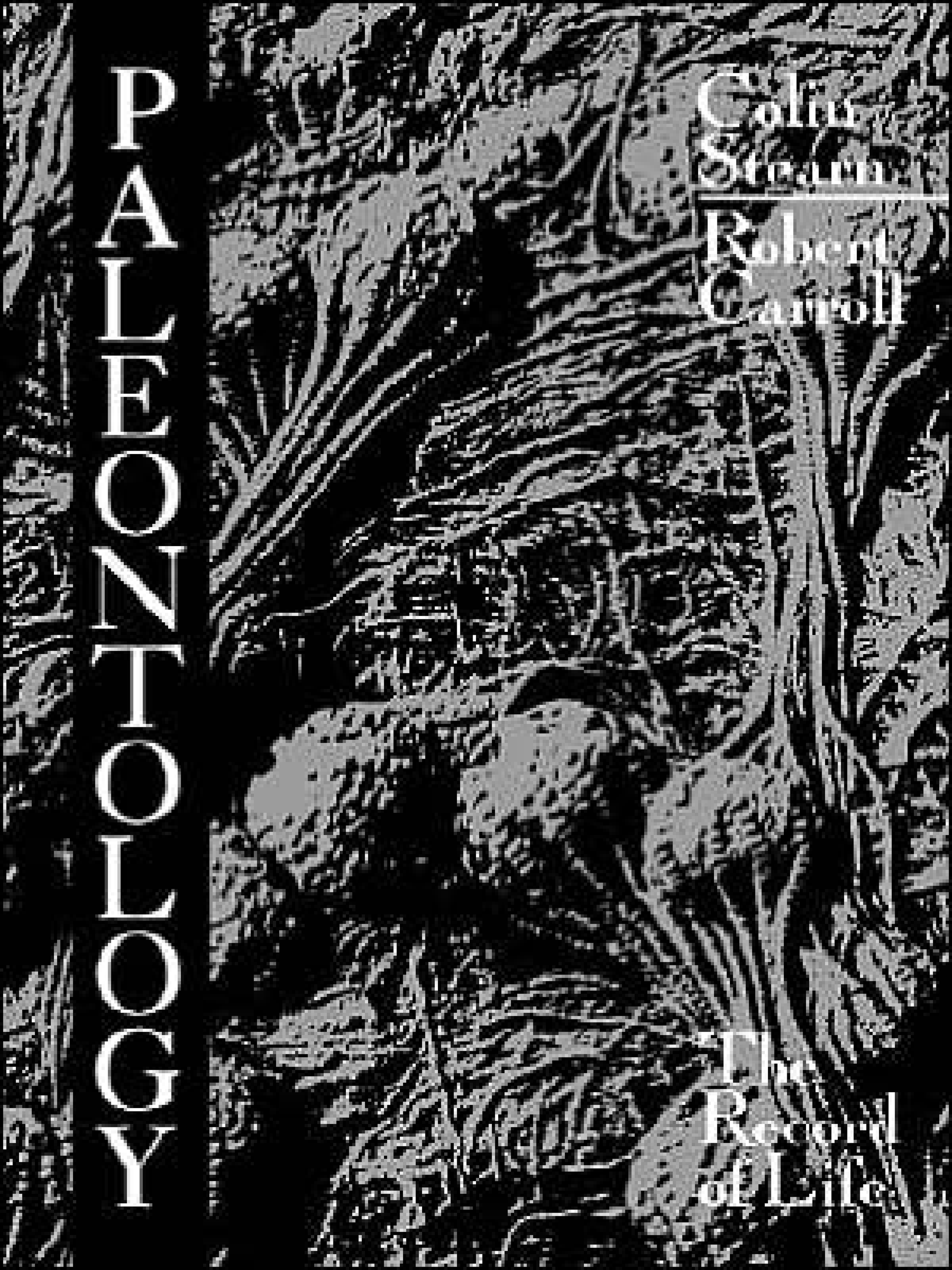
PALEONTOLOGY



Colin Stream

Robert Carroll

The Record of Life

Paleontology:
The Record Of Life

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To a pioneer in the study of the
record of life in Canada.

SIR WILLIAM DAWSON
(1820–1899)

Preface

This book is designed as a textbook for a first course in paleontology. Many students in such classes are geology majors, but majors in biology and other sciences also attend the courses we teach. We have written the book for a typical student of an elementary paleontology course who has a general science education up to the college level but little knowledge of geology and a high school preparation in biology. A short chapter on the geological time scale is included for students with no preparation in earth sciences. To make the text attractive to a wide range of students, we have not stressed classification and used as few technical terms as possible in describing the parts of organisms. We believe it is more important for the student to know how the organism lived than the names of its parts.

This book differs from most textbooks at this level in several important respects. First, it includes both descriptions of the organisms and their distribution in earth history and also extensive discussions of the principles of paleontology deduced from the fossil record. The descriptions of fossil animals and plants are presented first so that knowledge of the organisms can be applied to an understanding of the principles, which are given in the third part of the book, Lessons from the Record.

Second, the book integrates studies of invertebrates, vertebrates, and plants. The practice of dividing these aspects of paleontology into separate courses and teaching only invertebrate paleontology to geology majors, followed in many curricula, is unfortunate because the student needs to appreciate the interdependence and interaction of the various types of life in earth history. For example, no discussion of reefs can be complete without considering the role of algae, nor can any investigation of vertebrate evolution be complete without a knowledge of the plants that shaped the environment in which the animals evolved.

Third, we have emphasized the history of life by arranging the chapters in historical order rather than strictly taxonomically. This allows us to place chapters on Archean and Proterozoic life and the origin of the metazoans in a logical position. It also allows for discussions in the appropriate order of major events in the history of life, such as its origin, the evolution of skeletons, and times of adaptive radiations and extinctions.

Fourth, we have emphasized a biological approach to paleontology, for it is in this direction that we believe the science is moving. Information from fossil and living species is integrated to provide a unified view of the history of life. The interaction of extinct organisms with their environments, as reflected in

the sediments in which they are preserved, is emphasized not only in the chapter on paleoecology but also throughout the book. Paleontology has long been studied within the geological sciences, but biologists too need to study paleontology, for species that happen to be extinct may be of as much importance to a biologist as species that happen to be alive.

In the first part of the book we introduce the methodology of phylogenetic systematics as a means of determining relationships between modern and extinct groups. We discuss current controversies in evolution in three chapters in the third section. The influence of continental motions on paleobiogeography is discussed in Chapter 18. Because many geologists see more fossils in thin sections of limestones than in the field, a chapter on fossils as builders of rocks is included. The rapidly developing field of trace fossil study is surveyed in the last chapter.

The complete text can be used for a full-year course in paleontology, or chapters can be selected for semester or quarter courses. Although the teacher may choose to use only certain chapters as a direct supplement to lecture material, other chapters covering the larger spectrum of paleontology can be used for additional readings or reference. Teachers who do not wish to follow the emphasis on earth history in their lectures can select chapters in the book that are appropriate to a more taxonomically based approach.

The fossil drawings have been specially and carefully prepared for this book by Linda Sapienza, under our immediate supervision. We are grateful not only for her artistic talents but also for the enthusiasm with which she worked with both of us. Other illustrations have been supplied by our colleagues, museums, and other institutes, without whose contributions we could not have produced this book. The contributions of all these are acknowledged in the captions.

During the preparation of the book we have been helped by the advice and critical reading of the chapters by many fellow paleontologists. Without in any way holding them responsible for the final result, we would like to thank specifically the following: Carlton Brett, Thomas Bolton, Murray Copeland, Brian Chatterton, Owen Dixon, Felix Gradstein, Roger Hewitt, Hans Hofmann, Andrew Knoll, Alfred Lenz, Pierre Lesperance, Kenneth McNamarra, Alfonso Mucci, Guy Narbonne, Godfrey Nowlan, John Pojeta, Henry Reiswig, June Ross, and Gerd Westermann. In the preparation of a wide-ranging work such as this one, we have been impressed by the willingness of colleagues to share their time and knowledge. Without such sharing by the scientific community, textbooks could not be written.

Montreal
December 1988

Colin W. Stearn
Robert L. Carroll

Contents

Preface *vii*

PART ONE: INTRODUCTION *1*

1. Fossils 3
2. Time 14
3. Names, Relationships, and Classifications 21

PART TWO: THE FOSSIL RECORD *37*

4. The Time of Microscopic Life 39
5. Origin and Diversification of the Metazoa 54
6. The Invertebrates Dominate the Seas: Acoelomates and Lophophorates 75
7. The Invertebrates Dominate the Seas II: Schizocoelomates and Enterocoelomates 116
8. Land Plants and Their Ancestors 169
9. Paleozoic Vertebrates 184
10. The Second Wave: Invertebrates of the Mesozoic and Cenozoic Eras 213
11. Evolution of Vertebrates During the Mesozoic 243
12. Cenozoic Vertebrates 277

PART THREE: LESSONS FROM THE RECORD *315*

13. Biostratigraphy 317
14. Adaptation and Functional Morphology 327
15. The Mechanisms of Evolution 340

16. Evolution in Earth History 362
17. Paleoecology 374
18. Paleobiogeography 402
19. Fossils as Builders of Sedimentary Rocks 410
20. Paleoichnology: The Study of Trace Fossils 422

Index 433

PART ONE

INTRODUCTION

Chapter 1

Fossils

INTRODUCTION

Scientists recognize more than 3 million different kinds of plants, animals, and microorganisms in the modern biota, but these organisms are only the most recent products of almost 4 billion years of evolution. An immensely greater variety of plants and animals lived in the past but are now extinct and recorded only by their fossil remains. The study of modern plants and animals convinced Darwin that all shared a common ancestry and were the products of a long period of evolutionary history. The history of life can be established only through a study of the fossil record. Fossils document the emergence of humans from apelike predecessors and the changes in plants and animals from their origin in the seas to their emergence into terrestrial environments.

