29 December 1967, Volume 158, Number 3809 SCIENCE

Major Steps in Vertebrate Evolution

Alfred Sherwood Romer

In studies of animal form or function, there often seems to be an implication that the form studied was created *de novo* to fill the place which it occupies in the modern world. This is, of course, not the case. Every animal or plant living today has thousands of millions of years of history behind it and has been successively adapted to a long series of varied modes of existence; the structures and functions acquired by its ancestors as they passed through various stages have left indelible traces in its organization. It is my belief that the animals of today can be better understood and more reasonably interpreted if the investigator has an appreciation of their past history.

It is this evolutionary, historical approach, particularly as regards our own kin, the vertebrates, which has been the center of my research interests for half a century, and I propose here to give an outline of the present status of our knowledge of this field. The story is not, of course, fully known, but over the decades we have gained a fairly clear picture of most of its main events. There is general agreement as to the greater part of the evolutionary sequence. However, a number of points are still in dispute. Because space here is too limited for full discussion of them, I have selected, where there are alternatives, that interpretation which seems most reasonable in the light of current evidence.

The evidence in part is, of necessity, deduced from data obtained from the study of living animals. Their structures and functions often furnish suggestions of antecedent stages; the study of development can also give valuable information, for embryonic patterns in general tend to be conservative and to suggest the types of former adults to which these developmental processes once gave rise. But, early in their history, vertebrates acquired bony skeletons; this made it possible for them to be discovered in the fossil record. Particularly during the last half century, detailed studies have given important paleontological data on many crucial points of the evolutionary story which I wish to tell.

It might be assumed that the evolutionary story is a straightforward one, beginning with simplicity and going on to increasing complexity and "advance." Not so; it is highly complex. What an organism becomes is not due purely to its inherent potentialities; its fate is strongly modified by physical and biological factors successively met with in its career. Vertebrate evolution has undergone strange shifts due to conditions at various stages; it is not simply an unfolding of innate potentialities. Those who desire a teleological interpretation argue that the evolutionary developments among the vertebrates are so remarkable that they are inexplicable under ordinary theories of evolution. For example, how can we understand such a major shift as that from fish life in the water to vertebrate life on land unless there is some supernatural, directing force behind it? Those who believe that the changes occurring during this transformation are of no immediate selective value feel that a teleological interpretation is necessary. A typical example of this point of view is du Noüy's popular work (*1*). After demonstrating to his own satisfaction that no interpretation except a teleological one is possible, du Noüy discusses the future of man on the basis of supernatural direction in his development. However, I have failed to be interested in his discussion of our happy future; his conclusions are unsound, because his premises are faulty. Much of the evolutionary story which he believes to be insoluble except on the basis of design is readily interpretable under current neo-Darwinian theories of evolutionary progression.

Vertebrate history has been, of course, a continuum, a sequence of gradual changes and evolutionary development; but for present purposes we may divide this evolutionary story into about ten or so stages. And, abandoning any pretense of objectivity, let us direct the sequence of events toward the appearance of man.

Sessile Arm-Feeders

I shall not attempt to follow our history down to the protozoan level. At the beginning of Cambrian times, some 500 million years ago, there first appeared in the fossil record a considerable variety of invertebrate metazoan animals—trilobites and other arthropods, lamp shells, molluscs, echinoderms, and so on. But of our own ancestors at this time there are no sure traces; quite certainly the vertebrate ancestors were then soft-bodied creatures, not normally to be found in the fossil record. We are forced to rely on clues obtained from surviving lowly relatives of the vertebrates, often included with them in a major animal group known as the phylum Chordata (or in part separated as a lower but related phylum Hemichordata) (*2*).

What type of organism should a simply built, early metazoan ancestor of the vertebrates have been? Vertebrates are dominantly active animals,

This is the text of the presidential address delivered by Dr. Romer, retiring president of the AAAS, on 28 December 1967 at the New York meeting.

seekers of food, bilaterally built forms, and we would expect the early forms to have been of this nature. But while there are, among the oldest fossils, numerous forms of this sort (notably the abundant trilobites), the evidence suggests that our early origins come from a more lowly level.

Today, and in the early fossil record, we find remains of metazoans of very different build and habits—simple sessile forms which do not seek their food, but wait for food particles to come to them. The body, attached by a stalk to the ocean bottom, consists of little except a digestive tract; above this, arms extend out hopefully, along which ciliated bands catch food particles drifting past in the water and direct them down to a receptive mouth. Animals of this sort include (i) the bryozoans, or moss animalicules; (ii) the lamp shells or brachiopods, in which the ciliated arms are enclosed in a pair of shells; and (iii) the crinoids, primitive echinoderms in which the stalk, body, and arms are encased in rings of armor. And present today, as well, although not seen in the fossil record, is a fourth type of arm-feeder, the pterobranchs, tiny and rare deep-sea forms with a few structures which definitely show their relationship to the vertebrate pedigree.

Sessile Filter-Feeders

The tiny sessile pterobranchs are a far remove from what we would expect in a vertebrate ancestor in body form or function. A further stage, it would appear, developed among early ancestral forms before we reach anything remotely resembling our expectations of vertebrate ancestors. The ciliated arms of a pterobranch are fairly well adapted to picking up passing food particles and bringing them down to the mouth; but this is not too good an adaptation for actually bringing the particles into the mouth and on the way to digestion. This was accomplished by the development of gill slits—paired openings leading on either side from the throat (pharynx) out to the surface; bands of cilia draw inward a current of water containing food particles; in the pharynx, the food materials are strained out, to be carried down the gut, while the water is passed outward through the gill slits. In larger and later types of chordates, the gills are important, as breathing organs, for the absorption of oxygen; in small early types, however, breathing could be satisfactorily cared for by the skin in general; the primary gill function was as a feeding aid. With the development of the gill current, the "arms" could be—and were—lost; in front of the mouth, there was only a noselike proboscis (already present as a sign of chordate relationship in pterobranchs). A simple pair of gill slits is present in one genus of living pterobranchs, and only an increase in number of slits was necessary to attain this new stage. Departing but little from what we believe to have been the truly primitive filter-feeders are the balanoglossids, or acorn worms, essentially sessile burrowers found in modern seas; their name is derived from the fact that the proboscis nestling into a bandlike neck resembles an acorn in its cup. Filter-feeding has been a successful, if lowly, way of making a living, and a further stage in developing a filtering apparatus occurs in the little tunicates, or sea squirts, rather common in modern seas either as solitary or colonial attached forms or as free-floating types. They carry the filtering apparatus to an extreme; in a typical member of this group, almost the entire animal consists of a barrel-shaped pharynx comprising a complex set of gill filters.

