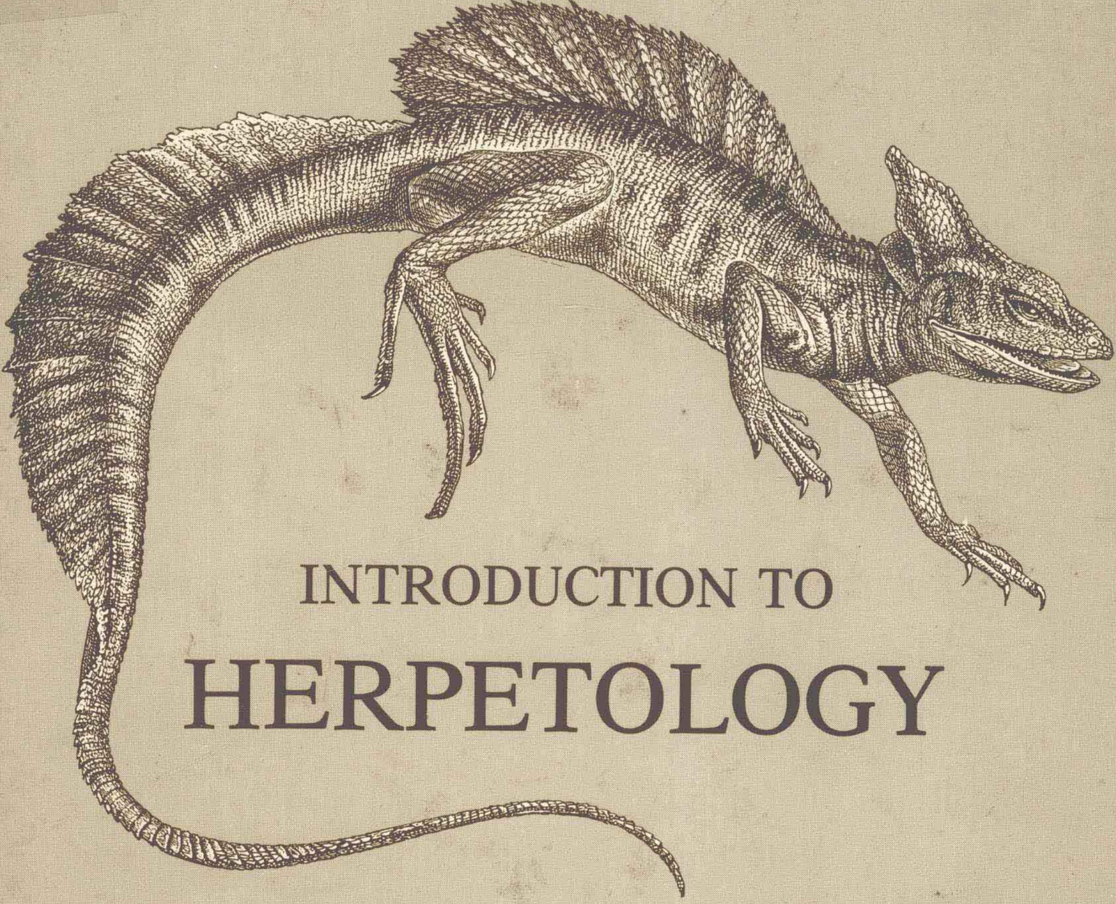

INTRODUCTION TO HERPETOLOGY

THIRD EDITION

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GEORGE R. ZUG

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PREFACE
TO THE THIRD EDITION

This edition of the *Introduction to Herpetology* follows the same organization and philosophy as the first two editions. Our intent is not to be encyclopedic, but rather to cover the wide spectrum of amphibian and reptilian biology. We believe that through this approach the reader will obtain a solid foundation in herpetology and a sense of the flavor of current herpetological research.

With the exception of the two chapters on structure, all chapters have been rewritten and reorganized. Speciation and geographic distribution have been combined into a single chapter because of the close relationship between the two subjects. Maps of the distribution of the major amphibian and reptilian families have been added.