The scientific study of fossil remains is paleontology. This book is an introduction to that study. It provides an outline of the history of life and discusses methods used in the study of fossils and the interpretation of fossils as the remains of formerly living organisms.

WHAT IS A FOSSIL?

Definition:

In the Middle Ages the word *fossil* applied to any specimen dug from the ground and included minerals and rocks. By the eighteenth century the word was used only for shells, bones, and other evidence of dead organisms found in rocks. The objects we now recognize as fossils are all remains of organisms that lived in the distant past and have been buried and preserved in sediments and sedimentary rocks. Fossils may be the whole organism or parts of it, impressions of the organism made as trails or footprints, and artifacts made by animals, such as excreta, burrows, and nests.

Although fossils are usually considered to be of prehistoric age, no strict lower limit to their age is recognized. However, studies of prehistoric human artifacts, such as arrowheads, are made by archeologists and those of the bones of ancient humans, by anthopologists.

Occurrence:

Geologists recognize three classes of rocks:

(1) Igneous rocks have cooled from a melted, or molten, condition. An example is lava.
(2) Sedimentary rocks consist of the products of the mechanical breakup and dissolution of other rocks when they are attacked by agents of weathering, such as rain, frost, wind, and ice. These products—mud, sand, gravel, and materials in solution—are carried by streams to lakes and the sea where they are deposited as shale, sandstone, and conglomerate or precipitated as limestone and evaporites.
(3) Metamorphic rocks are igneous and sedimentary rocks that have been changed in structure, texture, and composition by heat, pressure, chemically active fluids and gases, and stresses deep in the earth's crust.

Most sedimentary rocks contain fossils; those deposited in ancient shallow seas are rich in them (Fig. 1–1). Igneous rocks almost never contain fossils. Only rarely was an animal caught in a lava flow or overwhelmed by a fall of volcanic ash as were the inhabitants of Pompei in A.D. 79. Fossils may survive the drastic changes in texture that take place in the formation of metamorphic rocks, but these changes are often so intense that the fine structures are obscured and the fossils yield little information to the paleontologist.

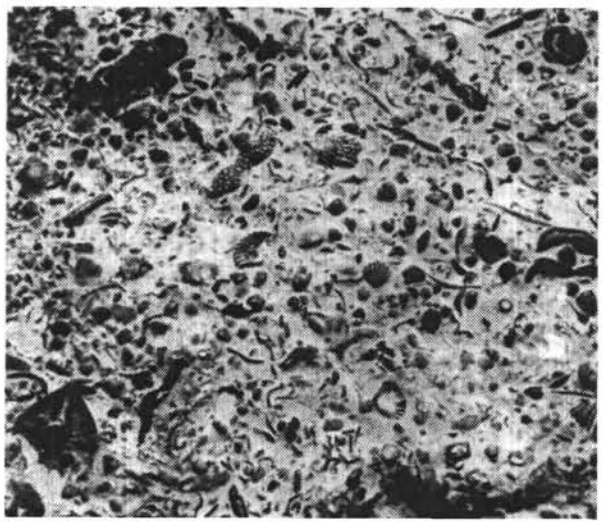

Figure 1-1 Fossils of marine invertebrates on the bedding surface of a limestone of Middle Silurian age. (Courtesy of Redpath Museum, McGill University.)

WHY STUDY FOSSILS?

People are curious about the history of the human race, the environment in which they live, and the animals and plants that share it. Fossils are an element of the natural world that require explanation. To understand ourselves we must know where we have come from and how we are related to other living things.

Evolution:

The chain that connects organisms to one another through the ages of earth history is referred to as evolution. Some of the processes of evolution have been discovered through the comparative study of living organisms, and some can be tested in the laboratory. Scientists disagree on the extent to which mechanisms of evolution are revealed by the fossil record, but all agree that the course of evolution can be followed only through a study of fossils. Without a knowledge of fossils we would be unaware of the many species of extinct animals and plants that formed the links in the evolutionary chain.

Geochemistry:

Without knowledge of the history of life we cannot understand many processes that have taken place on the surface of the earth. Since almost the beginning of geological time, life processes such as respiration, photosynthesis, and secretion of skeletons have influenced the conditions on this planet. Life has controlled the chemistry of the oceans and atmosphere for the last 3.5 billion years. For example, calcium and carbon have been removed by many different organisms and oxygen has been added by the photosynthesis of plants. Changes in ocean chemistry, probably caused by microorganisms, resulted in the precipitation of uranium and iron ores during one interval of geological time about 2 billion years ago.

Dating Rocks:

Because life has changed with time, and the major features and many of the details of this change are

now known, paleontologists can determine the relative age of most fossils with great precision. Many paleontologists, particularly those hired by oil companies and government services, are involved in this branch of paleontology, which is called biostratigraphy.

Environmental Reconstruction:

One of the principal objectives of geologists studying sedimentary rocks is the reconstruction of the environment in which the rocks were deposited. Correct reconstruction may result in the discovery of oilfields, deposits of salts, or base metals. As evidence of ancient environments the geologist has the structures, textures, and composition of the grains that make up sediments, and the fossils preserved in them. Organisms are far more sensitive to, and therefore diagnostic of, the environment in which they live than are the grains of sediment to the environment in which they were deposited. A study of the way of life and environmental requirements of organisms that became fossils therefore yields the most accurate information about the environment in which sediments were formed.

Paleogeography:

Reconstruction of the position of continents and oceans in the geological past is aided by a knowledge of fossil distribution. At present the distribution of animals and plants, both terrestrial and marine, is influenced by the pathways available for them to spread, and these pathways are dependant on the positions of land, sea, mountains, and lowlands—in other words, on the geography of the earth. In the past the earth's geography was different. Not only were the outlines of the continents unlike those of today, but the continents themselves were in different places on the globe. Many disciplines of the earth sciences contribute to the reconstruction of the geography of the past (paleogeography). Discontinuities in the distribution of modern organisms and fossils were among the first evidence that led geologists to suspect that continents in the past were in different positions from that of the present day.

Paleontology is the study of animals and plants that have lived in the past and their distribution in time and space. The information supplied by paleontological studies is essential to the understanding of earth history, evolution, paleogeography, and sedimentation. All these topics are examined in greater detail in subsequent chapters.

HISTORY OF PALEONTOLOGY

Neanderthals placed fossils around their dead in burials, perhaps attributing to them a magic that would conquer death. These primitive people could hardly have been able to appreciate the symbolism inherent in fossils which, though dead, have achieved the immortality of preservation in stone. The true significance of the strangely shaped stones that fascinated cave dwellers was not generally appreciated for tens of thousands of years after these burial ceremonies.

Fossils are sufficiently abundant that they must have caused our distant ancestors to wonder how rocks could take regular forms resembling living animals and plants. The first to record their speculations were Greek philosophers. The oldest recorded statement that fossils are remains of once-living animals that have been entombed in rocks was made by Xanthos of Sardis in about 500 B.C. Aristotle (born 384 B.C.), who passed down the most comprehensive account of Greek science, suggested that fossils of fish were remnants of sea animals that swam into cracks in rocks and were stranded there. These early speculations were neither added to, nor improved upon, for the next 2000 years, during which Roman civilization succeeded the Greek and itself passed into the intellectual night of the Dark Ages.

During the Middle Ages and the Renaissance, fossils were illustrated and described as figured stones by learned doctors and clerics (1). The origin of these stones was a matter of dispute. Some ascribed them to the working of an arcane force within the earth (*vis plastica*), others to the works of the devil, and still others thought they had fallen from the sky as thunderbolts during storms or as falling stars. The starlike form of the plates of fossil crinoids (see Chapter 7) and the radial patterns on fossil corals suggested the sky as their source, and these objects were called "star stones" (*Lapis stellaris* or *Astroites stellis*) (Fig. 1–2). By the middle of the eighteenth century, the similarity of fossils to living organisms had convinced many naturalists that figured stones were the remnants of animals and plants that had somehow been preserved in rocks. The more perceptive understood that the sea must have once covered large areas of the continents in order for

Figure 1-2 "Figured Stones" from the "Historia Lapidum Figuratorium Helvetiae" published in Venice, 1708. (*Source:* F. D. Adams, *Birth and Development of the Geological Sciences.*)

marine organisms to have been deposited as far inland as some fossils were found. Most attributed them to animals destroyed in the Biblical flood—a view still held by some fundamentalist Christians. The flood theory would not stand up to the evidence brought forward by paleontologists of the late eighteenth and early nineteenth centuries that the succession of sedimentary rocks reveals a progression of life forms and could not be the result of a single catastrophe. By the beginning of the nineteenth century the figured stones controversy was over, and knowledgeable naturalists agreed that fossils were remnants of organisms that lived in the distant past. By the middle of the century the groundwork had been laid for the recognition of fossils as evidence of evolution.

HOW ARE FOSSILS FORMED?

Some organisms are composed entirely of soft, unstable, organic compounds—largely of carbon, hydrogen and oxygen—but many have bodies reinforced with stable, hard compounds—commonly of calcium carbonate or calcium phosphate—that constitute a shell or skeleton. Paleontologists speak of unstable organic compounds as "soft parts" and shells and skeletons as "hard parts".