The Vertebrate Body Pattern

The tunicates are terminal members of this sequence of particle-gathering sessile types—the end of the line. It would seem that nothing further could well develop in an evolutionary sequence beyond the adult of this stage. Nothing did. But from the larva of a tunicate, or presumably a pretunicate, there arose the body type from which the true vertebrates sprang (Fig. 1).

We customarily think of evolutionary series in terms of adult animals; that change took place by gradual modifications in the structures and functions of mature individuals. But there is another possibility, that of paedomorphosis, emphasized especially by Garstang (*3*) as responsible for the further advance of the chordate-vertebrate series. Normally only a fully grown animal is capable of reproduction. But if immature forms should become sexually mature and reproduce, what then? It is quite possible that the previous adult stage might completely drop out of the picture, and a new evolutionary development might make its appearance.

In many tunicates, reproduction takes place by budding or by a normal direct development to the adult condition. But there is a different pattern in certain living types. Most tunicates make their livelihood where their parents live or where the local water currents carry them during their development. But some freedom of action has become available to certain tunicates by the introduction into the life cycle of a free-swimming, tadpole-like larva, so that the young have some freedom of choice to move to a favorable area for adult life. In a swollen "head" region, the gill apparatus, which is to constitute the major part of the adult body, develops. Behind, there is a muscular swimming tail, strengthened by a stout but flexible longitudinal cord, the notochord, predecessor of the vertebral column; the activity of the motile tail is supervised by a longitudinal dorsal nerve cord, which in the head region receives sensory information from rudimentary sense organs. The life of the larva is short; it swims about for a few hours or days and then settles down, to be attached to the sea bottom. Tail, notochord, nervous system, and sense organs degenerate and are resorbed, and the creature assumes the adult shape of a tunicate.

In this larva, we see the appearance, in simple form, of the typical body pattern characteristic of vertebrates, and it seems certain that we have here the beginnings of a new evolutionary series, radically different from that of the sessile series of which the adult tunicate is an end form. If, as seems surely to be the case, Paleozoic tadpoles of certain tunicates, or pretunicates, became sexually mature and no longer metamorphosed into sessile adults, a new mode of life opened up. Instead of passively waiting for food to come to it, the animal could go in search of food and could explore new areas or new habitats in which it might exist. *Amphioxus*, familiar to every student of biology, represents in slightly specialized fashion the stage in which sexual maturity of the tadpole has taken place, but not much progress toward higher evolutionary levels has occurred.

First Vertebrates: The Ostracoderms

These earliest stages in the vertebrate pedigree occurred, at the latest, in very early Paleozoic times, for in the Ordovician, second of the Paleozoic periods, remains of fossil true vertebrates are present. Such remains become abundant by the end of the following Silurian period, where numerous specimens of varied types of lowly vertebrates termed ostracoderms are found. Our knowledge of them dates from the thorough studies (in the 1920's) of members of the *Cephalaspis* group (*4*). No one of the late Silurian and early Devonian ostracoderms is to be regarded as a direct ancestor of "higher" vertebrates, but the cephalaspids, best known of ostracoderms, nevertheless show the general structure reasonably to be expected in an ancestral vertebrate. There is an expanded "head" region, exhibiting typical sense organs, and a powerful swimming tail. The "head," when dissected, is seen to be mainly occupied by an enormous gill chamber, terminated anteriorly by a small mouth. We have here, on a higher level, a structure not unlike that present in the tunicate tadpole. The ostracoderm was still a jawless filter-feeder, but it had the great advantage over its tunicate (or pretunicate) ancestor that the large feeding apparatus of the gill basket could be moved about to suitable food localities.

In what environment did the early vertebrates live? We assume that the ocean was the original home of life, and the seas are still the home of a great proportion of all animal types; further, the lower chordates and hemichordates are all marine forms. But many of the finds of early vertebrates are from sediments rather surely laid down in fresh waters, and I came to the conclusion, some decades ago, that early vertebrate evolution took place in lakes and streams rather than in the sea (*5*). At about the same period, Smith (*6*) reached a similar conclusion from a comparative study of kidney function. Our conclusions have not gone uncontested (*7*), and it may be long before definite agreement is reached. But while I must defer further discussion of this question to some future occasion, it still seems clear to me that a freshwater origin fits best into the general picture. With the invasion of the continents by plant life in the Paleozoic, freshwater streams and ponds gave a new area where animals might find food. Few invertebrates have been capable of entering freshwater environments—for successful life inland, the animal must be an active swimmer to avoid being carried back down to the sea. The vertebrates and their advanced chordate ancestors, with the swimming powers given them by their tail development, were one of the few types competent to enter fresh waters and to enjoy them profitably. Upstream invasion by vertebrates took place rapidly and successfully, so that by the late Silurian and the following Devonian period, fishes had become prominent dwellers in inland waters.

Because the "lowest" of living vertebrates—lampreys, hagfishes, and sharks —lack bone and have skeletons of cartilage, and since in the development of higher vertebrates the skeleton is first formed in cartilage and is only later replaced by bone, it was long thought that cartilage was the original skeletal material of vertebrates, and that bone developed only at a relatively late evolutionary stage. But our present knowledge of the fossil record shows that the oldest of known vertebrates already had bone, at least as an external armor. As a consequence, most (but not all) students of the subject will agree with Stensiö's conclusion that bone developed at the base of the vertebrate

