VERTEBRATE BIOLOGY

ORR

VERTEBRATE BIOLOGY

FOURTH EDITION

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W. B. SAUNDERS COMPANY
Philadelphia London Toronto

W. B. Saunders Company: West Washington Square
Philadelphia, PA 19105

1 St. Anne's Road
Eastbourne, East Sussex BN21 3UN, England

1 Goldthorne Avenue
Toronto, Ontario M8Z 5T9, Canada

Listed here is the latest translated edition of this book together with the language of the translation and the publisher.

Spanish (*2nd Edition*) — Nueva Editorial Interamericana S. A., de C. V., Mexico

Spanish (*3rd Edition*) — NEISA, Mexico City, Mexico

Library of Congress Cataloging in Publication Data

Orr, Robert Thomas, 1908–

Vertebrate biology.

Includes bibliographies and index.

1. Vertebrates. I. Title. [DNLM: 1. Vertebrates. QL605 075v]

QL605.07 1975 596 75–19850

ISBN 0–7216–7018–0

Vertebrate Biology ISBN 0-7216-7018-0

Last digit is the print number: 9 8 7 6 5 4 3

PREFACE TO THE FOURTH EDITION

This book is designed to give college or university undergraduates a comprehensive survey of vertebrate biology. Fairly brief accounts are given on the anatomy of major organ systems, with greater emphasis placed on their function, on special characters, and on behavior. An attempt is made to consider vertebrates as whole functioning organisms rather than as laboratory specimens to be dissected.

Since the first edition of *Vertebrate Biology* was published in 1961, I have attempted with each succeeding edition to present new data and concepts which are continually being published in the fields of vertebrate behavior, morphology, physiology, and systematics. Likewise, many significant new bibliographic citations have been added to enable students to delve deeper into various subjects if they so desire. Some chapters are less subject to change than others because of their contents. Anatomy obviously does not change, at least perceptively, between various editions of a text, but our knowledge of the functioning of organ systems does. It is, however, in such fields as ecology, ethology, and population dynamics that major advances have recently been made.

In the first edition of this text examples of the various principles discussed were selected primarily from North America. In subsequent editions I have tried more and more to increase the use of illustrations from other geographic areas. This not only broadens the scope for vertebrate students in North America but also makes the text more applicable to those studying this aspect of biology elsewhere.

A new chapter on vertebrate ancestry has been added to the fourth edition, in response to many requests from those who use this text in their courses. Hopefully, it will reduce the necessity for assigning additional reference books on this subject.

The majority of the illustrations used are original. Many of the line drawings were made by Edward Robertson and some were done by Jacqueline Schonewald. The diagram of avian bills was the work of Gene Christman. For permission to use certain illustrations owned or copyrighted by them I am indebted to the following: Academic Press, New York; The American Museum of Natural History, New York; Dr. Steven C. Anderson; Dr. David Caldwell; California Academy of Sciences, San Francisco; California Department of Fish and Game; David Cavagnaro; The Clarendon Press, Oxford; The Cleveland Museum of Natural History; Dr. Nathan W. Cohen; *The Condor; Copeia;* Arthur D. Cushman; Doubleday and Co., Inc., Garden City, New York; *Ecology;* Dr. W. I. Follett; Dr. Raymond M. Gilmore; Fritz Goro, *Life* magazine; Dr. Bruce Halstead; the late Dr. G. Dallas Hanna and Mrs. Hanna; Hanover House,

