassic times.

The term "Batrachia" is frequently used for the class Amphibia, as, for example, by Cope in his monumental "The Batrachia of North America." Linnaeus included crocodiles, lizards, snakes, and turtles in his group Amphibia, and he was followed by some later students. Brongniart was the first to distinguish the frogs and salamanders from the reptiles but his choice of the term batraciens for the group was unfortunate, as this name was already a synonym of Salientia. Various other names were later proposed for the class. It was not until 1825 that Latreille restricted the name Amphibia to the frogs, toads, and salamanders, leaving the caecilians with the reptiles. The term Amphibia, therefore, originates from the Linnaean name as restricted by Latreille, the caecilians being later added to the group. Rules of priority are not strictly applied to groups higher than genera, and as Linnaeus included reptiles in his category, there are some students who would use another name for the class. Since none of the later names proposed has met with wide acceptance, the majority of recent students utilize the Linnaean name Amphibia in its restricted sense. (Noble, 1929.)

The First Tetrapods.—If we compare a frog sitting on the edge of a pond with the perches, catfish, or eels in the water, the difference between a tetrapod and a fish seems tremendous. A scrutiny of their detailed structure brings forth such a series of differences in skull, appendages, and breathing apparatus that the change from fish to frog would seem to be one of the most radical steps in the evolution of the vertebrates.

This step does not seem less tremendous when we compare the aquatic newt with the fish, for the former is a typical tetrapod which has secondarily taken up a life in the water. It is no wonder that anatomists were puzzled for many years as to how the first tetrapod arose, and even today there is no agreement between those who study only the recent forms.

When the evidence from palaeontology is available, this must necessarily be placed ahead of all our other evidences. The gaps in the palaeontological record of the Amphibia are great, but the combined researches of recent years (especially Gregory, 1915; Watson, 1917, 1919, 1926; Williston, 1925) have thrown much light on the beginnings of land life among the vertebrates. Further, most amphibians pass their early life in the water. The morphological changes of metamorphosis would seem to reflect to a greater or lesser extent the changes which took place when the first vertebrate became established on land. As with all other problems of phylogeny, the evidence of palaeontology, of anatomy, and of development must be weighed one against the other for the final solution of the problem.

If the modern fish were to be changed into a tetrapod, a number of important transformations of structure would have to be accomplished. The gills would have to be lost, and the lungs developed and the nasal passage extended to form internal nares for the ingress of air when the mouth is closed. The fins and body would have to be modified for land locomotion and the integument changed to resist drying. The latter would mean the development of a cornified epidermal covering and a series of integumentary glands discharging by ducts on to the surface, at least over those parts not provided with an armored skin. Specialized glands would be required to keep the nasal passage and mouth from drying. The eyes, formerly bathed by the water, would be especially sensitive to the new conditions and must either develop a horny, protective cover as in modern snakes or produce softer eyelids out of dermal folds. In either case a lacrimal gland and drain would be needed for cleansing the eyeball. To keep the nasal passage clean a muscular closing device would be required at the outer end of each nasal inlet. If the first tetrapod were to succeed on land, the sense organs of the fish would have to undergo considerable modification, for, while the lateral-line organs would be no longer required, the auditory, optic, and olfactory centers would gain a higher importance, demanding in some cases fundamental changes in the structure of the organs. If the head were flat as that of many frogs, special muscles to raise the eyes above the surface of the skull would be needed if the eyes were to be at all efficient. Lastly, the loosely hung jaw of the majority of teleosts would have to be firmly fixed to the brain case.

How the first tetrapod accomplished all these changes will never be known. The evidence available shows conclusively that it was not by such sudden revolution as maintains in the metamorphosis of most modern forms. The outstanding contribution of the palaeontological data is the proof of how slight a structural alteration changed the primitive fish ancestor into the first land vertebrates. Similarly, the first reptiles evolved from the embolomerous amphibians and the first mammals from cynodont reptiles by very gradual steps.

Piscine Ancestors.—Today there are a few fish which live both in and out of water. Some of these have been recently carefully studied by Harms (1929) and it is interesting to note how closely they parallel the Amphibia in their adaptations to life on land. Protection against drying is secured by the development of a horny skin growth in the gobies and a cuticle in the blennies. Skin respiration is improved by the penetration of capillaries into the epidermis. An extensive saccular enlargement of the buccopharyngeal cavity increases the efficiency of buccal respiration. Gulped air is prevented from escaping through the gill slits by a modification of the gill covers. The eyes are modified to project above the surface of the head, and the limbs, especially the posterior, are strengthened by bony rays so arranged as to permit terrestrial locomotion. There are also changes in the cutaneous sense organs which protect them against drying. These fish undergo a certain metamorphosis into partly terrestrial animals, and Harms found that this metamorphosis was influenced by the thyroid hormone, as in the case of Amphibia.

The first tetrapods did not come from modern fish. Already in Carboniferous times three distinct orders of tetrapods—labyrinthodonts, lepospondyls, and phyllospondyls—had developed. The first two were both present in the Lower Carboniferous. Footprints are known from the Devonian of Pennsylvania. Hence the tetrapods must have arisen in at least Devonian and possibly Silurian times. The tetrapods arose from ancestors in the fresh waters, for their earliest remains are associated with fresh-water deposits. All fresh-water fishes of Devonian times were ganoids (in the broad sense), dipnoans, or