Life may be considered as the sum of the processes by which organisms keep inherently unstable carbon compounds together. When life ends, bacteria from within and without break down these complex compounds into simpler molecules, and eventually into stable compounds such as water, carbon dioxide, and methane. When these processes have been completed, no trace of the original soft parts of the organism remains. A visit to any marine or terrestrial environment in which organisms are abundant will illustrate the efficiency of decaying agents. Although organisms in such places are dying by the hundreds each day, no accumulation of their soft parts remains for more than a few days and usually no permanent accumulation of organic matter takes place. Living organisms build organic molecules from soils, gases, and water, and these molecules find their way back into the environment when the organisms that synthesized them decompose directly, or when the organisms feed a predator or scavenger, which in turn dies and decays. An organism composed entirely of soft parts can be preserved to enter the fossil record only if it is removed rapidly from predators, scavengers, and decayers.

Fortunately for the paleontologist, many marine organisms secrete shells of calcium carbonate, and many marine and terrestrial animals secrete skeletons of calcium phosphate. These are relatively resistant to postmortem destruction and are capable of survival while the soft parts of the organism decay. Almost the whole of the paleontological record consists of such hard parts that have persisted through millions of years, either in the state that they were secreted, or altered in various ways to be described.

Despite the relative resistance of these shells and bones to bacterial decay and their lack of appeal to predators and scavengers, only a small proportion of such hard parts formed by organisms are entombed in sediments to become part of the fossil

record. On the seashore where wave motion moves shells against each other and against mineral grains in the sand, abrasion reduces hard parts first to sandsized particles and then to mud. Other shells disintegrate into a muddy residue when the organic matrix that binds their crystals decays. Many marine organisms, including sponges, barnacles, gastropods, sea urchins, and a variety of "worms," bore into or abrade the surfaces of hard parts, reducing them eventually to unrecognizable particles. This process is called bioerosion and it may be so effective in tropical environments that it prevents any permanent accumulation of hard parts, even where animals that secrete shells and form skeletons thrive. In terrestrial environments many animals attack bones and horns left by dying animals. Although several groups of mammals, such as deer, moose, elk, and caribou, grow and discard large sets of antlers each year, complete sets can only rarely be found in forests where these animals live. The antlers are rapidly eaten by rodents and other small animals and bacteria infect them so that there is no permanent accumulation.

In order for hard parts to enter the permanent record, they must be protected from these destructive processes by being covered rapidly with sediment. Recycling of both soft and hard parts is the normal condition in most environments; removal of the remains from the recycling agents, enabling them to be preserved in the fossil record, is an exceptional event.

METHODS OF PRESERVATION

Unaltered Remains:

Few organisms are entombed and persist to the present day essentially complete with little change of form or composition. Ice Age mammoths found frozen in the tundra of North America and Siberia are so little changed that their flesh has been reported still palatable to wild animals, and their last meals remain undigested in their stomachs. A specimen of an Ice Age rhinoceros was preserved intact in a Polish oil seep because the petroleum penetrating the flesh had retarded bacterial decay. These are exceptionally rare specimens which are not representative of normal conditions of preservation.

After the soft parts decay, the hard parts of many organisms can be preserved essentially unaltered in sedimentary rocks. The shells of many marine organisms, once they have been entombed in sediments, are relatively stable. Some fossil shells formed millions of years ago cannot be distinguished from modern shells.

Permineralization:

Most shells and skeletons are not solid but contain canals and pores. The bones of land animals are generally highly porous, particularly in the central regions where marrow fills the voids when the animal is alive. When the soft parts decay and these porous materials are buried in sediments, the pores are filled with water that contains dissolved minerals. These waters precipitate calcium carbonate and silica in the pores of shells or bones, reinforcing and solidifying them. Almost all older fossils are subject to this process, which is called permineralization. Coniferous logs in the Petrified Forest of Arizona have been preserved through the infiltration of silica into the cellular structure of the wood, with so little disturbance that the microstructure appears to be that of a living tree. Yet these trees are millions of years old (Fig. 1–3).

Recrystallization:

After a shell has been covered with sediment and possibly also infiltrated with mineral matter, the crystals that were secreted to form the shell may be changed in form and size without changing in composition. In calcium carbonate shells, the original minute crystals often increase in size until the texture of the shell is a coarse calcite mosaic. The forms of the shell may remain faithfully defined, but the microstructure secreted by the organism has been destroyed. Such fossils are said to be recrystallized.

Replacement:

The water seeping through sedimentary rocks that contain fossil bones and shells may dissolve some of the hard parts and at the same time replace them with minerals that it carries in solution. The effect is to substitute another material for the original hard parts without changing the form of the shell or bone. Paleontologists cannot duplicate these processes, nor do they fully understand them, but the fossil record leaves no doubt that they occur. Commonly the replacing mineral is silica in its fine,

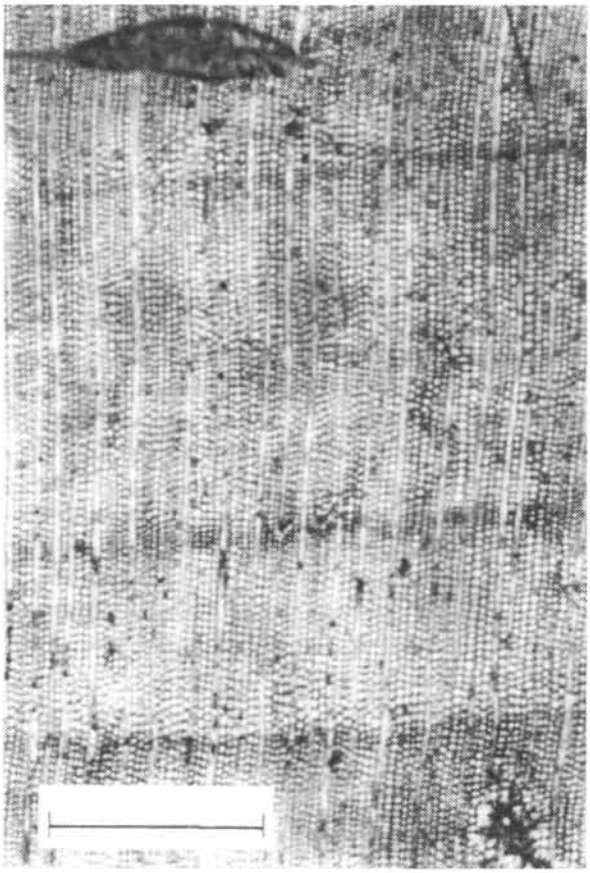

Figure 1-3 A thin section of silicified wood, showing the preservation of the cellular structure and the growth rings. Scale bar is 1 mm long. Locality unknown. (Courtesy of C. W. Stearn and Redpath Museum, McGill University.)

crystalline form of the mineral chalcedony. Where silica has replaced fossils in limestones, the silicified fossils can be separated by dissolving the surrounding carbonate rock in dilute hydrochloric or acetic acid (Fig. 1–4). Delicate spines and fine structures on fossil shells, which would be broken off were the shells cracked out of the rock with the geologist's hammer, have been revealed by dissolving silicified fossils from the rock around them.

Many different minerals can replace fossils. In shales, shells are commonly replaced by the brass-colored mineral pyrite, to produce attractive specimens (Fig. 1–5). Pyrite is an iron sulfide mineral. Delicate structures of organisms replaced by pyrite have been preserved in the Hunsrück Slate in western Germany (Fig. 1–6) and may be revealed by passing X-rays through thin slabs of the slate. Iron

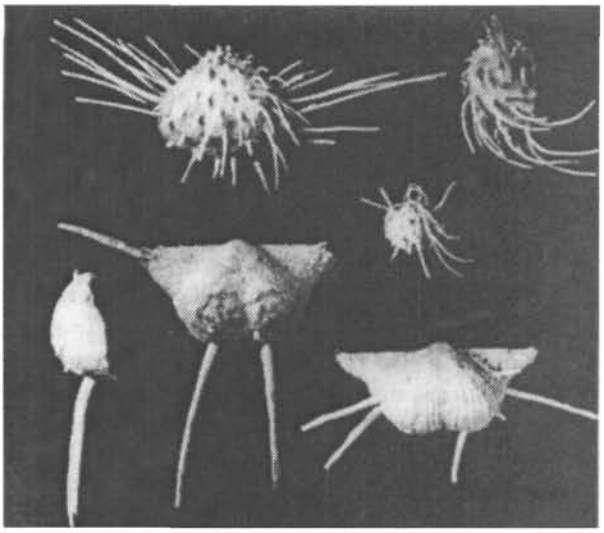

Figure 1-4 Silicified spiny brachiopods dissolved from Permian limestone. Permian of Texas. (Courtesy of G. A. Cooper and the Smithsonian Institution.)

oxide in the form of the mineral hematite may also replace fossils. Under rare conditions, both the soft parts and hard parts of animals may be replaced by calcium phosphates (Fig. 1–7). About twenty different minerals are known to have replaced fossils.