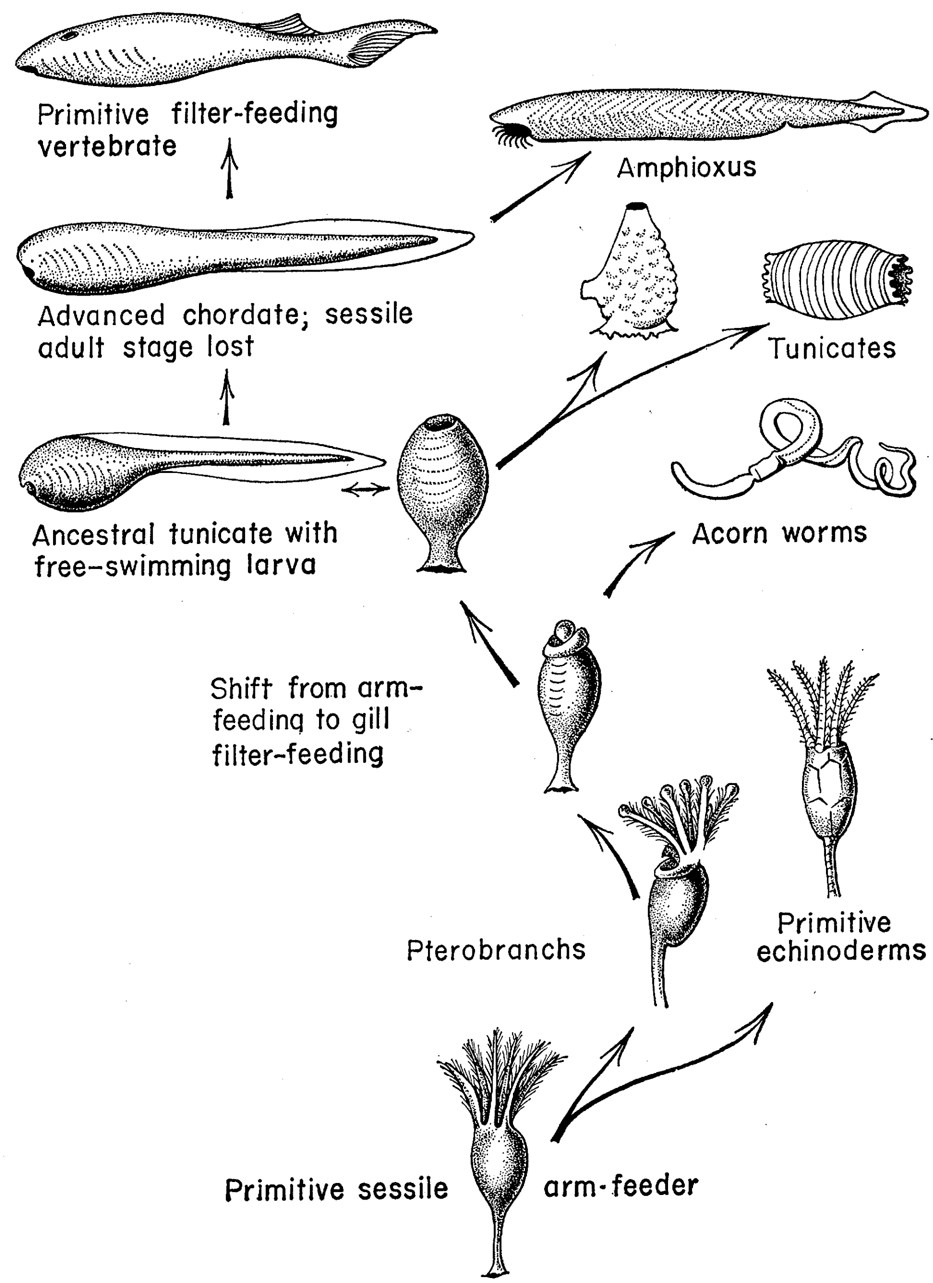

Fig. 1. Diagrammatic family tree suggesting the possible mode of evolution of vertebrates. The echinoderms may have arisen from forms not too dissimilar to the little pterobranchs; the acorn worms may have arisen from pterobranch descendants which had evolved a gill-feeding system but were little more 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. 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, *The Vetebrate Story* (University of Chicago Press)]

series and that the boneless condition in cyclostomes and sharks is a secondary, degenerate one; the prominence of cartilage in the young vertebrate is an embryonic adaptation (*8*).

Except for improvement of sense organs, the appearance of bone is the only major advance made by the earliest vertebrates over their higher chordate ancestors. Why bone? Calcium is physiologically important, and it has been suggested that its appearance has to do with a functional need. However, bone, as we see it in the oldest vertebrates, is not simply a calcium deposit, but an external covering of plates arranged in a complex pattern. It looks like armor; and very probably it was. In the late Silurian and early Devonian, we find numerous faunas in which nearly the only animals present are small armored ostracoderms and eurypterids—a type of predaceous arthropod distantly related to the horseshoe crab of today. The average eurypterid was much larger than most contemporary vertebrates—some as much as about 2.5 meters in length, compared with ostracoderms generally but several centimeters long. It seems clear that the lowly ostracoderms were their food supply and that the development of bony armor was an adaptive protective device. In later times, fishes became more advanced, more skilled in swimming, generally larger, and often predaceous themselves. Parallel with these advances, eurypterids became rare and (robbed, it would seem, of their erstwhile prey) extinct before the end of Paleozoic days (*9*).

It seems probable, then, that bone first appeared in the form of dermal armor, laid down in membrane fashion in plates within the skin. In many ostracoderms, there is no bone except in the surface armor (*10*). In the cephalaspids there is some development of internal bone within the head region, but even here it is of the same "membrane" pattern, laid down in sheets around the various internal canals and cavities. Only in higher fish groups, bone development progressed further, to the endochondral stage, when solid masses of bone are present in internal structure. It seems that, for the development of a bony skeleton, without which the evolution of the more advanced classes of vertebrates would have been impossible, we must thank the eurypterid enemies of our early ancestors.

The ostracoderms were, in general, small and feeble, doomed to extinction by the end of the Devonian period; they have survived only in the form of the degenerate and specialized lampreys and hagfishes in which the development of a peculiar, rasping, tonguelike structure has enabled them to persist in modest fashion as predators on other fishes. A new era in fish history opened with the development of jaws, formed by enlargement of a pair of skeletal bars which earlier had formed supports for gill slits. Armed with these new structures, fishes were released from the necessity of depending on filter-feeding for a livelihood, and a whole new series of potential modes of life was opened up for them. Early in the Devonian period we find, principally in fresh waters, a varied host of jawed fishes: placoderms, acanthodians, and, most especially, three major groups of advanced bony fishes which played an important role in later vertebrate evolution—the Actinopterygia (or ray-finned fishes), the Dipnoi (or lungfishes), and the Crossopterygii, of little account beyond Paleozoic days, but highly important as the progenitors of land vertebrates.

A persisting major gap in our paleontological record, however, is the almost complete absence of any trace of an earlier jawed fish. Although the common ancestor must have existed well before the Devonian, there is no earlier record of fish of this sort except for a few fragmentary remains of acanthodians in near-shore marine Silurian deposits. Why this gap? To one who believes that these early stages in fish evolution took place in salt water, there is no reasonable answer to this question. But to a believer in freshwater origins, the answer is simple. Earlier than the very late Silurian, continental strata are almost entirely absent from the known geological record. Without question, continental deposits had been formed in the earlier geologic times, but it seems that subsequent erosion has resulted in the destruction of such older beds in which remains of truly ancestral jawed fishes might have been found.