With each revision, our indebtedness increases. In addition to those acknowledged in the first and second editions, we wish to thank Charles J. Cole for the excellent photographs of karyotypes in Chapter 11 and Bart Kaveruck for help with the artwork. Edwin H. Colbert has been unfailingly kind and helpful. Rather than single out a few colleagues for special acknowledgment, we wish to thank all who have contributed ideas and

corrections through conversations, correspondence, and publications. Finally, special thanks to Pat Zug for her patient typing and retyping of this revision.

As always, we hope our readers will continue to point out errors, inaccuracies, and omissions.

Coleman J. Goin
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October 1977

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PREFACE
TO THE FIRST EDITION

This book is planned for use as a text in a one-semester course in herpetology. It is designed for students who have had one year of college biology, but who may have had no more than one year.

Courses in herpetology usually consist of two parts—a series of lectures or discussions in which basic principles are presented, and a series of laboratory and field exercises. We believe that laboratory work should be based primarily on local faunas and on the specimens available in local institutions. These differ from region to region. Techniques useful for collecting animals in one climate may be of little use in another; the season of the year at which animals are abundant and active varies from place to place; the characters used in identifying specimens from one faunal region may not apply to those from another. Moreover, excellent field guides, keys, and local lists are available for most places where courses of herpetology are presented today. We have therefore left the organization of the laboratory and field work to the individual instructor, and have concentrated instead on the major aspects of herpetology that apply throughout the world.

In these days when so much of biology is concerned with happenings at the molecular level within the individual cell, we believe there is a definite need for the student to appreciate that these processes have biological meaning only as they help us to understand the living, functioning animal. We agree with Professor Romer that:

"It is not enough to name an animal; we want to know everything about him: what sort of a life he leads, his habits and instincts, how he gains his food and escapes enemies, his relations to other animals and his physical environment, his courtship and reproduction, care of his young, home life (if any). Some aspects of these inquiries are dignified by such names as *ecology* and *ethology;* for the most part they come broadly under the term *natural history.* Many workers who may study deeply—but narrowly—the physiological processes or anatomical structure of animals are liable to phrase this, somewhat scornfully, as '*mere* natural history.' But, on reflection, this attitude is the exact opposite of the proper one. No anatomical structure, however beautifully designed, no physiological or biochemical process, however interesting to the technical worker, is of importance except insofar as it contributes to the survival and welfare of the animal. The study of the functioning of an animal in nature—to put it crudely, how he goes about his business of being an animal—is in many regards the highest possible level of biological investigation." (*The Vertebrate Story,* A. S. Romer, Univ. Chicago Press, Copyright 1959 by the University of Chicago.)

In preparing this volume, our task has been twofold: we have had first to decide on the basic organization that we felt a text in this field should have, and second to synthesize a mountain of original literature into a volume of modest size.

In the former task, we have worked under the firm conviction that the proper approach was to discuss basic biological principles as exemplified by amphibians and reptiles. This we have tried to do. In the latter task, we have of necessity shown a great deal of personal bias in deciding just what should and what should not be included. Because of the wealth of original literature, there are many fascinating facts of herpetology that we have had to leave unmentioned. We know that some of our professional colleagues will feel that, like good Anglicans, "we have left out those things which we ought to have put in, and we have put in those things which we ought to have left out."

In the first chapter we indicate the position of the amphibians and reptiles in the animal kingdom, discuss briefly certain basic principles of classification, and give a resume of the rise of herpetology as a science. The next four chapters deal with the structure and evolutionary history of the two classes. Chapters 6 through 11 are concerned with natural history and with the mechanisms of speciation and geographic distribution. The last six chapters give a summary of the living amphibians and reptiles to the family or subfamily level, with notes on life history and geographic distribution.

Since herpetology is a worldwide subject, we have tried, in our choice of examples and illustrative material, to strike a balance between native and exotic forms.

The references given at the end of each chapter are intended simply as suggestions to the interested student who may wish to pursue a particular topic further than is possible in an introductory text. Most are compendiums. Occasionally, we have included original papers that are of exceptional interest and importance and that give information not generally available elsewhere.

It is a pleasure to acknowledge the help we have received from so many people in the preparation of this text. We are indebted to M. Graham Netting for reading Chapters 8, 9, 11, 13, and 17, and to Archie Carr for reading Chapters 8, 9, and 14. We wish especially to thank Kenneth W. Cooper, not only for the critical reading of Chapter 10, but also for the continuing interest he has shown in this work, and for the many pertinent references he has sent us. Henryk Szarski read Chapter 4 and Carl Gans read portions of an earlier draft of the manuscript. Walter Auffenberg assisted us materially in dealing with the classification of the snakes and crocodilians.