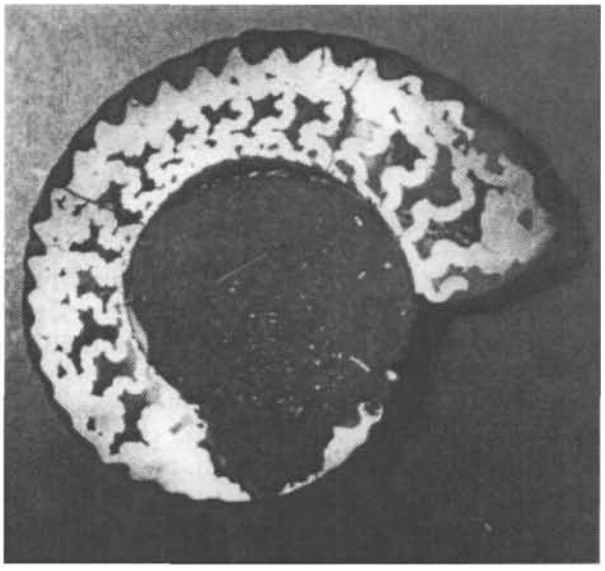

Figure 1-5 Polished cross section of a Jurassic ammonite whose outer whorl is replaced by pyrite and whose inner whorls are not preserved. (Courtesy of C. W. Stearn and Redpath Museum, McGill University.)

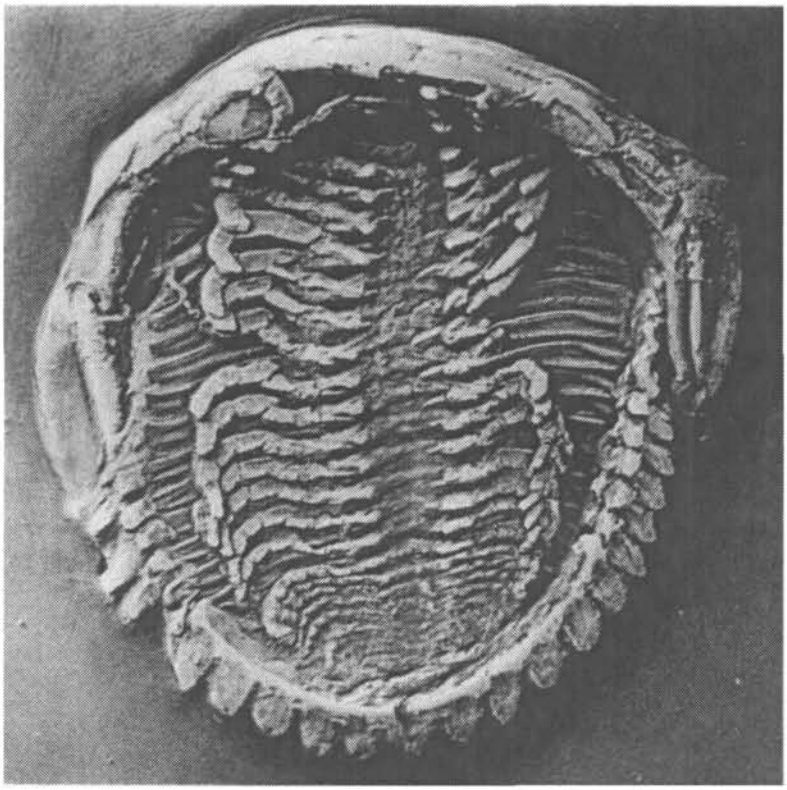

Figure 1-6 The ventral side of the Early Devonian trilobite *Rhenops* from the Hunsrück Slate, Germany. The skeleton has been replaced by pyrite, which has preserved the appendages, that are usually not preserved in unpyritized fossils. The specimen is about 3 cm across. (Courtesy of Jan Bergstrom and *Lethaia*, v. 17, p. 68.)

Molds and Casts:

Instead of replacing a fossil shell, water passing through the sediment may dissolve it completely. If the sediment packed around the shell has consolidated into rock before the shell is dissolved, a void will be formed. The walls of the void may preserve an impression of the face of the shell, which can be examined when the void is broken open (Fig. 1–8). These impressions are called molds. Their relief is opposite to that of the shell itself; knobs on the shell are represented by depressions and vice versa. If conditions change and the water deposits minerals into the void where a shell has been dissolved, the mold may be filled. The mineral deposit will take from the mold the external form of the fossil it has inherited but will have none of its internal structure. It is not a replacement of the shell but a cast that duplicates the shell after the original has been destroyed. The cast is a replica of the dissolved fossil. The mold is a negative impression of its surfaces.

Carbonization:

Plants are commonly preserved as thin films of carbon pressed on to bedding planes of sandstones and shales (Fig. 1–9). When a plant dies and is covered with sediment, the volatile constituents of the various carbohydrates of which it is composed disperse leaving a residue of coallike carbon—a black film which preserves the form of the fruit, leaves, or stem. The soft parts of marine animals have also been preserved in this way. Such preservation of soft parts rarely takes place, but when it does it is usually in environments where bacterial decay is inhibited by lack of oxygen. These environments are represented by black shales in the stratigraphic record.

Tracks and Trails:

Animals crossing the surface of sediment may leave behind footprints or impressions of parts of their body that are preserved when the sediment hardens

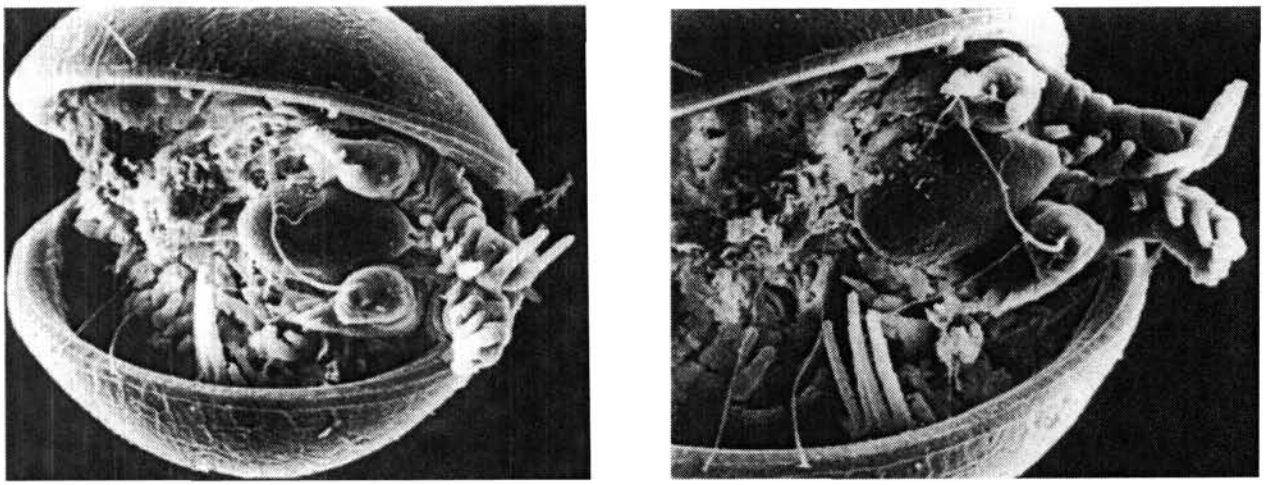

Figure 1-7 Late Cambrian ostracode, *Falites*, in which the soft parts have been preserved by replacement with phosphate. Four pairs of appendages and remains of the egg cases can be seen within the bivalved shell. Scanning electron micrograph. The specimen is about 0.16 mm across. (Courtesy of K. J. Muller and *Lethaia*, v. 12, p. 25.)