Garden City, New York; Harper and Brothers, New York; Ed N. Harrison; Holt, Rinehart and Winston, Inc., New York; Houghton-Mifflin Co., Boston; The Idaho Fish and Game Department; Richard Jennings; *Journal of Mammalogy; Journal of Wildlife Management;* Karl W. Kenyon; Dr. John Koranda; Dr. George E. Lindsay; Longmans, Green, and Co., London; The Los Angeles County Museum of Natural History; Dr. George H. Lowery, Jr.; Eric Lundberg; The Macmillan Co., New York; Bruce Markham; Marineland of the Pacific, Palos Verdes Peninsula, California; Dr. James A. Mattison, Jr.; McGraw-Hill Book Co., Inc., New York; Dr. Charles F. Mohr; C. F. W. Muesebeck; Dr. Dietland Müller-Schwarze; The National Audubon Society, New York; The New York Zoological Society; Oxford University Press, New York; The Peabody Museum of Natural History; Yale University, New Haven, Connecticut; Dr. E. T. Pengelley; the late Dr. Gayle Pickwell; Ronald Press Co., New York; Dr. Edward S. Ross; W. B. Saunders Co., Philadelphia; Dr. Arthur C. Smith; L. L. Snyder; Stanford University Press, Stanford, California; the late Dr. Tracy I. Storer; the late Cecil Tose; U. S. Bureau of Entomology and Plant Quarantine; U. S. Fish and Wildlife Service; U. S. Forest Service; U. S. National Park Service; U. S. Navy; U. S. Soil Conservation Service; University of California Press, Berkeley; The Wildlife Management Institute, Washington, D.C., John Wiley and Sons, Inc., New York; The Wyoming Game and Fish Commission.

Many friends and associates contributed to this work. I wish to mention especially the staff of the W. B. Saunders Co., particularly Richard H. Lampert; the late Butler O'Hara; Rollin D. Hemens and Carroll G. Bowen of the University of Chicago Press; Joy Bailey Osborn; the late Toshio Asaeda; Barbara Boneysteele Bortin; Lillian and Robert P. Dempster; Dr. W. I. Follett; the late Dr. Earl S. Herald; Dr. John Hopkirk; Dr. Alan E. Leviton; Dr. John R. Arnold; Jacqueline Schonewald. To these persons as well as other associates at the California Academy of Sciences and at the University of San Francisco with which I was formerly affiliated, I wish to express my sincere thanks for helpful advice and constructive criticism. I am most grateful to Charlotte Dorsey for her meticulous editing and proofreading of this text.

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San Francisco

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CHAPTER 1

INTRODUCTION

Biology as a science has gone through many phases since its beginning several thousand years ago. For centuries its aim was purely descriptive—to describe various forms of life and their component parts. Relationship and function were little understood. Following the rise of Darwinism systematic biology began to develop and replace what had been a nomenclatural science, and descriptive anatomy was gradually supplemented by functional anatomy. These were great advances that led to an understanding of the origin of species and their relationship to each other as well as of the functional performance of the various biological systems within the individual organism.

Today many biologists have gone into the molecular field, trying to understand the minute biochemical differences in animals and plants. Their contributions toward a clarification of the mechanisms by which evolutionary changes occur has been great. Nevertheless, continued study of organisms as a whole, commonly called "organismal biology" as contrasted with "molecular biology," is vital. It means little to know the structure of a protein molecule representing a gene if the organism whose chromosomes contain this gene is not identified. Both organismal and molecular studies in biology are vital and must be carried on together, each complementing the other.

A broader, more modern approach to biology is seen in the study of the relationship of organisms to their environment. This is called ecology, and it is not a new subject. Courses in ecology were given in universities at least as early as the 1920s. However, mankind is now realizing its great importance, not just for the advancement of knowledge but for the very survival of living things, including man himself, on this planet today.

In addition to all the basic knowledge that we have acquired on the structure and classification of plants and animals, it is necessary to know their environmental requirements. This involves many things for many kinds of organisms. Environmental temperature, both daily and seasonal, humidity, rainfall, altitudinal limitations, soil characters, water availability, plant and animal associations, food requirements, parasites, enemies, and diseases are just a few of the subjects needing investigation. The ecological requirements of some species are so limited that the changing of one of these environmental factors could spell extinction, as we are rapidly learning.

Vertebrate Biology is not meant to be a text on ecology, but its approach to backboned animals is ecological rather than morphological. In the early chapters a brief account is given of the organ systems of each class of vertebrates for the benefit of students who have not taken comparative vertebrate anatomy. Much emphasis in each of these chapters, however, is upon special characters. Most of these are adaptations of the integumentary system and the appendages or are special sensory perceptive devices for particular modes of living. The major part of the book is concerned with the principles of systematic biology, factors governing distribution, methods used by vertebrates to solve environmental problems, reproductive physiology and behavior, and population dynamics.