Mr. and Mrs. J. C. Battersby, Charles M. Bogert, Robert F. Inger, and Alfred S. Romer all responded most kindly to appeals for special information and material.

Not least have been the intangible benefits we have received from discussions with these and other colleagues, among whom we should like to mention in particular Doris M. Cochran and Ivor Griffiths.

Except where otherwise indicated, the excellent photographs were made by Isabelle Hunt Conant, many of them especially for this volume. The line drawings are from the gifted pen of Evan Gillespie, many of them from sketches made originally by Ester Coogle.

To James E. Bohlke, Alice G. C. Grandison, W. S. Pitt, Oswaldo Reig, and Charles K. Weichert we are indebted for special illustrative material.

We wish to thank Dean George T. Harrell for the use of a dictaphone during the preparation of the first draft, and Mrs. Sue P. Johnson for her careful typing of the final draft.

Since everything we have ever done has had imperfections, we feel sure that this book will have its share. We would like to request that our friends be kind enough to point out to us our errors, both of omission and of commission, so that in the future we may mend our ways.

Coleman J. Goin

March 1962 *Olive B. Goin*

CONTENTS

CHAPTER ONE

INTRODUCTION

THE SCIENCE OF BIOLOGY has become enormously complex. No longer is it possible for the work of one person to encompass all of its ramifications. To keep up with advances, biologists have been increasingly obliged to limit themselves to various subsciences, such as anatomy, genetics, embryology, or ecology. These subsciences can be visualized as extending vertically through the parent science. But this is not the only way biology can be approached; it can be subdivided according to the kinds of organisms studied. These subdivisions include such disciplines as ornithology, entomology, and herpetology. They extend across and interweave with the primary divisions mentioned above.

Biology might thus be visualized as a vast tapestry, with the threads of the warp formed by the many subsciences and those of the woof formed by the groups of organisms under study. Whether one wishes to follow a thread of the warp and study something like the anatomy of one or more structures in many different kinds of animals (comparative anatomy) or to follow a thread of the woof and study the anatomy, behavior, and distribution of a particular group of organisms (such as the snakes) is a matter of personal inclination. When we study herpetology (*herpeton* = crawling thing, *logos* = reason or knowledge), we follow those threads of the woof that consist of the amphibians and the reptiles. Any aspect of the biology of these animals is legitimately part of the subject of herpetology.

ZOOLOGICAL POSITION OF AMPHIBIANS AND REPTILES

We cannot profitably study any of the broader aspects of zoology until we know just what animals we are dealing with and where they fit in the whole pattern. No one knows exactly how many different kinds of animals there are, but one careful estimate gives 1,120,000, and this is within reason. To bring order and meaning into this bewildering array of forms, we must classify and divide them into groups and categories. There are a number of different schemes of classification that we might adopt. We could, for example, divide animals according to their habitat, such as forest, desert, lake, or ocean. Some studies require this kind of classification, but the standard, universally accepted classification today, the one we mean when we speak of animal classification, is based on the degree of relationship through descent from a common ancestor. Closeness of relationship is usually judged by similarity of morphological characters.

The animal kingdom is divided into a number of large groups called phyla (e.g., phylum Mollusca: shellfishes, like the oysters, clams, snails, and squids; phylum Arthropoda: joint-footed animals, such as insects, spiders, centipedes, and lobsters). The phylum Chordata comprises animals that at some stage in their life history have pharyngeal pouches, a hollow dorsal nerve cord, and a notochord (a stiffening rod running along the back). The phylum Chordata is divided into several small subphyla and one large one, the subphylum Vertebrata, to which belong the animals most familiar to us—the fishes, amphibians, reptiles, birds, and mammals. Vertebrates are animals in which the notochord, though still present in the early embryonic stages, has been largely replaced in the adult by a jointed vertebral column composed of a number of separate structures, the vertebrae. The anterior end of the nerve cord is expanded to form a brain, which is enclosed in a protective box, the cranium.