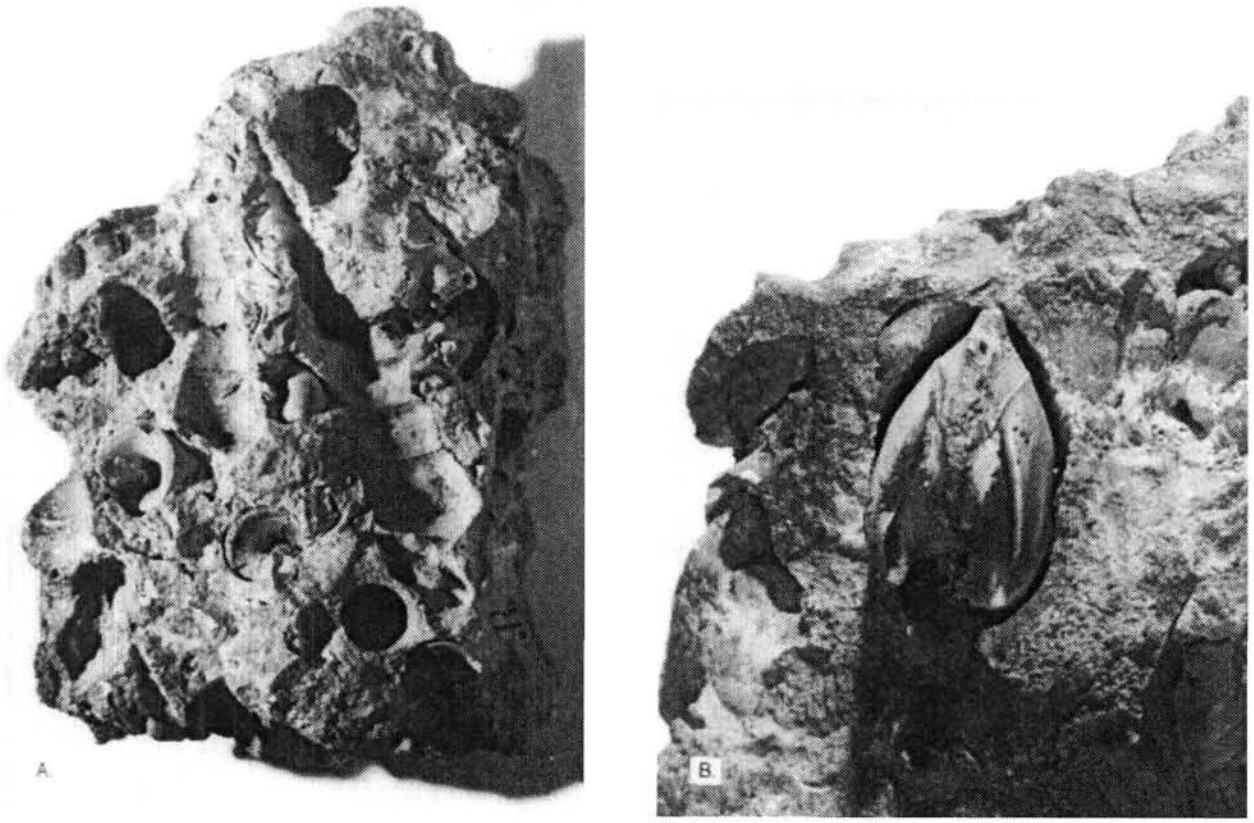

Figure 1-8 Preservation of fossils as molds. A. Gastropods in a Cenozoic sandstone. The long specimen is a mold of the exterior. In some specimens the interior of the shell has been filled with sand to produce a mold of the interior. B. Mold of the interior of a bivalve. Sediment has filled the space between the two valves producing a mold of their inner surfaces, and the shell has then been dissolved, leaving only the dark space around the internal mold. (Courtesy of Redpath Museum, McGill University.)

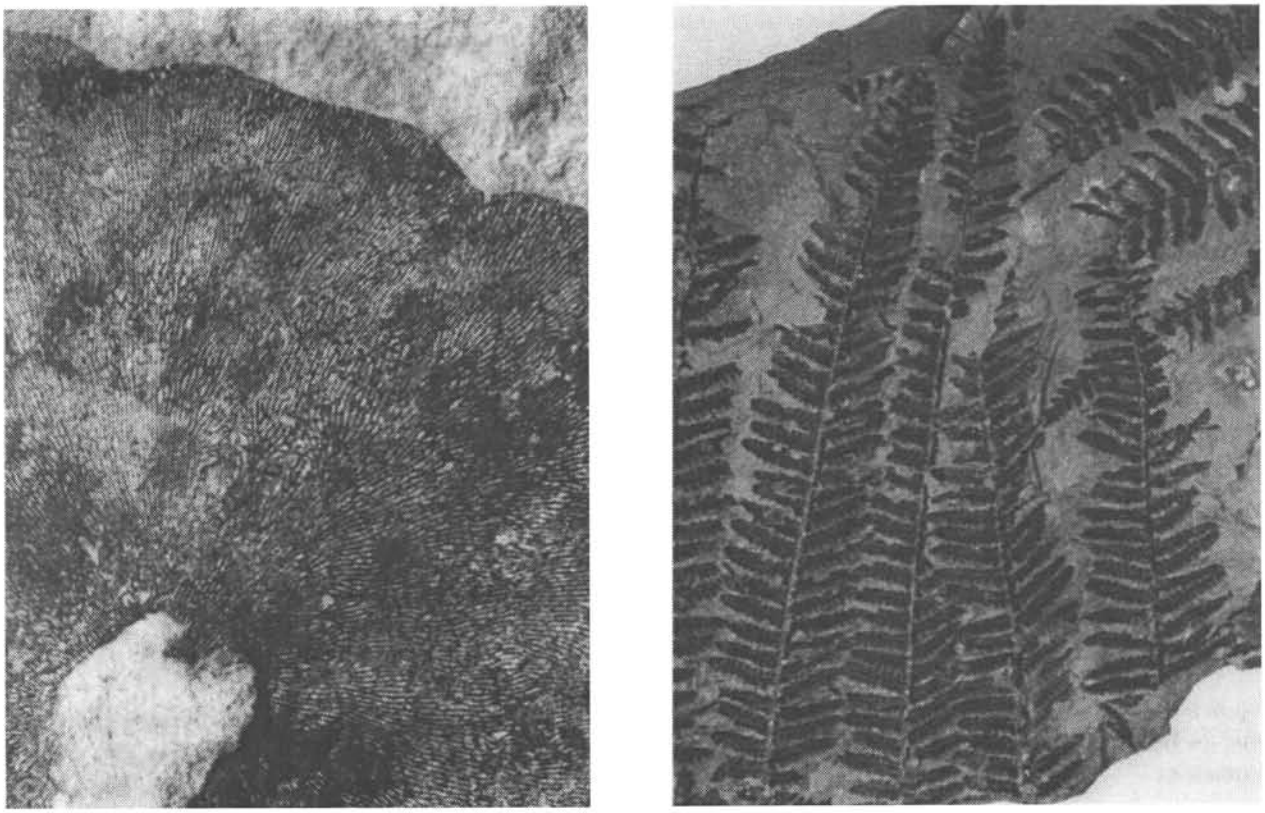

Figure 1-9 Preservation by carbonization. A. Dendroid graptolite *Rhabdinopora* from Silurian dolomite. B. Fernlike leaves of the Carboniferous plant *Pecopteris*. Both shown about natural size. (Courtesy of Redpath Museum, McGill University.)

to rock (Fig. 1–10). Animals living or feeding in soils or sediment leave behind burrows and tunnel systems that may become part of the fossil record. These types of fossils are called ichnofossils or trace fossils.

These seven ways in which fossils are preserved—unchanged, permineralized, recrystallized, replaced, carbonized, as molds and casts, and as ichnofossils—are those that the paleontologist is likely to encounter. Other mechanisms for preservation are confined to particular times and places and are considered in appropriate places in the following chapters.

BIASES OF THE FOSSIL RECORD

Soft-Bodied Organisms:

The variety of barriers to entry into the fossil record discussed in this chapter suggest that the chances of preservation for an individual are extremely small and that all organisms do not have an equal chance. The soft parts of animals and plants, and whole organisms composed completely of soft organic matter, cannot be preserved unless some unusual condition inhibits bacterial decay. As a result, large groups of living invertebrate animals that do not secrete hard parts are unrepresented, or scarcely represented, in the fossil record. Jellyfish are examples of marine organisms that are abundant at present but have a poor fossil record. We know from impressions of their surfaces that they existed half a billion years ago, and we suspect that they have been abundant since then without leaving a significant record. Table 1–1 illustrates the direct relation between the paleontological representation of marine invertebrates and the possession of hard parts. All animals with hard parts have a good representation, and those without are poorly represented.

Figure 1-10 Trackway of the Permian amphibian *Laoporus* from the Grand Canyon. (Courtesy of the Smithsonian Institution.)

Sediment Burial:

Animals and plants that do not live in environments where sediments can bury them when they die (out of the reach of scavengers, bioeroders, and agents of decay) are unlikely to become fossils. Land animals and plants living in highlands where erosion rather than deposition is taking place are unlikely to be preserved unless they are washed into lowland swamps and lakes. The fossil record therefore entombs a far larger proportion of land organisms that lived in lowlands than those that lived in hills, high plains, or mountains.

Collection Biases:

Deposits of the past are not equally available to paleontologists for collection of fossils. Most of the marine sediments whose fossils have been studied were laid down in shallow seas that flooded the interiors of continents. Although organisms are assumed to have existed in the abyssal depths of oceans, where sediment accumulates to entomb them, most of these deposits remain at abyssal depths and are difficult to sample except by expensive techniques of deep-sea drilling. As a result our knowledge of shallow marine faunas far exceeds that of abyssal faunas.

TABLE 1-1 Estimates of the total number of living marine invertebrate species described and of the number of these that may be fossilizable because they have hard skeletons.

	Total living species described	Total described species "fossilizable"
Foraminiferida and Radiolaria	20,000	20,000
Porifera (sponges)	2,250	1,750
Cnidaria (largely corals)	9,500	6,200
"Worms"	20,000	1,000
Bryozoa	3,000	3,000
Brachiopoda	225	225
Mollusca	54,300	53,100
Arthropoda	23,000	10,500
Echinodermata	6,000	5,000
Others	2,000	
TOTALS	140,275	100,775

Source: Modified from Valentine.

Our knowledge of the paleontology of Europe and North America is more extensive than that of the southern continents because more scientists live in the northern hemisphere. Therefore, a fossil organism from the south is less likely to come to the attention of paleontolgists than one from the north. Our knowledge of the paleontology of large areas of the earth is limited because they have few outcroppings of sedimentary rocks. Tropical areas beneath rain forests and polar areas beneath ice are examples of such limitations.

Inadequacy or Bias:

Citing these deficiencies, some have claimed that our knowledge of the fossil record can never be adequate to supply a detailed history of life on our planet. The adequacy of the fossil record to supply answers depends on the nature of the questions we ask. The record is effective in solving some problems and is unable to solve others.

Paleontologists prefer to describe the record as biased rather than inadequate. A biased record of events has come to mean one that is slanted by the observer's prejudices. The fossil record is biased against the recovery of soft-bodied organisms, highland organisms, and abyssal organisms, but, if these prejudices are recognized, paleontologists can make corrections for them in order to arrive at a balanced view of the life of the past.