Amphibians—The Beginnings of Land Life

With the radiation of jaw-bearing fishes, vertebrates had obtained a dominant position in life in the water. But a further major advance was presently to come—the conquest of the land, initiated by the amphibians and completed by their reptilian descendants. In recent decades, much of the general picture of this major evolutionary advance has been worked out (Fig. 2).

What fish group gave rise to the early four-footed animals, tetrapods, represented today by the surviving orders of amphibians? Quite surely, all would agree, some type of the higher bony fish of the class Osteichthyes. One may immediately rule out the ray-finned fishes—the actinopterygians—for a variety of reasons; because of various specializations, the lungfishes, despite anatomical and embryological similarities to amphibians, are to be regarded as the "uncles" of the tetrapods rather than as actual ancestors. It has become increasingly certain in recent decades that the ancestors of land vertebrates lay among the Crossopterygii and, particularly, an early central group of crossopterygians, termed the Rhipidistia. The crossopterygians flourished during the Devonian but rapidly declined in numbers, and beyond the Paleozoic they survived only in the form of an aberrant side branch, the coelacanths, of which a single form, *Latimeria*, survives in the Indian Ocean. We know nothing firsthand of the soft anatomy or embryology of rhipidistians, but in regard to the skeleton, the evidence is clear that the older crossopterygians are proper ancestors for the tetrapods. The fin skeleton is of just the type to develop into a land limb, and, in general, a crossopterygian skull can be compared bone for bone not only with amphibians, but also with reptiles, mammals, and man.

The tie-in of crossopterygians with the Amphibia is close, not so much with the living orders as with a great group of forms, the Labyrinthodontia, which began their career at the end of the Devonian, abounded in the Carboniferous and Permian, and survived, before extinction, into the Triassic (*11*). Over the last half century, a long series of finds has yielded a fairly complete story of the labyrinthodonts. They are of importance in their own right, but one group of them, the anthracosaurs, are especially important in that they show a series of stages leading onward to the reptiles (*12*).

But whereas we have a fairly clear story of the relationship of the crossopterygians to the labyrinthodonts and through them to the reptiles, the history of the surviving orders of amphibians is still obscure. These consist of (i) the

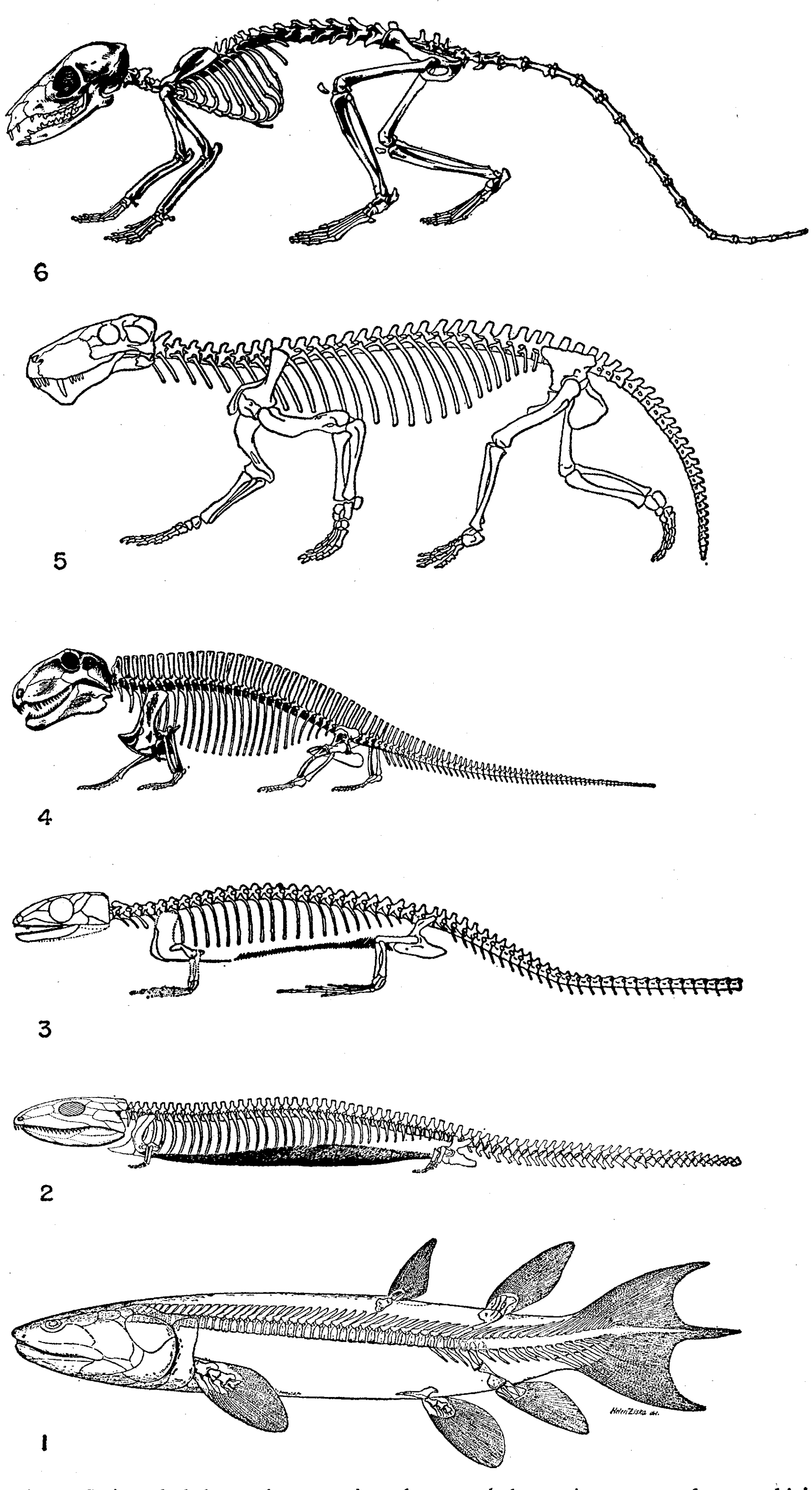

Fig. 2. Series of skeletons in approximately true phylogenetic sequence from a rhipidistian crossopterygian to a placental mammal. (1) Crossopterygian *Eusthenopteron*; (2) *Pholidogaster*, an early labyrinthodont tending in a reptilian direction: (3) *Hylonomus*, one of the oldest and most primitive of known reptiles; (4) *Sphenacodon*, a Permian pelycosaur pertaining to the group from which therapsids were derived; (5) *Lycaenops*, a generalized therapsid, with improved four-footed locomotion; (6) The tree shrew *Tupaia*, a generalized placental mammal. [(1) and (6) after Gregory, (3) after Carroll, (4) after Romer and Price, (5) after Colbert]