Members of the subphylum Vertebrata are divided into a number of classes. Included are several classes of fishlike vertebrates plus the classes Amphibia, Reptilia, Aves, and Mammalia. These comprise about 38,000 kinds of living animals:

Fishlike vertebrates	17,000 ± species
Amphibians	3,000 ± species

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Reptiles	6,000 ± species
Birds	8,600 ± species
Mammals	3,500 ± species

Amphibians

Amphibians are vertebrate animals whose body temperature is dependent upon the external environment; that is, they are ectothermic. They have soft glandular skins that are for the most part without scales. They lack the paired fins of the fishes: instead, most have limbs with digits, as have the higher animal forms, the reptiles, birds, and mammals. These four classes of animals with limbs are sometimes linked in the superclass Tetrapoda (four-footed). The amphibian egg lacks a shell and, to prevent the developing embryo from desiccating, must be laid in water or in humid surroundings.

Ancestral amphibians were derived from primitive fishes. They were the first vertebrates to move onto land, and they gave rise to all the other terrestrial vertebrates: the reptiles, birds, and mammals. Two hundred fifty million years ago, they were a prominent element in the world's fauna; today, they are the smallest tetrapod stock with only about three thousand living members. These are divided into four orders:

Order Gymnophiona (Apoda), caecilians	150 ± species
Order Meantes (Trachystomata), sirens	3 species
Order Caudata (Urodela), salamanders	310 ± species
Order Salienta (Anura), frogs and toads	2,510 ± species

Reptiles

Reptiles, like amphibians, are ectothermal vertebrates that do not have paired fins. They differ from amphibians, however, in that they all have scales. The reptilian egg usually has either a parchmentlike or a calcareous shell and is laid on land. In addition to a yolk sac, the embryo has three extraembryonic membranes—the *amnion, chorion,* and *allantois*—that are not present in amphibian and fish embryos. Since these membranes are also present in birds and mammals, these three classes are sometimes called amniotes, to distinguish them from the anamniotes, the fishes and amphibians.

Reptiles are descendants of the early amphibians and were the dominant animals on the earth during the Mesozoic era; they gave rise to the two classes of endothermic vertebrates with internal temperature control, the birds and mammals. Reptiles have lost the dominant position they held during the Mesozoic, although they are still far more numerous than amphibians. Living reptiles are divided into the following orders:

Order Testudines (Testudinata), turtles	230 ± species
Order Rhynchocephalia, tuatara	1 species
Order Squamata	
Suborder Amphisbaenia, worm lizards	140 ± species
Suborder Serpentes (Ophidia), snakes	2,700 ± species
Suborder Sauria (Lacertilia), lizards	3,000 ± species
Order Crocodylia, alligators and crocodiles	21 species

Amphibians and reptiles have traditionally been studied together. This is partly for historical reasons—at one time the differences between the two groups were not recognized as being important enough to justify their placement in separate classes. It is also partly a matter of convenience—amphibians are a small group, and the methods of collecting and preserving them are similar to those used for reptiles. To avoid repeating the rather cumbersome phrase "amphibians and reptiles," we will hereafter use "herps" as a general term for the members of both classes.

With our knowledge of biology becoming more and more detailed and the literature more and more voluminous, it is difficult for a worker even in the restricted field of herpetology to keep abreast of current developments. Some modern herpetologists restrict themselves almost entirely to the study of amphibians, or of reptiles, or perhaps even of a single order.

SYSTEMATICS AND TAXONOMY

Historically, the task of naming, describing, and classifying amphibians and reptiles has necessarily had priority, and even at the present time a portion of the literature of herpetology is concerned with such studies. Here herpetology interweaves with taxonomy and systematics. These two terms are often used interchangeably, but it seems better to restrict *taxonomy* to the frequently very complicated task of assigning names to groups of animals, and *systematics* to the formulation of a classification that will describe the relation of the animals to one another. The two do overlap, of course. Current taxonomic practice requires that the taxonomist describe the form he is naming and include in the description an indication of the animal's relationships. The systematist frequently finds that he must name one or more new forms or resolve a nomenclatural problem before he can discuss intelligibly the relationships of the animals he is classifying.