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Chapter 2

Time

Paleontology is an historical science. From fossils paleontologists reconstruct long-dead organisms and the world in which they lived. Unlike chemists, physicists, or biologists, they cannot experiment with the materials they study but, like all scientists, they examine the products of past events and try to reconstruct what happened. Chemists can combine solutions, whose properties are known, repeatedly under controlled conditions in order to understand the product of their reaction. The events that paleontologists study are unique in time. They do not recur under exactly the same conditions in earth history because the earth and its inhabitants have progressed along an irreversible course. Paleontologists observe in the fossil record the interaction of organisms with one another and with the physical environment. Their behavior can be deduced from the behavior of similar living organisms. Although paleontology does not deal with repeatable events, it shares with all sciences the gathering of data, its interpretation according to recurring patterns, and the formulation of general laws or relationships. These describe the manner in which life has changed through the millennia.

Events of the past must be placed in a sequence and calibrated with a time scale if their direction and rates of change are to be assessed. The succession of the beds that contain fossils must be determined, as well as their ages in years. Since the beginning of the twentieth century geologists have developed methods of dating many types of rocks in years.

DATING BY RADIOACTIVE ISOTOPES

Principles:

The regularity of decay of radioactive atoms makes dating of ancient rocks possible. The atoms change to daughter atoms by emission of alpha particles and beta rays, altering the number of protons and neutrons in the nucleus at rates that are unaffected by chemical or physical conditions. Once deposited in a rock, a mineral containing such radioactive atoms continues to accumulate the products of its change (daughter products), regardless of heat, pressure, or its chemical bonding to other atoms. If the rate of change can be measured in the laboratory and the amount of the parent and daughter atoms can be obtained by analysis, a relatively sim-

ple calculation yields the time at which the parent was emplaced and began to accumulate products. Since they came into existence, parent elements have been generating daughter products. The age measured is the time at which the parent, separated from its previously accumulated daughter products, began to accumulate them again in a new environment.

Materials Used in Dating:

The first minerals used to calculate ages were those containing uranium. The element uranium exists in two forms of different atomic weights that are called isotopes. Each of these decays through a series of unstable daughter products to a stable isotope of the element lead. Thorium, which is associated with uranium in most natural deposits, also decays to an isotope of lead different from those produced by uranium isotopes. Determination of the rates of decay, and analysis for parent and daughter products of the two uranium isotopes allow the geologist not only to determine the age of the mineral, but also to correct for loss of accumulated lead that may have taken place.

Elements other than uranium and thorium also have radioactive isotopes and have been used in dating. Potassium–40, an isotope that is widespread in small quantities in the earth's crust, changes into an isotope of calcium and one of argon. The amount of argon accumulated from this transformation is measured. The element rubidium, commonly associated with potassium in minerals, has a radioactive isotope which decays to an isotope of strontium. Several rare earth elements, such as samarium and neodymium, have also been used to measure the age of rocks (Table 2–1).

Rates of Radioactive Decay:

In order to be useful for dating rocks millions of years old, transitions must take place at a rate low enough that even very old rocks retain both parent and daughter isotopes, that is, the decay process must still be continuing. For short-lived isotopes the radioactive decay is completed and the radioactive "clock" "runs down" before a significant interval of geological time has passed. Rates of decay are measured by an interval called the half-life. During the first half-life interval, one-half of the parent atoms change into daughter products; in the next interval, one half of the remaining half, and so on (Fig. 2–1). Most of the half-lives of the commonly used decay series are of the order of billions of years (Table 2–1).

TABLE 2–1 RADIOACTIVE ISOTOPES USED IN DATING ROCKS AND THEIR HALF-LIVES

Parent Element	Atomic Wt. of radioactive isotope	Ultimate daughter element	Atomic Wt. daughter	Half life
Uranium	238	Lead	206	4.5×10^9
Uranium	235	Lead	207	0.7×10^9
Thorium	232	Lead	208	1.4×10^{10}
Rubidium	87	Strontium	87	5.0×10^{10}
Potassium	40	Argon	40	1.3×10^9
Samarium	147	Neodymium	143	1.0×10^{11}

These measurements have shown that the earth is about 4600 million years old; that complex animals first arose about 700 million years ago; that animals possessing skeletons and shells first left their hard parts behind in the sea about 570 million years ago; that dinosaurs walked the earth between 200 and 66 million years ago; and that since then mammals have dominated the fauna of the land. These dates for salient events in life history are representative of the type of information available from

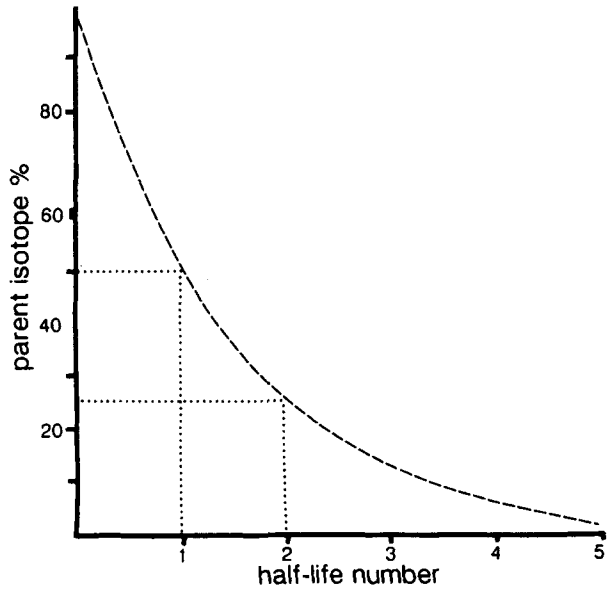

Figure 2-1 Radioactive decay curve to show the significance of the half-life. In one half-life interval, 50 percent of the parent changes into the daughter isotope; in another interval, a further 50 percent of the remainder changes, and so on.

the work of geochronologists, as those who date rocks are called. By dating many thousands of rocks annually, they provide paleontologists with a time scale for the history of life

ROCKS THAT CAN BE DATED

Sedimentary Rocks Are Difficult:

Not all rocks contain minerals that are radioactive. Unfortunately for paleontologists, the sedimentary rocks that contain the record of life rarely contain radioactive minerals suitable for dating. Most sedimentary rocks are the products of the chemical and physical destruction by the atmosphere and organic agencies (weathering) of other rocks. Sands and silts inherit, from the rocks that were weathered, particles containing radioactive minerals and daughter products that they have accumulated. The ages of such grains are the ages of the rocks weathered to produce the sediment, not of the time of deposition of the grains, because the processes producing the grains do not separate parent isotopes from their daughter products. Some sediments, like limestone, are deposited biochemically or chemically from seawater and are ultimately the product of weathering by dissolution. Unlike sedimentary rocks composed of grains weathered from other rocks, their mineral constituents are formed when they are deposited. However, the minerals are not, with one or two exceptions, composed of atoms that have radioactive isotopes. The exceptions, sediments that can be dated by their radioactive isotopes, are some highly organic shales that contain uranium, some sandstones composed of the potassium-rich mineral glauconite, shales in which the strontium isotopic composition has been homogenized during their consolidation, and some evaporites rich in potassium salts.

Most of the rocks that contain radioactive isotopes sufficient for dating are igneous and metamorphic rocks. Igneous rocks cool from a molten liquid in which the radioactive parent atoms are separated from the daughter products that accumulated before the melting. The processes that metamorphose sedimentary and igneous rocks, such as heat, pressure and shearing stress, do not affect the decay of radioactive isotopes, but the disruption of the rock may physically disperse accumulating daughter products. The dispersal of the gas argon resets the clock of the potassium–argon method so that analyses yield the date of metamorphism, not the date of formation for the rock that was metamorphosed.

Using Igneous Rocks to Date Sedimentary Rocks:

The general lack of direct dating methods for sedimentary rocks means that their age must commonly be related to that of igneous rocks. If the extrusion of a submarine lava flow or the fall of ash from a volcanic eruption interrupted the accumulation of sediment in a marine basin, then the sediment below it must be slightly older than the date determined from the flow or ash bed, and the sediment above must be slightly younger. If sedimentation is essentially continuous, the beds above and below can be accurately dated by the flow or ash. In a sedimentary succession interrupted by repeated lava flows, the ages of most of the sedimentary beds can be accurately determined.

More commonly, the age of a sediment must be determined by the relation between igneous rocks that intrude a sedimentary succession and igneous rocks that are overlain unconformably by sedimentary rocks. The relationships are shown in Figure 2–2. Sedimentary rocks that are intruded by an igneous body are older than that body, and those that overlie the eroded surface of an igneous body are younger than that body.

RELATIVE TIME SCALE

Development of the Scale:

By the time geologists had developed methods of dating rocks by radioactivity, they had already outlined the physical and biological history of the earth. This was accomplished without knowledge of the age of the rocks in years.

