Vertebrates of the United States

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PREFACE

The need for a new, usable manual covering the vertebrate groups of the United States became particularly evident with the unavailability of Pratt's manual in the late forties. About this time the senior author, in consultation with a representative of the publisher, worked out the basic plan for such a work, and in the fall of 1950 a conference was held between the authors and the publisher at which more definite plans for collaboration were formulated. Additional meetings were subsequently held in order to coordinate more fully the work of the authors in matters pertaining to style, format, etc. As originally planned and, the authors hope, finally realized, the book was to facilitate the identification of all known United States vertebrates through the assembling of taxonomic keys, check lists, descriptions, and ranges. It was intended that the book might serve as both a text and a reference for courses in vertebrate classification, ecology, and natural history. We hope it will fill this niche.

Geographic coverage is limited to the continental United States and its adjacent waters except that marine fishes and turtles have been omitted. Approximate extralimital distributions are given, however, for taxons which occur in the United States and range outside. Each taxon is characterized as it exists on a world-wide basis. Geologic range is indicated by citation of the earliest known record for each higher category.

Scientific names and phylogenetic arrangements generally follow these check lists: Berg's *Classification of Fishes, Both Recent and Fossil* (1947); Schmidt's *A Check List of North Amerian Amphibians and Reptiles* (1953); Miller and Kellogg's *List of North American Recent Mammals* (1955); A.O.U. *Check-list of North American Birds* (1931) and Supplements (1944–1956). Each author has had to make decisions regarding controversial scientific names and taxonomic allocations, particularly at the species level. We have generally avoided trying to settle doubtful cases of relationship by authoritarian decree, but have attempted instead to direct attention to unsolved problems of affinity. The length of species descriptions has been governed by spatial limitations imposed by the fact that all known vertebrates of the United States are covered.

Although the book is presented in six parts with each author dealing in his particular specialty, careful plans were made to have some unanimity in the work. All sections follow the same general plan and have been read and criticized by each of the other authors. In cases where differences occurred, they were carefully analyzed and discussed before a governing decision was reached. It is hoped that this method has enabled us to present a generally authoritative work. As is inevitable in cases of this kind, however, errors will creep in, and each of the authors would appreciate having them called to his attention.

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PART TWO (FISHES). Reeve M. Bailey made available his manuscript keys to the families of fresh-water fishes and to the genera of the family Percidae. He also criticized the section on the family Percidae and with Robert R. Miller arranged the cyprinid genera in a linear manner. The entire section was criticized by Robert R. Miller, who also supplied the key to the genus *Salmo,* a portion of the key to the Coregonidae, and, from his notes, many counts pertinent to the identification of western fishes. The keys to the family Amblyopsidae were modified from a manuscript furnished by Loren P. Woods and Robert Inger. Criticisms were offered by Royal D. Suttkus and Clark Hubbs. Mrs. Leah Moore typed the section and assisted in reading proof. Her help and encouragement are deeply appreciated.

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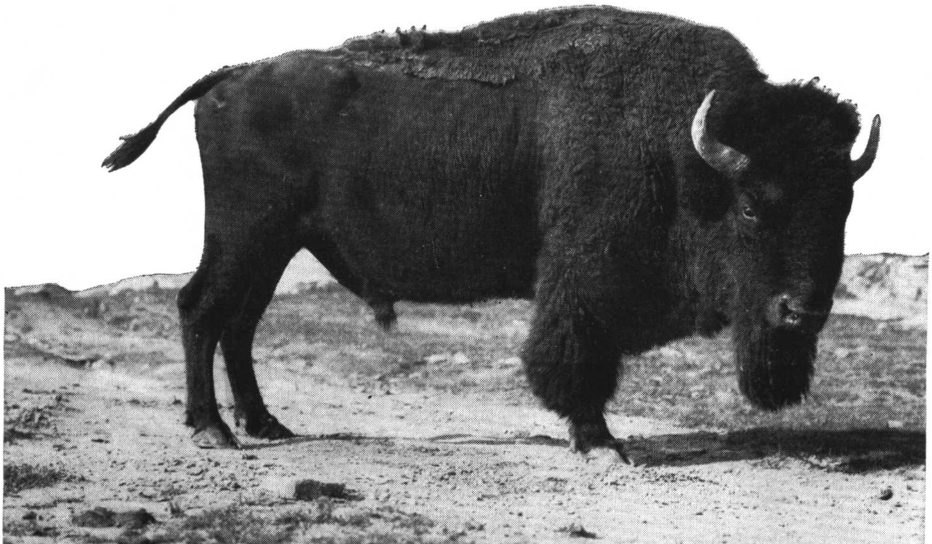
PART FIVE (BIRDS). George H. Lowery, Jr., critically read the completed manuscript. All original illustrations are by Esther Coogle.