The demand for persons trained in this field has increased greatly in the last few decades, and the need will be even greater in the future. Vertebrate species have long played a major role in human economy. They have provided man with food, sport, and clothing. Their utilization for these purposes has increased constantly with the enormous growth in human population that continues unabated year after year. How long we can continue the uncontrolled harvest of any living vertebrates is problematical, but surely it is not for very long. More than a century ago it was learned that such animals as fur seals, sea lions, elephant seals, bison, pronghorns, passenger pigeons, and many other species that seemed to be present in limitless numbers could withstand man's ruthless slaughter of their populations only for a relatively short time. The result for many was final or near extermination. Today we are still slaughtering whales to the point where the very existence of the largest creatures to inhabit the earth is threatened. We continue to overfish the sea because most of it is outside of territorial waters and a depletion in its population seems far off to many. It is estimated that since the year 1600, 36 species of mammals have become extinct, and at least 120 are presently in danger of extinction. During the same period of time 94 species of birds have become extinct and 187 have been in danger of complete extermination. Natural causes have accounted for some of this, but extinction of about three quarters of these birds and mammals in a little less than 400 years has been directly or indirectly caused by man.

Biologists are needed to study all aspects of vertebrate life. Many intensive investigations already have been conducted and others are under way, but vastly more information is needed on the environmental requirements, behavior, and reproductive activity of most vertebrates. Man himself, through air, land, and water pollution, is

FIGURE 1–1. A beaver dam and pond in Rocky Mountain National Park.

changing many environments to such a degree and so rapidly that native species are being eliminated at an alarming rate. In order to know the effects of pollution we must have a knowledge of the natural composition of the environment. This is becoming increasingly difficult because there are few if any parts of Earth today that have not been affected by human activity to some degree.

More studies have been made on land and freshwater vertebrates than on marine forms because among these are the principal game species as well as those that conflict with agricultural activities. A few investigations are concerned with the transmission of disease. In order to manage game fishes, birds, and mammals properly a very detailed knowledge of their lives is essential. The value of these animals in terms of dollars is enormous. This is obvious when we realize that tens of millions of persons go hunting or fishing in the United States each year. The equipment as well as the cost of travel and lodging to accomplish this runs into billions of dollars annually. Fishing and hunting with their associated activities are big business. As a consequence national governments as well as individual states and provinces have set up special bureaus to engage in wildlife management and carry on research as well as to recommend legislation in order to protect wildlife adequately. Tens of thousands of biologists are in the employ of the United States Government alone.

Apart from the commercial and sporting value of vertebrates, they provide an important part of the recreational value of the out-of-doors. These are intangible assets which are difficult to measure in dollars and cents. In our national and state parks, wilderness areas, and wildlife refuges man has a chance to see relatively untouched segments of the land with living things in their natural setting. The sight of trumpeter swans with their young on a lake or bighorn sheep moving across a mountainside is a thrill long to be remembered. Deer, moose, elk, pronghorns, black bears, and even grizzlies are among the more dramatic mammals in such reservations, but smaller species such as beavers with their dams, muskrats, and otters are equally enjoyable to watch in an undefiled environment where they seem to know they have little to fear from this strange tall, two-legged species which elsewhere seems to spell their doom.

CHAPTER 2

VERTEBRATE ANCESTRY

INVERTEBRATE ORIGIN

To understand the ancestry of vertebrates one must go back more than half a billion years to a time when a great division arose in the invertebrate world. Most students now believe that two lines of development branched from a primitive coelenterate-like stock somewhat resembling the hydras or sea anemones. One of