The first classifications of sedimentary rocks were based on the principle of superposition, which simply states that the oldest of a succession of layers is at the base and the youngest is at the top. In central Europe the lowest rocks that can be seen are metamorphic and igneous rocks that were called Primary in the eighteenth century. Layered sedimentary rocks that were called Secondary overlie these rocks, and over them are poorly consolidated sands and gravels called Tertiary and Quaternary. When additional layers were found that overlie the Pri-

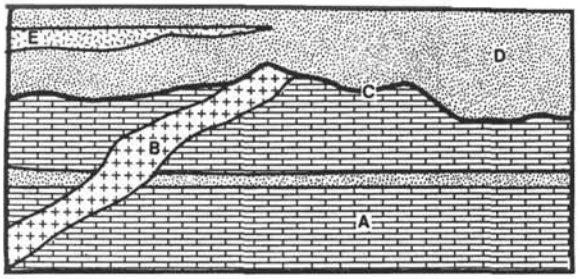

Figure 2-2 Use of igneous rocks that can be dated in years to date sedimentary rocks. The rocks labeled B and E are igneous rocks. Because B intrudes A, it must be younger than A. After the intrusion, A and B were eroded to a surface labeled C. Sediments of D were deposited over C to produce an unconformity. These sediments contain a lava flow, E, that may record the time of their deposition.

mary and are overlain by the Secondary, these were called the Transition. Fossils were found in many of these layers, and by 1825 the names Transition, Secondary, Tertiary and Quaternary were being replaced by terms that refer to life form: Paleozoic, Mesozoic, and Cenozoic (ancient, middle and recent life, respectively). Near the beginning of the nineteenth century William Smith (and, independently, Georges Cuvier and Alexandre Brongniart) discovered that the fossils found in sedimentary layers always occur in the same order so that certain fossils always characterize certain layers. They had discovered that life changed in time, and that these changes are recorded in successive sedimentary layers. Once the succession of fossils was known, isolated fossil-bearing layers, whose positions with respect to other layers were unknown on the basis of superposition, could be determined as either younger or older than other fossil-bearing layers.

As knowledge increased, the first divisions were broken up into smaller units and these units fitted into a continuous succession on the basis of their fossils. The smaller divisions of the Paleozoic, Mesozoic, and Cenozoic were called systems. In Britain the lower part of the Paleozoic was divided into the Cambrian, Ordovician, and Silurian systems, which were based on rocks in Wales and named after ancient tribes that lived there. The upper part of the Paleozoic was divided into the Devonian System, named from the English county; the Carboniferous System, which included and was named after the coal-bearing beds of Britain; and the Permian System, named from a province of Russia. The names of the divisions of the Mesozoic were based on the threefold nature of the lower part in Germany (Triassic), the outcrops in the Jura Mountains between France and Switzerland (Jurassic), and the chalk (Latin, *creta*) beds of the English Channel (Cretaceous).

The divisions of the Cenozoic were first defined on the basis of the percentage of living (as opposed to extinct) molluscan species in the rocks. The Eocene was defined as the sedimentary rocks whose molluscan fauna included 3.5 percent molluscan species that are still alive today; the Miocene as the beds whose molluscs included 17 to 18 percent living forms; and the Pliocene, more than 35 percent. Further subdivisions were added to make the six listed in Figure 2–3, and recognizing divisions by percentage of surviving species was abandoned. These divisions of the Cenozoic are not as large as systems and are called series. The younger four (Miocene, Pliocene, Pleistocene, and Holocene) are recognized as comprising the Neogene System and the older three (Paleocene, Eocene, Oligocene), the Paleogene.

Periods Are Based on Systems:

As the succession of systems was being established in Europe, the names were also applied to sedimentary rocks in other parts of the world. For example, the term Silurian System was used in North America for rocks containing fossils similar to those of the Silurian rocks of Britain; the similarity of fossils demonstrated that the two had been deposited during the same time interval. The names of the systems that originally referred only to local successions of sedimentary layers came also to have time significance. The list of successive systems had become a time scale by which sedimentary successions all over the world could be related. The rocks deposited during the interval of the Silurian System in Wales, and identified as such by their fossils, were then said to be deposited during the Silurian Period. Specific systems are now recognized as the succession of rocks deposited anywhere in the world during a specific interval of geological time (a period), and the periods are defined by the boundaries of the system in the area where they were first described but the boundaries may be extended by information from other areas. Although this definition appears to be circular, it is not, because the areas where the systems were first described are unique standards called type sections.

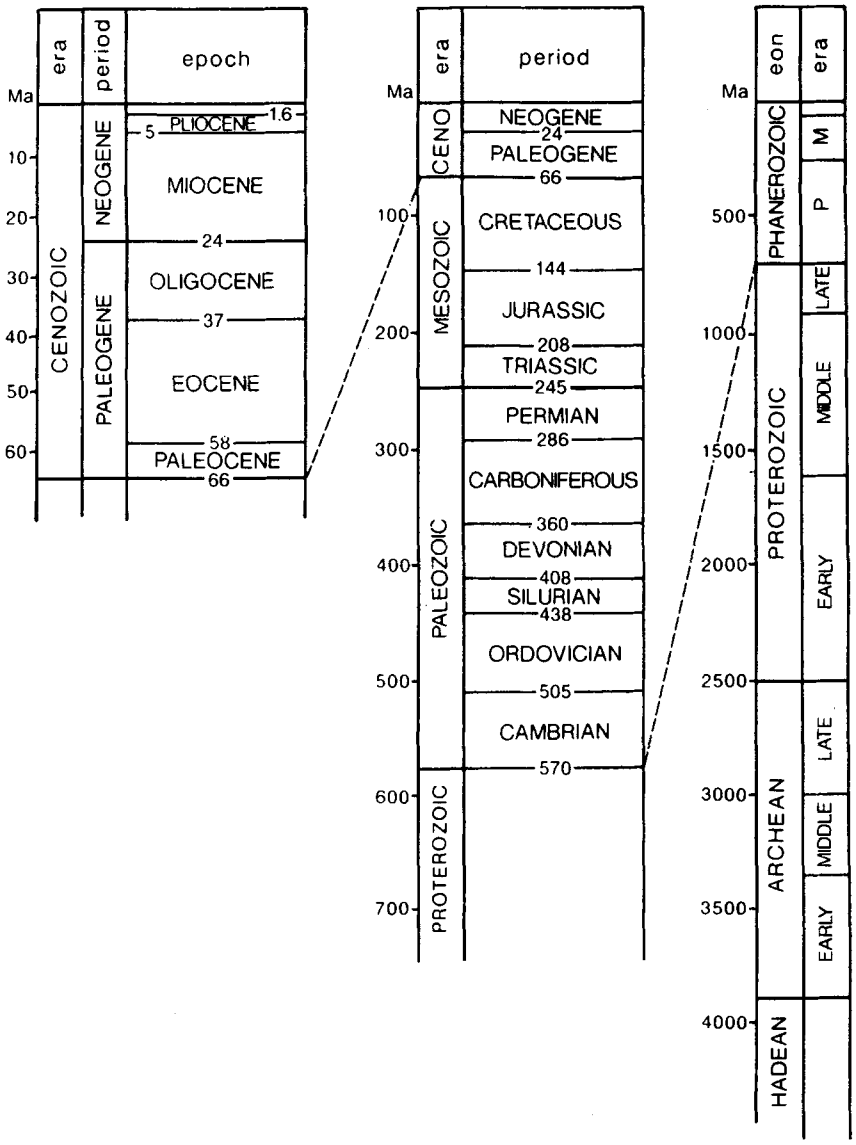

Figure 2-3 Time scale used in this book. The scale of the columns changes by a factor of 5 between each column. The last two epochs of the Neogene, the Holocene (last 0.1 Ma) and the Pleistocene (1.6 Ma), are too short to be shown clearly on this scale. Dates of boundaries between time units are from the *Decade of North American Geology Time Scale*. (*Source:* A. R. Palmer, *Geology*, v. 11, p. 503–504.)

This time scale was a relative one. That is, for all the nineteenth and part of the twentieth century the lengths of the various periods were unknown. Throughout this time most scientists thought that the total age of the earth was only one percent of what isotopic dating has now shown it to be. Despite this major misconception, the main outline of the earth's physical history and the history of life were established, but the time scale of events remained uncalibrated. No one appreciated how slowly the events had actually taken place or how long the history really was.

Although the succession of life-forms that allows the systems to be recognized worldwide is now ascribed to the processes we call evolution, the succession was recognized 60 years before the publication of Darwin's *The Origin of Species*. The establishment of the succession of life did not depend on Darwin's proposal of a mechanism to explain the change but on a simple observable fact; older beds contain fossils that are different from those in younger beds.

MAGNETIC REVERSALS

The earth's magnetic field is modeled as a bar magnet whose poles approximate the geographic poles of the planet. For over a hundred years geophysicists have known that this field has at times been reversed; that is, the end of the compass needle

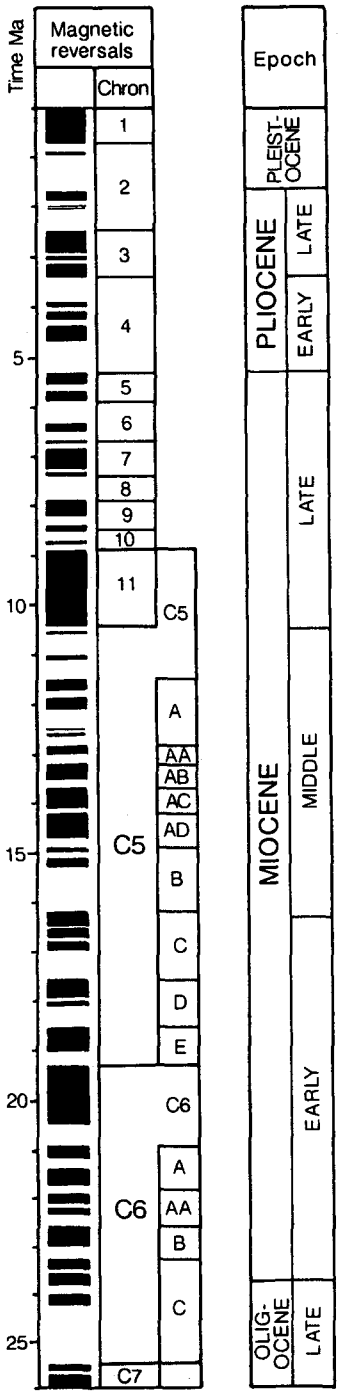

Figure 2-4 Magnetic reversal time scale for late Oligocene time to present. Intervals of normal polarity are represented by the black pattern. The intervals of magnetic polarity (chrons) are given in numbers and letters. (*Source:* W. Berggren and others, *Bulletin of the Geological Society of America*, v. 96, p. 1407–1418.)