Our present system of classification comprises a series of categories, each less inclusive than the preceding one. Phyla are divided into classes, classes into orders, orders into families, families into genera (singular genus), and genera into species (singular species). A Box Turtle is thus classified:

Phylum Chordata
Class Reptilia
Order Testudines
Family Emydidae
Genus *Terrapene*
Species *Terrapene carolina*

These are the standard categories. Each category is intended to represent a distinct level of evolutionary relationship. We can visualize the evolutionary history of a group (its phylogeny) in the form of a branching tree (the phylogenetic tree). The species are the twigs of the phylogenetic tree. As the categories become higher, the branches they represent extend further back in time and represent older points of divergence. Ideally, all forms placed in a given category should represent a single, monophyletic lineage (a clade), all of whose members are descended from the same ancestral population. All the species (twigs) placed in one genus should arise from a single small branch, and all the genera placed in one family should arise from a single larger branch. Since the fossil record is woefully incomplete, our classification is necessarily based largely on similarities among extant species. As a result, convergence may trick us into linking together species or higher groups that share many features because of a similar way of life, but do not have a common ancestor. Such a group is polyphyletic and is called a grade. Usually, when a systematist decides he is dealing with a grade rather than a clade, he reclassifies the group. For example, the Australian tree frogs closely resemble some South American tree frogs of the genus *Hyla*, and were long placed in that genus. But recent work indicates that the former evolved from a different branch of the phylogenetic tree, so they have been removed from *Hyla* and are placed in the genus *Litoria*.

The superclass, infraorder, subfamily, and other intermediate categories reflect a more detailed knowledge of relationship. They are categories of convenience. Every animal is a member of a species, genus, family, order, class, and phylum; not every animal belongs to a superclass or subfamily. The latinized name applied to a category designates a particular group of organisms, called a taxon (plural taxa). For example, the taxon *Rana pipiens* refers to all populations of frogs that belong to that species; the taxon Serpentes includes all snakes.

Of all the taxonomic categories, the species is the only one that can be objectively defined, at least for bisexual vertebrates. *A species is a population or group of populations of similar animals that interbreed, or are potentially able to interbreed, and produce fertile offspring.* This definition formalizes our intuitive impression that like tends to breed with like and produce more of the same. Species—or, rather, their component populations—are the units of evolutionary change. Evolution is change in the genetic composition of a population through natural selection. As such, evolution operates on the population, although natural selection operates on individuals. Natural selection must not be viewed as "nature red in tooth and claw," but as a process of differential reproduction, by which one set of parents are able to place more of their offspring into the breeding pool for succeeding generations than can another set of parents.

Because of evolution, species are not static units of life. They possess both spatial and temporal dimensions, and owing to these extensions in space and time, they are often difficult to delimit. Since most species are spread over large geographic areas, they are divided into small, semi-isolated populations by geographic barriers, such as rivers or mountains, and by the discontinuous nature of their preferred habitats. Each population is subjected to a different physical and biological environment and becomes adapted to that specific environment. The differences between populations may range from small variations in gene frequency to striking differences in morphology or physiology. The extent of the differences is largely determined by the amount of gene exchange between adjacent populations, the intensity of selection, the length of time since the founding of a population, and the genetic composition of its founding members. When the differences between populations of a given species are evident and occur more or less abruptly, these populations are considered to be distinct geographic races or subspecies. For example, the Spring Peepers in most of the eastern United States are uniform pale pink below, while those of northern Florida are heavily spotted below. The two populations are therefore regarded as different races.

No matter how different two populations may be, if they are capable of freely interbreeding, they are members of the same species. This criterion is very precise in principle, but often extremely difficult to apply in practice. Too often we simply do not know whether two given forms can or do interbreed in nature. The systematist must use his judgment, must decide whether specimens collected from two populations perhaps many kilometers apart are similar enough to represent a single species. But mere morphological similarity is not always a reliable guide. The Leopard Frog of the southeastern United States does not differ markedly from that of the northeastern United States, and the two were long thought to be separate geographic races of a single species. Then it was found that the two forms, though they may inhabit the same pond, do not interbreed. It is now known that the Leopard Frogs, once considered a single, wide-ranging species, *Rana pipiens,* in reality comprise at least four, and probably more, separate species.