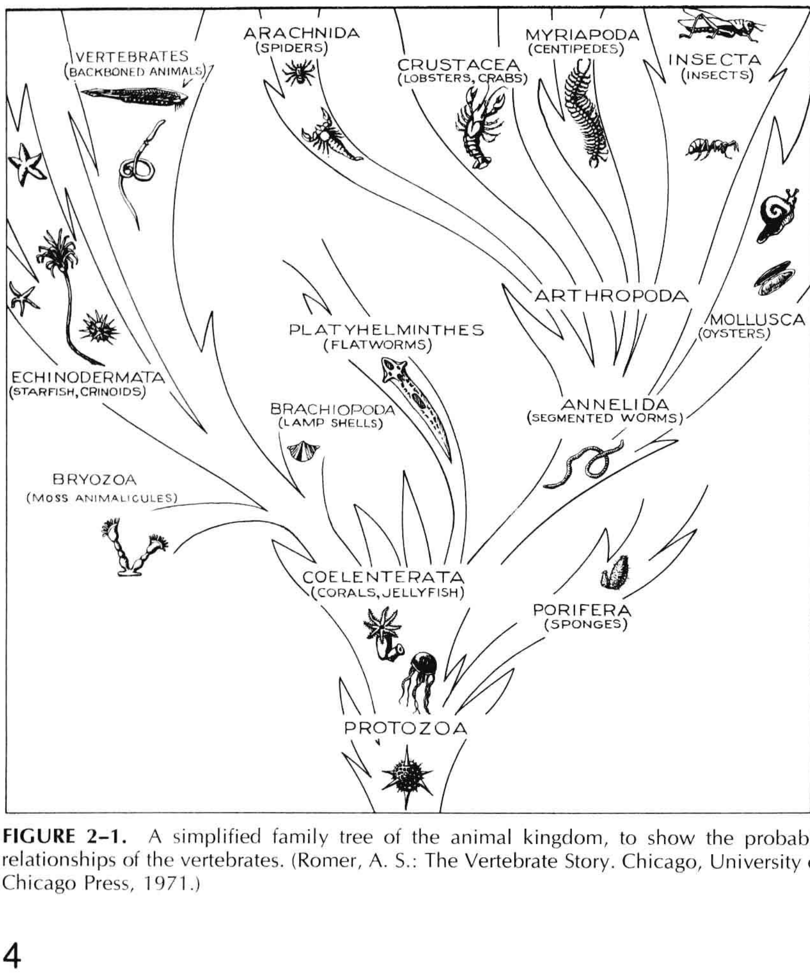

FIGURE 2–1. A simplified family tree of the animal kingdom, to show the probable relationships of the vertebrates. (Romer, A. S.: The Vertebrate Story. Chicago, University of Chicago Press, 1971.)

these led to the segmented worms or annelids, the mollusks, and to the arthropods, while the other gave rise to moss animalcules (bryozoans), lamp shells (brachiopods), starfish and their relatives (echinoderms), and finally to chordates, which include the vertebrates. These two divergent lines, each containing very different kinds of or-