PART SIX (MAMMALS). William J. Hamilton, Jr., critically read the completed manuscript. Byran P. Glass also read the manuscript and offered valuable comments. All original illustrations in the section were drawn by William F. Pyburn.

CONTENTS

PART ONE **INTRODUCTION** W. F. BLAIR



Bison, *Bison bison*. (New York Zoological Society photo.)

INTRODUCTION

Vertebrates possess a notochord and pharyngeal gills or pouches at some stage of development, and they have a dorsal, hollow, fluid-filled nerve cord. These characters are shared with some small marine animals, which, with the vertebrates, are classified in the phylum Chordata. These relatives of the vertebrates include 3 subphyla, which are often referred to collectively as protochordates:

FIG. 1-1. Acorn worm, a representative of the subphylum Hemichordata. (After Bateson, from Neal and Rand, *Chordate Anatomy,* The Blakiston Division, McGraw-Hill Book Company, Inc.)

Subphylum Hemichordata. Acorn worms. Marine, burrowing animals, with superficially wormlike body form. Body divided into proboscis, collar, and trunk. Dorsal, hollow nerve cord in collar. Diverticulum at base of proboscis thought to represent notochord. Gill slits in pharyngeal region.

Subphylum Cephalochordata. Lancelets. Small, free-swimming, translucent, marine animals, with fishlike body form. A well-developed notochord extending length of animal. Well-developed, dorsal, hollow central nervous system. Numerous gill slits. Muscular, digestive, and circulatory systems are simple prototypes of these systems in vertebrates.

Subphylum Urochordata. Tunicates. Small, marine, free-floating or sessile as adults. Some with free-swimming larval stage in which there is a well-developed notochord, a dorsal, hollow central nervous system, and rudimentary brain. Notochord and part of nervous system degenerate in adult.

The vertebrates are placed in the separate subphylum, Vertebrata. They differ from the protochordates in having a vertebral column of cartilage or bone, which supplements or replaces the notochord as the main support of the long axis of the body. They also have a cranium, or braincase, of cartilage or bone, or both, for support and protection of the brain and major special sense organs. No living protochordate may be seriously regarded as ancestral to the vertebrates, but the common ancestry is evident. The structure of lancelets is suggestive of a stage in the evolution of the ancestors of the vertebrates. These animals, along with the other protochordates, however, seem to have reached an impasse in evolution. The vertebrates, on the other hand, have progressed to a dominant place in the living world in part because of the advantages conferred by their light, internal, continually growing skeleton.

VERTEBRATE HISTORY

The earliest remains of vertebrates are known from Ordovician rocks, indicating that this group has been in existence for more than 400 million years. These earliest remains are mostly remnants of bony armor such as has been found in the jawless ostracoderms of Silurian and Devonian age. These earliest known vertebrates apparently lived in fresh water. The small group of living jawless fishes (Cyclostomata) appear to be a highly specialized