Anura, frogs and toads; (ii) the Urodela, including newts and salamanders; and (iii) the Apoda or Gymnophiona, tropical wormlike forms. The three orders are quite diverse in structure and body form, but recent work suggests that they are, as the Lissamphibia, a phylogenetic unit (*13*). Possibly related to their ancestry are small Carboniferous and early Permian amphibians known as the Lepospondyli (*14*); but this does not solve the question, for the pedigree of the lepospondyls themselves is quite uncertain. This is a chapter of vertebrate evolution where further data are needed.

How did the major evolutionary step from water toward and to land take place? Those who favor teleological interpretations insist that some divine or mystical driving force must have underlain this radical shift in habitus and structure since, they say, the development of adaptations fitting the fish descendants for future life on dry land would have had no immediate adaptive value to a water dweller. Here, however, as in other cases, there is no need to call upon the supernatural, for it can be shown that under some special condition such adaptations could have been of immediate selective value. This special condition seems to have been seasonal drought (*8*). More than half a century ago, Barrell (*15*) pointed out that the numerous red beds of the late Paleozoic (and Triassic) gave evidence of the widespread prevalence of regions subject to seasonal drought. At certain times of the year (as today in some tropical areas), rainfall would be abundant; at other seasons, the rains would cease, streams slow down, and ponds become stagnant.

There are many structural and functional changes necessary to turn a typical fish into an amphibian and, eventually into a reptile; let us merely take two of the most obvious "improvements" needed—lungs and land limbs. To a fish under normal climatic conditions, gills suffice for breathing purposes. But under drought conditions, with stagnation of waters and low oxygen content, it would be highly advantageous for a fish to be able to come to the surface and avail itself of atmospheric oxygen. Today only five genera of fish have retained true lungs (they live in seasonal drought areas), but our evidence suggests that in the late Paleozoic the great majority of freshwater forms possessed lungs.

But legs? Why should a water dweller

have these structures, so essential for land life? The answer seems to be that legs did not evolve as a mystical "preadaptation" for a future life on land, but (seemingly a paradox) as structures which would aid a water-dweller, under drought conditions, to continue his life in his own proper element. In early stages of a severe drought, a fish with lungs would survive stagnant water conditions without trouble. But suppose the drought worsened and the water in a pond dried up completely? An ordinary fish would be literally stuck in the mud and would soon perish unless the rains soon returned. But a form in which there had been some trend for enlargement of fins toward the tetrapod limb condition might be able to crawl up or down a river channel, find a pond with water still present, happily splash in, and resume his normal mode of life. Most fossil amphibians had legs developed to at least a moderate degree. But as far as we can tell, most of them had no yen for life on land; legs were, for the time being, simply an adaptation for bettering the animal's chances for surviving in his proper aqueous environment (*16*).

The First Reptiles

Modern reptiles and modern amphibians can be readily told apart. But increased knowledge of the fossil record has brought us to the point where it is almost impossible to tell an advanced fossil amphibian from a primitive reptile on the basis of its skeletal structure. The first reptiles, it now seems clear, were a group of "stem reptiles" (cotylosaurs) known as the Captorhinomorpha, well known in the Permian and now known to have been present far back in Carboniferous times (*17*). The real distinction, of course, between amphibians and reptiles lies in the mode of reproduction. The typical frogs, toads, or salamanders in our temperate regions gather in the spring in ponds where the eggs are laid and develop, as those of their fish ancestors did, into water-dwelling and water-breathing larvae. Only later, with metamorphosis, lungs develop, and land life becomes possible. In contrast, reptiles are notable in that they lay an amniote type of egg. This is prosaic to us (since it has been retained by the avian descendants of the reptiles), but it is actually the most marvelous "invention" in vertebrate history. This egg can be laid on land; the water stage of development is eliminated. Externally, there is a protective shell; internally, a complex series of membranes protects the growing embryo, and there is an abundant supply of nourishing yolk; a larval stage is eliminated, and the young reptile (or bird) hatches as a miniature replica of the parent, already well adapted to take up a fully terrestrial mode of life.

At what evolutionary stage did this new and revolutionary egg type enter the picture? Certain amphibians of ancient days had well-developed limbs and were apparently ready for a fully terrestrial existence. But they were chained to the water (splendid phrase) by the necessity of the old-fashioned aquatic mode of development. Finally (went the story as it was long told, and as I used to tell it myself), the amniote egg was developed, the chains were broken, and the reptiles burst forth upon the land!

A good story, but, it would now seem, a false one. It is probable that the egg came ashore before the adult was fully ready for land life (*18*). Study of certain members of the oldest-known reptilian faunas seems to indicate that although they quite surely laid an amniote type of egg, the adults, like their amphibian ancestors, were still amphibious in habits, spending much of their time in the water, with a sustaining diet of fishes. Why, then, a land egg? A review of breeding habits of modern amphibians furnishes a clue. I have mentioned the "typical" mode of reproduction of frogs, toads, and salamanders. But if we survey these types as a whole, we find that the "typical" mode is really exceptional rather than common. Particularly in the tropics, modern amphibians adopt any device possible to avoid laying the eggs in the water. Why? Avoidance of enemies is probably a major objective; to a variety of forms, ranging from insects to other vertebrates, eggs in a pond are a desirable amphibian caviar. But to some degree among modern forms and, I think, to a major extent among the ancestral Paleozoic reptiles, the reason was seasonal drought; if eggs are laid in a pond, drought leads to larval death. Here again, an adaptation which was to be exceedingly useful in terrestrial life appears to have evolved, not with this end in view, but as an immediately useful adaptation to an animal still leading an amphibious life.