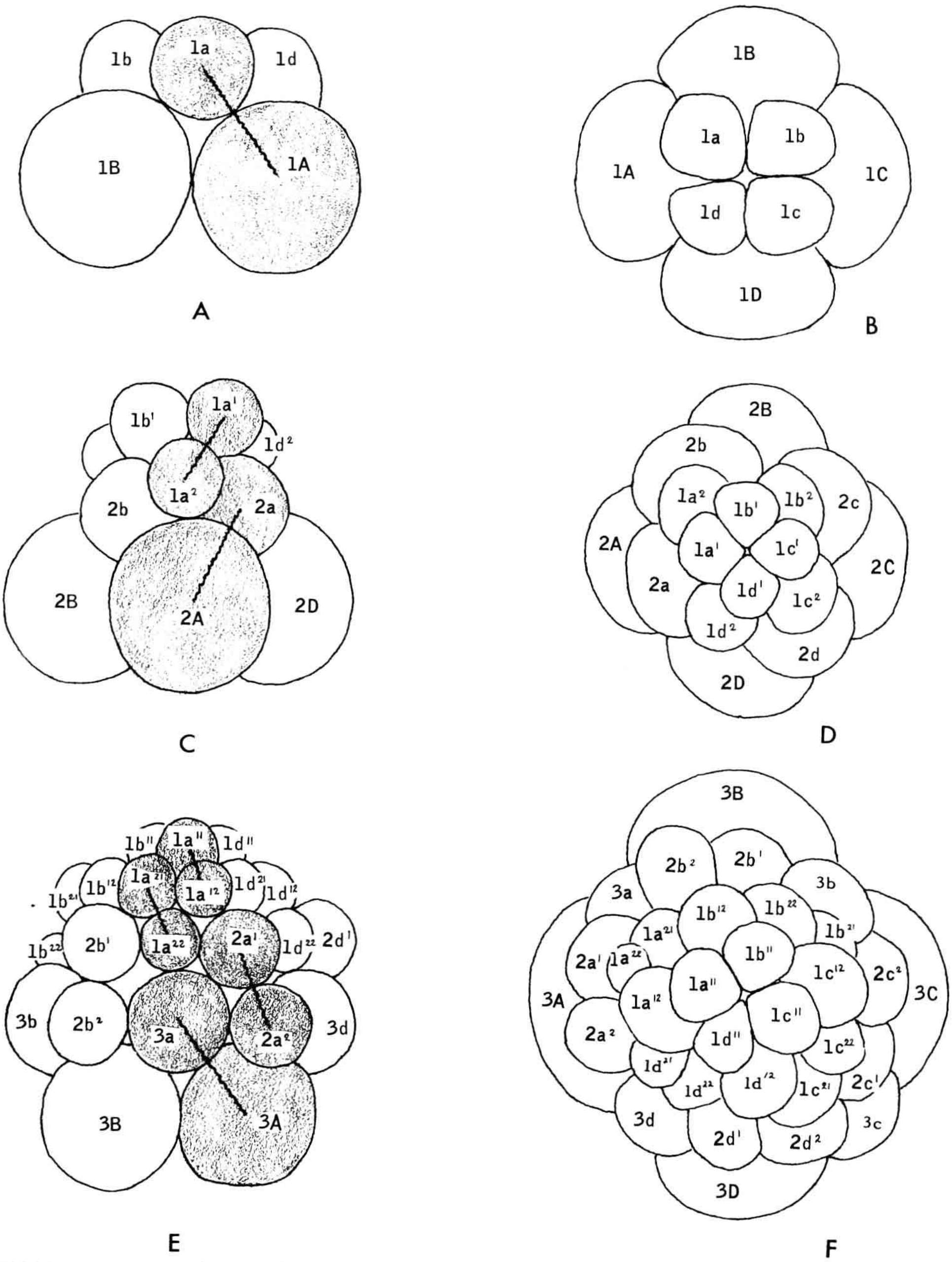

FIGURE 2–2. *A, C,* and *E.* Spiral cleavage (lateral views). All cells derived from original *A* blastomere are shaded. Wavy black lines indicate orientation of spindles at each cleavage. (After Villee, Walker, and Smith.) *B, D,* and *F.* Same stages viewed from animal pole. (After Hyman. From Barnes, R. D.: Invertebrate Zoology, 3rd Ed. Philadelphia, W. B. Saunders Company, 1974.)

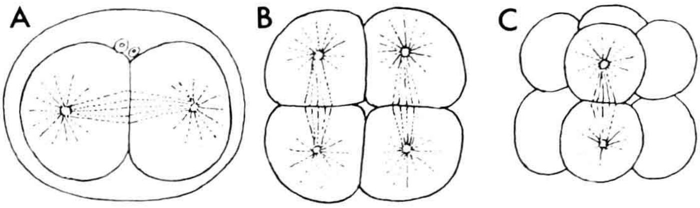

FIGURE 2–3. Radial cleavage in the sea cucumber, *Synaptia*. *A*, Polar view. *B* and *C*, Lateral views. (After Salenka. From Balinsky, B. I.: An Introduction to Embryology. Philadelphia, W. B. Saunders Company, 1975.)

ganisms, differ fundamentally from one another in the manner of cleavage of the fertilized ovum as well as in certain features of embryonic development (Fig. 2–1).

The annelid-molluscan-arthropod line is characterized by *spiral cleavage* of the egg so that the blastomeres have a spiral arrangement (Fig. 2–2). The mesoderm develops as solid masses of cells, and the body cavities originate by separation within these solid mesodermal blocks. The echinoderm-chordate groups, in contrast, have a *radial cleavage* whereby the early cleavage planes are either at right angles or parallel to the polar axis (Fig. 2–3). Later, body mesoderm arises in echinoderms and lower chordates as outpocketings from the upper mesodermal wall of the primitive gut. The cavity or cavities originally formed from these mesodermal evaginations remain and give rise to the future coelomic cavities. There are also variations in later larval development that tend to differentiate these two great groups.