Such failure or inability to interbreed results from the evolution of barriers to the production of fertile offspring. These reproductive barriers, or isolating mechanisms, may operate either before or after mating. Typical premating mechanisms are seasonal or habitat isolation, behavioral isolation, and mechanical isolation. Males and females of different species may not interbreed, even though they live in the same area, because they occupy different habitats or because their reproductive periods occur at different times. Two species may also fail to interbreed because the reproductive signal given by members of one sex of one species is not recognized by members of the opposite sex of the other species. If these isolation mechanisms fail, mating may still be impossible owing to mechanical incompatibilities such as differences in size.

Postmating mechanisms may cause failure to fertilize the egg, death of the embryo, or sterility of the offspring. Selection favors premating mechanisms, for postmating mechanisms waste an individual's gametes (sperm or eggs) and energy, which could have been spent more productively mating with one of its own kind. The selection for premating isolation mechanisms is sometimes overtly apparent in areas where two species are sympatric (occur together). Reproduction-associated characters of two species may become strikingly different in the sympatric area, yet remain similar in allopatric (where the two species do not occur together) areas. This kind of character displacement occurs frequently in the calls of frogs.

Since many pairs of closely related species (sibling species) cannot be recognized by differences in morphology, systematists have been enlarging their repertoire of technical tools. Experimental cross-fertilization was one of the first such tools to be used in anuran systematics. Using the techniques of embryology, the eggs of different species were fertilized with testicular extracts. Cross-matings could then be compared by the degree of successful development of the embryos. It was discovered that the offspring from crosses between closely related species are frequently as viable as those from intraspecific crosses. Thus this technique may fail to distinguish species, although the survivorship of the embryos does demonstrate the degree of genetic compatibility of different species, which in turn indicates the degree of relationship. Recording and analysis of frog voices has become an important technique in the recognition of sibling species. The breeding calls are species-specific, and a female will only go to a calling male of her own species. Different calls identify different species. *Hyla versicolor* and *Hyla chrysoscelis* can be distinguished only by their calls and their karyotypes (chromosome complements); in external appearance they are identical.

Techniques for measuring protein similarity are rapidly gaining prominence in the analysis of the genetic composition of species and the degree of genetic relationship between species. Since immediate products of the genes are being compared, these techniques provide a more direct measure of the genotype (genetic constitution) of the animal than do morphological or behavioral traits. They have the additional advantage over cross-fertilization and vocal analysis that they can be compared at all life stages and for all types of animals, not just frogs. These techniques, combined with morphological and natural-history observation, enable herpetologists to identify species more clearly.

NOMENCLATURE

Our system of nomenclature is based on the one first universally applied to all animals by Linnaeus in the tenth edition of his *Systema Naturae,* published in 1758. Linnaeus gave each species known to him a name consisting of two parts, the name of the genus to which it belonged, plus a specific epithet, the trivial name (e.g., *Rana esculenta*). Over the years, other biologists adopted the Linnaean system of designating species. But as more and more new species were found and named, and more and more papers were published using these names, confusion inevitably crept in. Sometimes a biologist, either deliberately or through ignorance, gave a name to a species that had already been named something else, creating a *synonym.* Sometimes two investigators, working on different groups, happened to give the same name to entirely different forms. Such a name is called a *homonym.* But if we, as biologists, are to understand one another, we must be sure that each species has only one name and that each name applies to only one species.

The need for a set of rules for taxonomists to follow in proposing new names, or in deciding which of several names already in use should be accepted, soon became acute. A number of codes were drawn up in different countries and for different groups. The English followed one code, the French another, the Germans still a third; ornithologists had a code of their own, and so did paleontologists. Finally, in 1895, the Third International Zoological Congress appointed a committee that drew up the *International Code of Zoological Nomenclature,* commonly known as the Code. This Code was accepted by the Fifth International Zoological Congress in 1901 and is now universally followed. It has been revised from time to time, most recently in 1961. A permanent International Commission of Zoological Nomenclature serves as a "supreme court" to resolve the knotty problems of interpretation that seem to be inevitable under any code of laws.

Most of the rules and recommendations of the Code deal with technicalities of interest only to professional taxonomists. A few of them, however, should be familiar to every zoologist, if only because an understanding

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