Mammal-Like Reptiles

Once lungs, limbs, and, finally, the amniote egg were developed, full terrestrial existence became possible. The early tetrapods were eaters of animal food; the rise of the insects toward the end of the Carboniferous furnished a basic food supply for early land-dwellers. Soon there was under way a great radiation of reptilian types which were to dominate the world during the Mesozoic era—a radiation leading not merely to the familiar surviving reptilian orders, but also to a host of forms now extinct, such as the great marine reptiles of the Mesozoic, dinosaurs, flying reptiles, and bird ancestors. Curiously, however, the first great development from the primitive reptilian stock was not the one that led to any of these forms, but was the rapid emergence of the Synapsida, a group from which the mammals were destined to evolve. The first synapsids appear in the record almost as early as the first reptiles of any sort, and from the late Carboniferous on through the Permian and into the early Triassic they were the commonest of land animals. From time to time, there sprang from this stock successful, herbivorous, side branches, but the main evolutionary line consisted of forms which were the dominant carnivores, large and small, of late Paleozoic and earliest Mesozoic times. The more primitive representatives of this group were the pelycosaurs, forms to which I have devoted a considerable part of my scientific life (*19*), and which are best known from the early Permian red beds of Texas. In structure, pelycosaurs had departed little from the most primitive reptiles; they still walked, quite inefficiently, with the sprawled-out pose of the limbs characteristic of all early four-footed animals. During the Permian, there developed from one pelycosaur group a more advanced mammal-like type, that of the therapsids. Here locomotion was greatly improved; the elbows were turned back, the knees forward, the trackway narrowed, the stride increased with resulting greater speed. These therapsids are best known from the Great Karroo deposits of South Africa, from which hosts of therapsids have been described by Broom, Watson, and many other scientists.

Therapsid dominance lasted until the Triassic. But as this period progressed, the therapsids dwindled in numbers and variety, to disappear completely in the Jurassic. The cause of their downfall appears to lie in the rise of a rival reptile group, the archosaurs, or "ruling reptiles." In this reptile subclass, there was a strong trend toward the solution of the problem of efficient locomotion in a fashion different from that adopted by the synapsids. Instead of evolving an improved quadrupedal gait, the front limbs were abandoned in locomotion, and fast bipedal running was attained by elongation and adaptation of the hind legs. This new stance came into being among archosaurs during the Triassic, when early carnivorous archosaurs, known as thecodonts, began a successful competition with the therapsids; by the late Triassic there had evolved carnivorous dinosaurs, which were to dominate the earth during the 100 million years or more which constituted the remainder of the Mesozoic era.

The Rise of Mammals

The mammal-like reptiles, then, disappeared from the scene, to give way to the dinosaurs, but not without having left behind, as their descendants, the mammals, small early representatives of which, not too far from therapsids in structure, have recently been found in deposits of late Triassic age. These mammalian descendants of the therapsids persisted through the next 100 million years of dinosaurian dominance, but survived only as small and inconspicuous forms. Their history during this long period (*20*) is sparse and fragmentary; except, perhaps, for the late Cretaceous, all known materials (should one treat them so irreverently) would probably little more than fill a derby hat. But this time of tribulation under the constant menace of the dinosaurs was not a wasted one. The first mammals were probably little above the reptilian level; by the close of the Cretaceous, when the dinosaurs became extinct, they had reached a high degree of organization and were competent to take over the rulership of the world.

If we were to attempt to define a mammal briefly, it could perhaps be done in two words—activity and intelligence. We mentioned earlier body improvements in therapsids which made them swift-running quadrupeds; in mammals generally, this four-footed gait is retained and improved. Maintenance of body temperature (toward which end a hairy or furry covering is one adaptation) enables a mammal to be active (quite in contrast to a reptile) at any temperature. Therapsids were active forms, but, as the fossils show, still small-brained, still essentially thoughtless automata. By the end of the Mesozoic, the mammal brain had become highly developed; the cerebral hemispheres were large and complex; learning and training were possible, so that, in a broad sense of the word, intelligence had come into the world. Because the cerebral cortex is a complex organ, as much time as possible should be allowed in the development of the individual so that this important structure may reach its full potentialities before it is put to use. Reproductive improvements in mammals work toward this end. Mammals (except for two archaic types) bear their young alive, and in the higher mammals—generally termed the placentals—there had developed by the end of the Mesozoic a highly efficient nutrient connection, the placenta, between the mother and the fetus within her uterus, so that birth can be delayed until the young reach a much larger size and more mature structure than it was possible for them to do in an egg-laying form. The nursing habit extends further the time before the youngster is forced to live its own life. During this period, the young mammal can be trained and taught; in a sense, we can say that in the nursing habit we see the establishment of the world's first educational institution.

Some of these features, which were to be eventually responsible for mammalian success, were quite surely developed by their therapsid ancestors; most, however, appear to have been brought about as adaptations and advances necessary for the survival of our feeble mammalian ancestors under the reptilian tyranny. As mammals, we owe a debt of gratitude to the dinosaurs for their unintended aid.

Life in the Trees: Primates

By the close of the Mesozoic and the dawn of Cenozoic times, the evolution of higher mammals had been completed, and there were forms well equipped to take over world dominance from the ruling reptiles. The small ancestral placental types of that day were (as their ancestors had been for innumerable millions of years) potentially carnivores, but we believe that, due to their modest size, they must have contented themselves with insects and grubs as food staples. Forms surviving today with similar diets are considered members of an order Insectivora, of which the shrews are the most characteristic representatives. But while the shrews, in their small size and in-

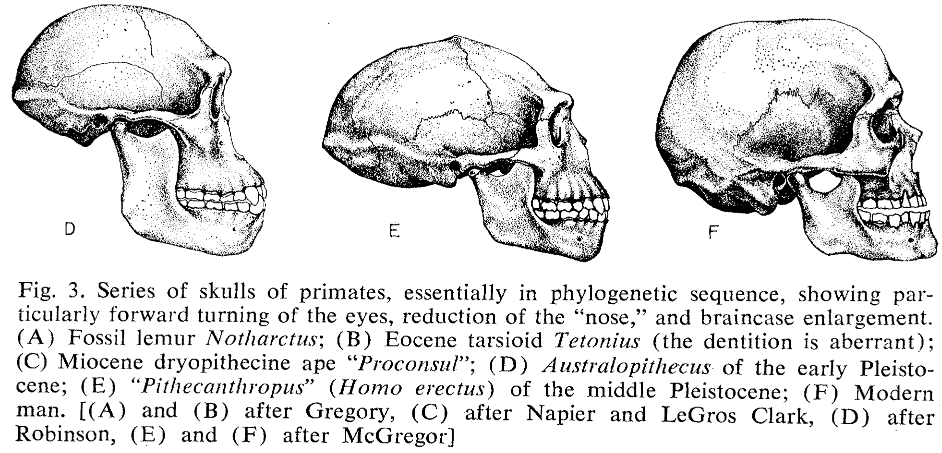

Fig. 3. Series of skulls of primates, essentially in phylogenetic sequence, showing particularly forward turning of the eyes, reduction of the "nose," and braincase enlargement. (A) Fossil lemur *Notharctus*; (B) Eocene tarsioid *Tetonius* (the dentition is aberrant); (C) Miocene dryopithecine ape "*Proconsul*"; (D) *Australopithecus* of the early Pleistocene; (E) "*Pithecanthropus*" (*Homo erectus*) of the middle Pleistocene; (F) Modern man. [(A) and (B) after Gregory, (C) after Napier and LeGros Clark, (D) after Robinson, (E) and (F) after McGregor]