Two other theories presented to account for the origin of vertebrates are the arthropod theory, based on a superficial resemblance between the ancient ostracoderms and certain arachnids such as *Limulus*, the horseshoe crab, and the annelid theory, which speculates that if one were to reverse an annelid a vertebrate-like body plan would result. However, the echinoderm-coelenterate line of development is the most plausible. Even protein serum studies indicate that the lower chordates are more closely related to echinoderms than to any other invertebrate group.

LOWER CHORDATES

Before one can understand the *phylogeny* or ancestral history of vertebrates it is necessary to know something of the lower members of the phylum Chordata to which they belong. The principal characteristics of chordates are the presence of a *notochord* or flexible rodlike structure which represents a primitive axial skeleton extending from the anterior to the posterior part of the body dorsal to the gut, a dorsal hollow nerve cord above the notochord, and the presence of pharyngeal gill slits, at least in embryonic life. The Vertebrata or vertebrates represent only one of four subphyla. The others are the Hemichordata, the Urochordata, and the Cephalochordata.

The hemichordates include the acorn worms, whose lives are spent in tidal mudflats. Although they are wormlike in body shape, any further resemblance to segmented worms ceases. These chordates have pharyngeal gills somewhat like those of the lower vertebrates, a short, hollow dorsal nerve cord, and a small, thick pouch at the base of the conspicuous proboscis that some believe represents a possible notochordal structure.

The urochordates are the tunicates or sea squirts, either sessile or free-floating organisms that are often colonial (Fig. 2–4). Like the hemichordates they are filter feeders with pharyngeal gill slits housed inside a tough barrel-shaped covering or tunic, which is the source of the name tunicate. While adult urochordates show no evidence of a notochord or dorsal hollow nerve cord, many species pass through a