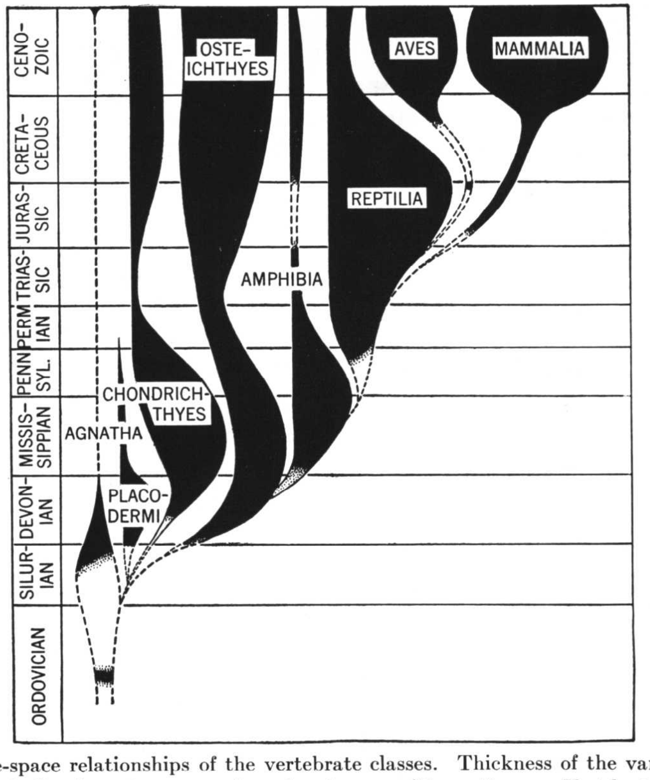


FIG. 1-2. Time-space relationships of the vertebrate classes. Thickness of the various branches gives a rough indication of comparative abundance. (From Romer, *Vertebrate Paleontology*, University of Chicago Press.)

(mostly parasitic) remnant of this primitive vertebrate stock. Much modification of body form, of organ systems, and of life habits has occurred during the long history of the vertebrates. Outstanding developments in the progressive evolution of the vertebrates have been (1) appearance of paired appendages, (2) appearance of jaws, (3) movement to land, and (4) development of homoiothermy.

A

B

C

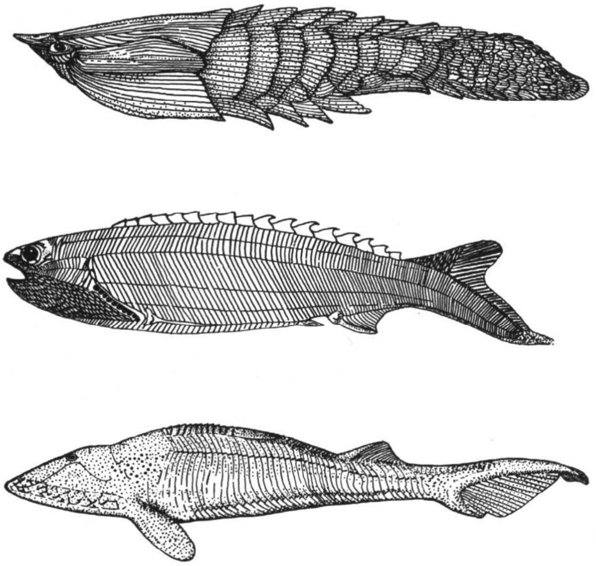


FIG. 1-3. Representative ostracoderms (jawless fishes). (*A* and *C* after Heintz, *B* after Kiaer; from Romer, *Vertebrate Body*, W. B. Saunders Company.)

PAIRED APPENDAGES. Unpaired fins were present in the ostracoderms as accessory organs of locomotion. Such structures have persisted through the fishlike vertebrates, and analogous structures have developed in terrestrial vertebrates which have reinvaded the aquatic environment. Paired fins were developed as stabilizers. The beginnings are seen in the ostracoderms, which developed paired flaps, spines, or folds. In the class Placodermi, which flourished in the Silurian and Devonian and persisted into the Permian, various combinations of paired fins were present. Some placoderm fossils show evidence of as many as 7 pairs of fins. In the cartilaginous fishes (class Chondrichthyes) and bony fishes (class Osteichthyes), which apparently branched from placoderm ancestors in the Devonian or earlier, there is an anterior (pectoral) and a posterior (pelvic) pair except where the fins have been secondarily lost. While useful to fishes as stabilizers in the water, the paired appendages were vitally important as locomotor organs when the move came to land life.

JAWS. The development of jaws came early in vertebrate history, and the possession of such structures conferred important food-getting advantages on the aquatic vertebrates. More importantly, this development was an essential forerunner of the migration to land. The jawless ostracoderms were probably limited to the ingestion of small organisms and dead organic material which could be sucked into the pharynx and strained out by the gill mechanism. The jaws of placoderms and higher vertebrates permitted the grasping, holding, and ingestion, and in some cases the crushing or chopping up, of food organisms of enormously wider variety than was available to the jawless ostracoderms.