conspicuous habits, give us a picture of the life which the early placental mammals must have led under the reign of the dinosaurs, even they have developed certain specializations which remove them from a truly central position in placental evolutionary history. The actual ancestors, of 20 million or so years ago, are extinct; but if we look about us for living forms which appear to be closest to the primitive stock, the choice, I believe, falls on the tree shrews; *Tupaia* and related genera, of the Oriental region. These attractive little animals are often considered as possible ancestors of the primates; but there is little in their structure to prevent them from being considered as playing a still more important role, that of forms approaching most closely the parental stock of all higher mammals.

Once the dinosaurs passed from the scene, the ancestral placental mammals rapidly began a radiation into the varied mammalian types which are with us today—from rats to cats, to bats, to whales, to hoofed mammals of all sorts, and so on. All of these types have had interesting and often spectacular careers in the approximately 70 million years of the Cenozoic Era, the age of mammals. But if we wish (conceitedly) to continue our story in the direction of ourselves, the one mammalian order which comes into focus is that of the Primates, including lemurs, monkeys, apes—and men (Fig. 3).

The primates are (with a few exceptions, such as men and baboons) tree-dwellers, and such success as man and his primate relatives have had can be attributed in great measure to features associated with arboreal life (*21*). Locomotion in the trees, as practiced by primates, demands flexibility and agility, and the primate skeleton is much more generalized in nature than is that of most other mammals. Small tree-dwellers, such as squirrels, may climb trees by digging in their claws; primates, generally of rather larger bulk, have adopted another method—they have developed an opposable thumb and big toe, so that a branch may be grasped. Arboreal life has caused a marked change in the development of sense organs. In most mammals, smell is highly developed, while vision, as far as one can tell, is of a rather fuzzy nature. In the trees, olfaction is unimportant and is greatly reduced (as the snout is) in higher primates. Accurate vision, on the contrary, is essential for safe locomotion in the trees; we find that, in all but the lowest of primates, the eyes, primitively rather laterally directed, are turned forward so that the two fields of vision are identical, and stereoscopic vision, with depth effects and distance judgment, is developed. Further, higher primates have in each retina a central area in which detail is clearly perceived.

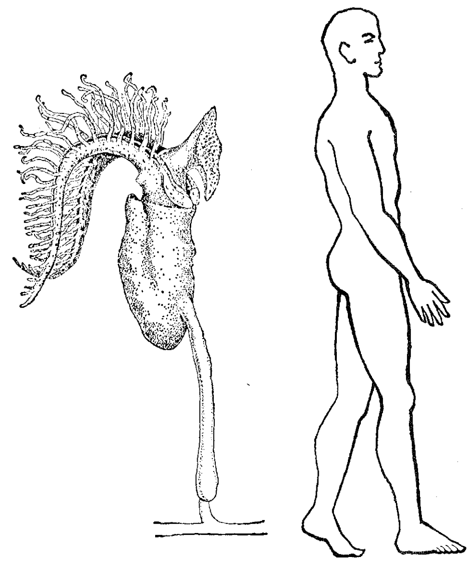

Fig. 4. Beginning and end of the story. (left) Pterobranch *Rhabdopleura,* much enlarged, showing the simply built, stalked body, with food-collecting arms above; (right) modern man. [*Rhabdopleura* after Delage and Herouard]

The brain of mammals is, in general, highly developed; in primates, its development is of a still higher type than in most other placentals. Locomotor agility in the trees demands a high development of motor centers in the cerebrum, and it is suggestive that the major brain area devoted to the highest mental faculties develops in an area (frontal) alongside the motor centers. Again, the development of good eyesight has rendered possible a far wider knowledge of their environment for primates than for forms which depend upon smell. Also important in primate mentality has been the development of the grasping hand as a sensory aid in the examination of objects. With the potential advantages to be gained from any trend toward increased mental ability, it is not surprising that, in monkeys, apes, and men, selection has resulted in the development of large brains and greatly extended areas of the gray matter of the cerebral cortex.

In early Tertiary times, numerous remains of primitive primates in the lemur stage of primate evolution were present in the fossil beds of both North America and Europe. In the lemurs, which today survive mainly in the protective isolation of Madagascar, primate evolutionary trends have but begun; for example, there is still a large muzzle, and the eyes are directed more laterally than anteriorly. But, early in the fossil record, there are remains of a more advanced primate type, of which the living *Tarsius* of the East Indies is a surviving member. *Tarsius* itself is a somewhat specialized little animal, but shows clearly the advances already present in its early Tertiary relatives. Smell is reduced, and the nose is a mere nubbin; the large eyes are turned straight forward, with the development of stereoscopic vision; the brain is quite large in proportion to body size.

Beyond the *Tarsius* stage, the evolution of higher primates occurred in two separate lines. The next higher level of organization, seen in the monkeys, was attained in one group of tarsioid descendants which migrated to South America and in a second group that developed in Eurasia. In Oligocene rocks of the Egyptian Fayum are found remains (if fragmentary) not only of ancestors of Old World monkeys, but also of small ancestors of the great apes which are man's closest relatives (*22*).

Of the living great apes, the gibbons and orang presumably split off at an early time. However, in mid-Tertiary rocks, widespread in Eurasia and Africa, there are found remains (mostly fragmentary, unfortunately) of a rather advanced type of great ape. The term *Dryopithecus*, the "oak ape," is generally applied to such remains; an East African member of the series is generally given the special name of *Proconsul.* In members of this group, we are dealing with apes of modest size which are relatively little specialized. As far as we know them, the oak apes appear to be potential ancestors of the chimpanzee, of the gorilla, and, not improbably, of man as well.