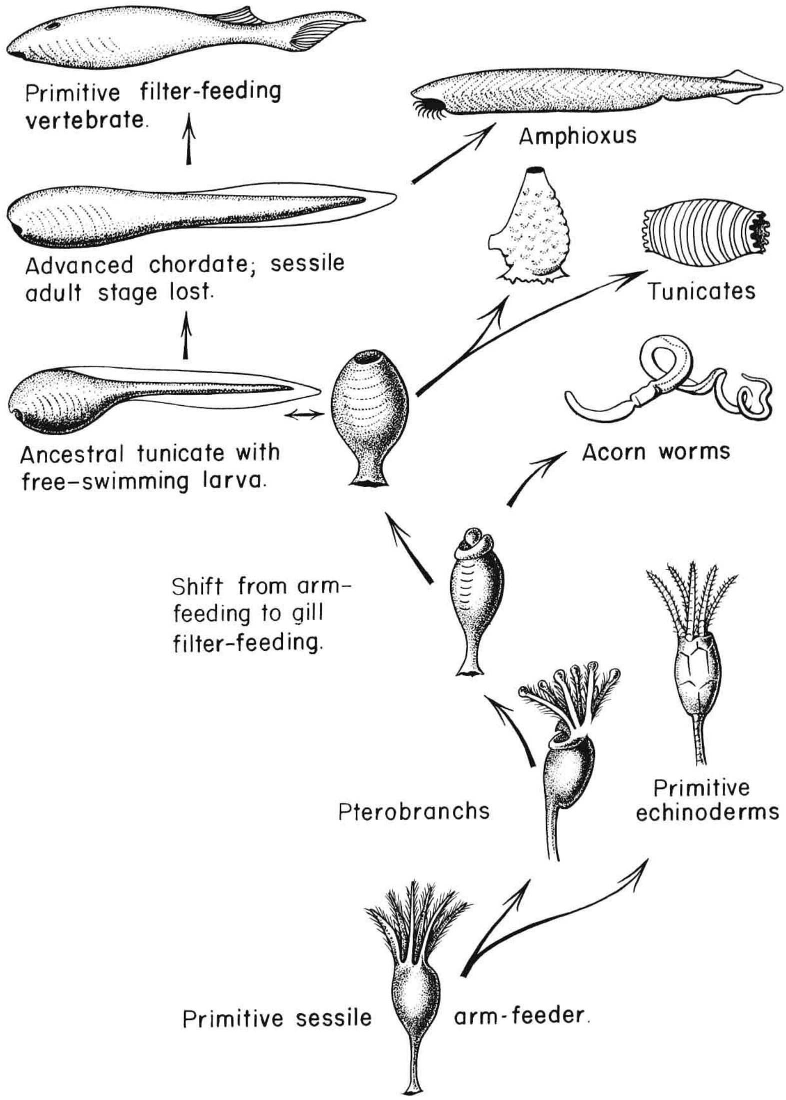

FIGURE 2–4. A diagrammatic family tree suggesting the possible mode of evolution of vertebrates. The echinoderms may have arisen from forms not too dissimilar to the little pterobranchs; the acorn worms, from pterobranch descendants which had evolved a gill-feeding system but were little more advanced in other regards. Tunicates represent a stage in which, in the adult, the gill apparatus has become highly evolved, but the important point is the development in some tunicates of a free-swimming larva with advanced features of notochord and nerve cord and free-swimming habits. In further progress to Amphioxus and the vertebrates the old sessile adult stage has been abandoned, and it is the larval type that has initiated the advance. (From Romer, A. S.: The Vertebrate Story. Chicago, University of Chicago Press, 1971.)

free-swimming larval stage somewhat similar to that of most amphibians. The larval body develops into the adult body while the larval tail, which provides a means of locomotion, is ultimately absorbed. While it functions, however, the tail has a well developed notochord, which gives the name Urochordata to the subphylum, as well as a hollow dorsal nerve cord.

The cephalochordates are known from a small group of organisms called Amphioxus. The relationship of these animals to vertebrates is much more obvious than that of either the acorn worms or the tunicates. The body shape of Amphioxus is fish-like with a well developed notochord that extends its entire length. Above the notochord is a long, hollow nerve cord. Numerous pharyngeal gill slits function for filter feeding as well as respiration. These slits are important, since these animals live in shallow marine situations where they burrow into the sandy bottom, leaving only the front part of the body exposed to take in water containing tiny food particles as well as oxygen. The water passes out through the pharyngeal gill slits. Although certain features in the body of the cephalochordates differ markedly from vertebrates, such as their excretory and reproductive organs, in many respects they resemble larval lampreys, which are true vertebrates.

FOSSILS

Our understanding of this orderly sequence of the appearance of life on earth is largely based upon fossil remains of former living organisms. Fossils are formed in a number of ways, although the chances of any one organism becoming fossilized are extremely small. Most fossil remains are those of animals that possessed hard parts such as shell or bone. It is also necessary in most instances that a dead organism be buried rapidly in sand, mud, or other sedimentary deposits which in time will harden into a stony matrix. Ultimately, under favorable conditions, the skeletal parts become petrified and minerals replace the bony parts to produce a complete replica.

Casts and molds represent other types of fossil remains. Many molluscan and brachiopod fossils are of this type. Shells encased in sandstone may ultimately dissolve, leaving a perfect cast which may show the shape and markings of the original structure. Plant structures such as leaves are most often preserved by carbonization, a process whereby an organic part is pressed so hard that the liquid and gaseous contents are expelled and only a thin layer, consisting mainly of carbon, remains. The detailed veins of leaves as well as their shape are often beautifully preserved in this manner. Footprints of animals, left in mud, may harden under favorable conditions and become covered with sediment, which ultimately turns to stone. Many dinosaur tracks have thus been preserved.

While most fossils are found in sedimentary rock, there are other methods of fossilization. Numerous animals were trapped in tar pits in western North America during the Pleistocene, furnishing an excellent picture of the terrestrial vertebrate fauna of that time. Frozen remains of animals preserved in ice for thousands of years have been found in the Far North. Amber, which is fossilized resin, provides a perfect means of preserving insects.

GEOLOGICAL RECORD

The oldest known rocks on earth date back over 3 million years, although most evidence indicates the age of the earth to be about 4 and one-half billion years. Life itself on this planet is thought to have originated over 3 billion years ago, but most of our knowledge of life from the fossil record dates back little more than one-half billion years ago.

To understand the story of the earth geologists have divided its history into various