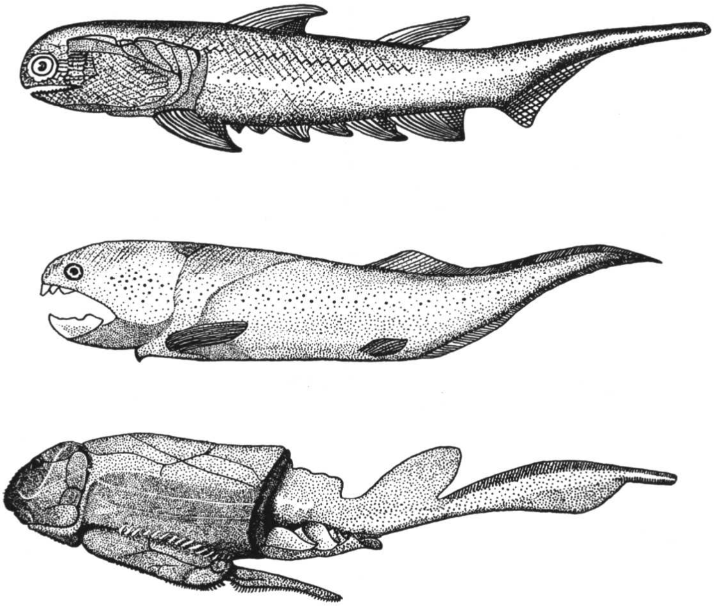


FIG. 1-4. Representative placoderms (primitive jawed fishes). (From Romer, *Vertebrate Body*, W. B. Saunders Company.)

MOVE TO LAND. The movement of vertebrates to land life may have been a by-product of adaptations to permit the aquatic ancestors of the land vertebrates to survive in water. It has been theorized that the modification of the paired fins of crossopterygian fishes into tetrapod appendages came as an adaptation to permit overland movement of the primitive amphibians from a drying pool to the nearest pool still containing water. The change to land life began in the Devonian, which was apparently a time of periodic drought. The crossopterygian fishes possessed simple lungs, but only those which were able to move overland participated in the migration to land. The gradual change to land life could have resulted from selectional pressures when the primitive amphibians tended to linger longer and longer on land as they moved from pool to pool.

The migration of vertebrates to land life posed many adaptational problems. The new and previously unexploited environment had many advantages. There was a plentiful and constant supply of oxygen. There was a solid substratum on which to move, and air was a much less dense medium in which to live and move about than had been water. The new environment also had formidable disadvantages. There was the constant danger of drying up, of losing a fatal amount of water from the body protoplasm. There were

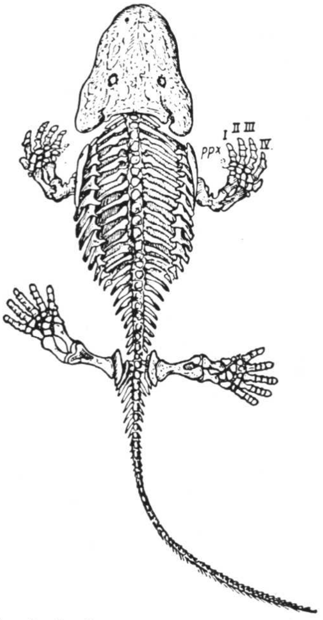


FIG. 1-5. *Eryops*, an extinct labyrinthodont amphibian. (From Gregory, *Evolution Emerging*, The Macmillan Company.)

great ranges of temperature to be adapted to or avoided. The change to land life, consequently, resulted either directly or indirectly in marked changes in virtually every organ system of the vertebrate body.

The amphibians have not become well adapted to life on land. The thin stratum corneum of their epidermis and their numerous skin glands render them susceptible to water loss through the skin. Even the most land-adapted must seek out moist environments to replenish and to reduce their water loss, and many have remained closely associated with the aquatic environment. Their unshelled eggs must be deposited in water or in moist soil on land.