Down to Earth—Man

Lower primates in general and even such higher apes as the gibbons and orang are definitely tree-dwellers. But the trend was reversed at the top of the primate series. The chimpanzee is less of an arboreal acrobat than the lower great apes, and the mountain gorilla of central Africa has almost completely abandoned tree-dwelling (but is essentially quadrupedal in locomotion on the ground). As yet, we know almost nothing of the late Tertiary history of the specific ancestors of man, but it is suggested, not unreasonably, that his abandonment of the trees may have been associated with reduction, in some of the Old World regions in which his ancestors lived, of a forest covering to a savanna-type of environment, with open areas between the copses; this would have encouraged ground locomotion and introduced prehumans to the possible advantages of terrestrial over arboreal life (*23*). In recent decades, a part-way step from ape to man has become known with discovery of the australopithecines, whose remains are primarily from South African caves (*24*). *Australopithecus* and his kin are, unquestionably, morphologically antecedent to man, and with one or two exceptions, all competent investigators in this field now agree that the australopithecines of the early Pleistocene are actual human ancestors. From mid-Pleistocene times, half a million or so years ago, we find remains of forms, such as *Pithecanthropus* and *Sinanthropus*, which are definitely human types, although with brains still well below modern levels and with many primitive features. Later in the Pleistocene, there appear more advanced forms and, toward the end of the Pleistocene Ice Age, some tens of thousands of years back, there appear in Eurasia and Africa representatives of our own species, *Homo sapiens*, fully as advanced as any living race.

Summary

We have come to the end of our story—a long one, covering some half a billion years, it appears. A modern man or other higher vertebrate has traveled far from the simply built insensate type of creature seen in his ultimate metazoan ancestor among the pterobranchs. The course of this evolutionary progression is far from direct and simple, as some might believe to be the case; it is a trail with many twists and turns. Nor is there the slightest reason to attempt a teleological interpretation; there is no trace of design and direction toward an obvious goal. Quite in contrast, it seems clear in many stages of the series that the changes which have taken place are immediately beneficial ones, strongly subject to selection. Obvious, too, is the fact that special environmental factors, biological and physical, have added unexpected quirks to the story. The development of a motile "tadpole" larva at an early chordate stage led to a sharp shift in an evolutionary sequence which otherwise might have simply ended in a sedate filtering form of tunicate type. The development of plant life on the continents opened up to motile chordates a new environment into which few invertebrates could enter and in which the chordates flourished to progress to the vertebrate level. The need for armor as defense against eurypterid enemies appears to have initiated the development of bony skeletal structures, without which the higher vertebrates could never have developed. The widespread late Paleozoic condition of seasonal drought favored progressive developments which, with the attainment of a reptilian stage, had the happy accidental result of the vertebrate conquest of the land, a conquest aided by the emergence of the insects as a basic food supply. The long period of dinosaur dominance seems to have been responsible for the sharpened wits which made the mammalian descendants of the therapsids competent for terrestrial dominance when the reign of the ruling reptiles ended. The arboreal life of primates was finally abandoned by man, but tree-dwelling had endowed his ancestors with advances in brain, eyes, and hands that were highly advantageous when this relatively feeble creature descended to the ground. It has been a long and tortuous journey; but every stage of it shows its effects in the structures and functions of such an end product as ourselves (Fig. 4).

References

1. L. du Noüy, *Human Destiny* (New American Library, New York, 1947).
2. An excellent account of prevertebrates is given by C. Dawydoff [in *Traité de Zoologie XI*, P.-P. Grassé, Ed. (1948), p. 367].
3. W. Garstang, *Quart. J. Microscop. Sci.* **72**, 51 (1928); J. Z. Young, *The Life of Vertebrates* (Oxford, 1950), chap. 3.
4. E. A. Stensiö, *Skr. Svalbard Nordishavet* No. 12 (1927); *The Cephalaspids of Great Britain* (British Museum of Natural History, London, 1932).
5. A. S. Romer, *Amer. Midland Natur.* **16**, 805 (1935); *Deep-Sea Research* **3** (suppl.), 261 (1955).
6. H. W. Smith, *Quart. Rev. Biol.* **7**, 1 (1932).
7. For example, R. H. Denison, *Fieldiana Geol.* **11**, 359 (1956); J. D. Robertson, *Biol. Rev.* **32**, 156 (1957).
8. A. S. Romer, *Science* **78**, 114 (1933).
9. ———, *Amer. Natur.* **76**, 394 (1942).
10. ———, in *Bone Dynamics*, H. M. Frost, Ed. (Little, Brown, Boston, 1964), p. 13.
11. ———, *Bull. Mus. Comp. Zool.* **99**, 1 (1947).
12. ———, *ibid.* **131**, 129 (1964).
13. T. S. Parsons and E. E. Williams, *Quart. Rev. Biol.* **38**, 26 (1963).
14. A. S. Romer, *Amer. J. Sci.* **248**, 628 (1950); D. Baird, *Amer. Zool.* **5**, 287 (1965).
15. J. Barrell, *J. Geol.* **16**, 159, 255, 363 (1908); *Bull. Geol. Soc. Amer.* **23**, 377 (1912).
16. A. S. Romer, *Proc. Amer. Philos. Soc.* **100**, 157 (1956).
17. R. L. Carroll, *J. Linn. Soc. London Zool.* **45**, 61 (1964); D. Baird and R. L. Carroll, *Science* **157**, 56 (1967).
18. A. S. Romer, *Sci. Mon.* **55**, 57 (1957).
19. ——— and L. I. Price, *Geol. Soc. Amer. Spec. Papers 28*, (1940); A. S. Romer, in *International Colloquium on the Evolution of Mammals*, (Brussels, 1961), vol. 1, p. 9.
20. Summarized by G. G. Simpson, in *International Colloquium on the Evolution of Mammals* (Brussels, 1961), vol. 1, p. 57.
21. G. Elliot Smith, *The Evolution of Man* (Oxford, 1927); W. E. LeGros Clark, *The Antecedents of Man: an Introduction to the Evolution of the Primates* (Chicago, 1960).
22. E. L. Simons, *Amer. Mus. Novitates* No. 1976 (1959); *ibid.* No. 2051 (1961); *Postilla* No. 64 (Yale Peabody Museum, 1964).
23. See, for example, G. Heberer, *Die Evolution der Organismen* (Gustav Fischer Verlag, Stuttgart, ed. 2, 1959), pp. 1110–1142.
24. An excellent review of this and later stages in the human story is by W. E. LeGros Clark [*The Fossil Evidence for Human Evolution* (Univ. of Chicago Press, ed. 2, 1964)].