The reptiles, derived from amphibian ancestors in the Carboniferous, were the first vertebrates which were really well adapted for land life. The most significant advance was in the type of egg, which was now adapted to survive on land. The amniote egg of these and higher vertebrates is protected by a hard or tough porous shell. The embryo is surrounded by a series of membranes, of which the amnion provides the embryo with its own minute aquatic environment, the allantois serves as respiratory and excretory tissue, and the chorion encloses and protects the whole lot of embryonic structures. The newly emerged young are similar in general to the adult and are ready to meet the problems of survival in the terrestrial environment. The adult reptile is much better adapted than the adult amphibian for land life. Loss of most of the skin glands and thickening and cornification of the epidermis render reptiles highly resistant to water loss through the skin. Many excrete their metabolic wastes as crystalline uric acid rather than in urine as an adaptation that conserves body water.

The birds and mammals are offshoots of reptilian stocks and, like the reptiles, are well adapted to resist desiccation on land. The birds apparently branched from archosaurian reptiles in the Jurassic or possibly earlier. The mammals appear to have branched from synapsid reptiles in the Triassic. These groups have gone beyond the reptiles in adaptation to the terrestrial environment, as they have also adapted to control their body temperatures in the variable temperature environment on land.

HOMOIOTHERMY. Birds and mammals have acquired the ability to control their body temperatures within narrow limits and so maintain internal temperatures that are independent of the external environment. Among the bony fishes, it has been suggested that the tunas, which inhabit warm seas, may maintain constant body temperatures, but homoiothermy is in general an adaptation to the variable temperatures of the terrestrial environment.

It has been theorized that the giant Mesozoic reptiles were essentially homoiothermal in the sense that their great body mass in relation to their heat-radiating surfaces resulted in fairly stable internal temperatures. Unlike true homoiotherms, however, the dinosaurs did not possess effective insulative coverings. The great bulk of these reptiles was disadvantageous in that progressive warming of climate might have exceeded their tolerance of high temperatures, or progressive cooling might have exceeded their tolerance of low temperatures. The reptiles which have persisted to the present are mostly small, or at most, moderate-sized animals. Their internal temperatures remain close to the external temperatures, and their activities are consequently controlled by the dictates of the external temperature environment.

The acquisition of homoiothermy has rendered birds and mammals relatively free of dependence on the external temperature. The constant maintenance of body temperatures at optimal temperatures for metabolic processes permits more sustained activity than is possible for poikilotherms. The higher intelligence of homoiotherms, culminating in the reasoning forebrain of man, is largely made possible by this constant maintenance of high metabolic activity. The ability to maintain body temperatures above that of the external environment has enabled the birds and mammals to spread into parts of the world which are closed to terrestrial poikilotherms because of sustained cold temperatures.

Heat conservation is effected by integumental structures, feathers in birds, hair in mammals, which trap an insulative coat of air next to the body surface. Mammals which have reinvaded the aquatic environment have tended to lose the hair and to replace it with an insulative layer of fat (blubber) beneath the skin, as in the whales. The principal mechanisms to cool the body below that of the environment are heat loss through a highly developed skin vascular system and through expired air. The presence of a well-developed skin vascular system is the chief evidence that tunas may be essentially homoiothermal fishes. The evaporation of water from the moist skin of amphibians may result in the cooling of the body below the temperature of the environment. Some mammals use this method by evaporating water which reaches the surface through sweat glands.

VERTEBRATE CHARACTERS

Body form. Most fishes are fusiform (torpedo-shaped), which permits the body to pass through the dense medium of water with a minimum of resistance. The anteriorly tapering head passes gradually into the trunk with no constriction or neck, and the trunk narrows gradually into the caudal region. The greatest diameter is near the middle of the body. Various modifications have occurred. Many bottom-living fishes have the body flattened dorsoventrally; other fishes have the body laterally compressed. Some fishes have the body greatly elongated (auguilliform) and flexible. Larval amphibians have the fusiform body of generalized fishes. Adult aquatic salamanders do not differ far from it, and some are anguilliform. Mammals which have reinvaded the aquatic environment (e.g., whales) tend to be fusiform.

The change to land life and to locomotion in air, which offers relatively little resistance to movement, brought major changes in body form. The head became readily movable on the constricted and more or less elongated neck. Streamlining was lost, and the body became relatively compacted. The caudal region became progressively constricted in diameter, but it usually remained as a balancing organ. The bipedal method of locomotion appeared as a specialization in ancient reptiles, in birds, and in some lines of mammals, and brought changes in body form. Saltatorial (jumping) locomotion reached high development in modern anuran amphibians and brought additional foreshortening of the body, great development of the posterior appendages, and loss of