that now points north would then have pointed south. Today's condition of the earth's field is said to be normal, the changed position reversed. Discovery of field reversal was possible because sedimentary and igneous rocks containing minerals susceptible to magnetic fields (mainly those containing large proportions of iron) preserve a record of the earth's field. When grains of these minerals in a sediment are deposited from a fluid, or crystals of them are frozen into place in a lava, they are aligned with the magnetic field around them and preserve a record of that field after it has changed. The phenomenon is called remanent magnetism. By dating the remanent magnetism of many samples, geologists have determined that the earth's field reversed itself frequently in some intervals of the past and at other times remained relatively stable. As more detailed work has been done, intervals that were once considered to represent a time of magnetic stability have been shown to be divided by several polarity changes. The larger intervals defined by magnetic polarity have been called chrons and the smaller ones events. Not many reversals of polarity have been dated isotopically. The relatively few chrons that have been dated in years are used through interpolation and extrapolation to calibrate the record of polarity reversals preserved in the crust of the ocean floor as it is formed at mid-ocean ridges and moved away. Polarity changes have been defined in this way back to Late Jurassic time. Figure 2–4 shows the polarity reversal record for Neogene time, which includes chrons 1 to 7. Forty eight polarity changes are recognized in this interval of 26 million years.

The polarity of a sample may help to place it accurately in the time scale if the approximate position is known from paleontological evidence. Unless a relatively precise age is available, knowledge of the normal or reversed polarity is useless, because polarity change has been so common in earth history.

STANDARD TIME SCALE

Events in earth history are now universally related to a standard time scale (Fig. 2–3). By dating igneous rocks that are associated with sedimentary rocks bearing fossils characteristic of the various systems, geologists are now able to determine the ages of the boundaries between periods of the relative time scale. The scale that once could be used

only to place sedimentary layers in their relative position in earth history, that is, as older or younger than other layers, can now be used to estimate how many years ago a fossil-bearing layer was deposited. For example, if a sedimentary deposit contains a fossil that is known to occur only at the top of the Silurian System, the deposition of that bed can be dated as about 410 million years ago, even though no igneous rock near the layer can be isotopically dated. The end of Silurian time has been dated as 408 million years ago by the relationship between igneous rocks and Silurian layers bearing similar fossils at some other locality.

Subsequent discussion of life history in this book will be in terms of this standard time scale. The dates of the boundaries between the periods are constantly under review as new age determinations are made; the time scales in books may differ by a few million years. The methods of using fossils to divide sedimentary successions and determine their ages are considered in greater detail in Chapter 13.

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Chapter 3

Names, Relationships, and classification

NAMES

Botanists and zoologists give the various kinds of plants and animals Latin names. These names allow scientists of different countries to understand one another despite the fact that the common names of animals and plants are different in each language. Latin was the language of science and the church through the Middle Ages into the Renaissance and many organisms were given Latin names in the treatises of these times. Carl von Linné (1707–1778), a Swedish naturalist who published many editions of a book called *Systema Naturae* in the middle part of the eighteenth century, systematized new and old names into this catalogue of plants, animals, and fossils. Linné (or as he is sometimes called, Linneus, his Latinized name) used two Latin names for each organism. The first name indicated the type of animal or plant being named and was somewhat analoguous to our family names but, like Chinese family names, it was placed first. He gave all cats the first name *Felis*, the Latin for cat. Because this name identifies the type of animal, it is called the generic name (Latin *genus* = race or kind, plural is genera). The various cats were distinguished from one another by different second names. *Felis leo* was the name given to the lion; *Felis domestica*, to the house cat; *Felis tigris*, to the tiger, and so on. Lions, tigers, and house cats were recognized as various kinds, or species, of cat and the second name was therefore referred to as the species name (plural = species), or sometimes as the trivial name. This name may be a Latin adjective (*domestica*) modifying the genus name which is a noun, or it may be another noun (*leo, tigris*), but in either case the species name does not start with a captial letter as does the generic name. In addition to hundreds of living animals and plants, Linné named in his *Systema Naturae* many fossils common in northern Europe. Such was the logic of Linné's scheme of uniform genus and species names that within a generation it was accepted by biologists throughout the world and has been systematically applied to both living and fossil organisms.

Describing and Naming Newly Discovered Organisms:

Since the time at Linné, biologists and paleontologists have been describing new species, genera, families, and so on, as they have recognized different forms of life. The description of newly rec-

ognized species is one of the most important activities of the research paleontologist. We are far from documenting all the forms of life that have been preserved, and new fossil species are discovered every day. Descriptions of new fossils are published in scientific journals. After a collection of fossils is made, the paleontologist determines whether the fossils present have been previously described by consulting these journals which together constitute what is called the paleontological literature. This literature, which has accumulated over the past 200 years, is so vast that no one can be familiar with it in its entirety, and most paleontologists therefore specialize in mastering small fractions of it. Most are experts in a single group of fossil organisms, and some are specialized to the extent that they are familiar only with those organisms for a particular interval of the geological past.

If the paleontologist finds that the fossil specimens belong to a species that has not yet been described, he or she may describe it for the first time and give it a name. Usually a new species can be assigned to a genus that has already been described, but if the paleontologist believes that no previously described genus can include the new species, he or she may decide that a new genus must also be established. The naming and describing of newly discovered forms of life are governed by Codes of Botanical and Zoological Nomenclature, which are administered by international commissions. These codes are complex documents but are based on the simple concept that the person who first recognizes a new form has the right to name it, and that the specific name once given, cannot be changed unless the proposal is proved incorrect. In order to help people search the literature, the name of the describer, the species author, is usually attached to the binomial name. For example, the house cat is *Felis domestica* Linné.

Biologists have found that the divisions originally proposed for classifying organisms, such as family, order and class, are insufficient. Since Linné's time subdivisions have been used so that we now have subspecies, subgenera, superfamilies, superorders, and so on. To illustrate how this set of terms is used to place an organism in relation to similar organisms, consider the classification of a familiar animal, man's best friend. All domestic dogs, despite the variety produced by manipulative breeding, belong to the species *familiaris* of the genus *Canis*. The genus also includes some species of wild dogs such as the jackal, *Canis aureus*. The genus *Canis* is united with other such genera as *Lupus* (the wolves) and *Vulpes* (the foxes) in the family Canidae. The Canidae are one family of the suborder Arctoidea which also includes the bear, panda, and racoon families. This suborder is within the order Carnivora, the meat-eating mammals. The carnivores are a member of the class Mammalia to which all mammals belong. With reptiles, amphibians, and the various fish groups, the mammals are included in the phylum Chordata whose members are characterized by a supporting structure, the notochord, along the back. Finally, the chordates share membership with a host of different animals without backbones in the kingdom Animalia. Although this may seem like a large number of divisions to use in classifying an organism, in fact, several subgroupings and supergroups have been left out of the preceding summary. Note in this account that the Latin name of a division is capitalized but its English equivalent is not, and that the Latin names above the level of genus are not placed in italics.

The term *taxon* (plural taxa) refers to any group in the classification, such as family, order, species, or genus. The science of naming and classifying organisms is taxonomy.

Family names can be recognized by the ending "idae" which is unique to this taxonomic rank. Subfamily names end in "inae". The ending "oidea" is used consistently for superfamilies, but it is used for some suborders as well. Names of vertebrate orders frequently end in "formes," but this is not a formal rule. There is no consistency in the endings for higher taxonomic groupings.

Biological classification is not static, but changes as new species are discovered and new knowledge makes the revision of old classifications and the subdivision of old groupings necessary. For example, since Linné, biologists have found new forms of cats, such as the North American puma (*Felis concolor*), and have agreed that is it no longer appropriate to consider all the large cats species of the genus *Felis*. At present some are placed in the genus *Panthera* and the lion is now known as *Panthera leo* (Linné). To indicate that the generic name is not the one assigned by the original describer, his name is placed in parentheses.

ESTABLISHING RELATIONSHIPS

Linné not only distinguished species and genera but grouped the genera into larger divisions called

families to indicate relationships among them. The families were grouped into orders, the orders into classes, the classes into phyla, and the phyla into kingdoms. In this way a unified system that reflected similarities and differences between organisms was established.

In Linné's time, the observed similarities among species were attributed to some systematic aspect of their creation by God. With the acceptance of Darwin's evolutionary hypothesis in the mid-nineteenth century, the relative degree of similarity among species was attributed to the closeness of descent from a common ancestor. Animals and plants that are similar to one another were thought to have evolved from a common ancestor more recently than did those which differ from each other to a greater extent.

Evolutionary biologists agree that systems of classification should reflect the genetic relationships of organisms as closely as possible. Such systems of classification are referred to as natural, as opposed to an arbitrary system that might be based on similarities not resulting from descent. An unnatural classification might unite sharks and whales on the basis of the similarity of body form, but it would not reflect the fact that whales evolved from terrestrial ancestors only very distantly related to sharks.

A formal system of classification depends on establishing the relationships of organisms. Establishing relationships is consequently one of the most important activities of both paleontologists and biologists who study the diversity of living organisms.

From the time of the Greeks, systems of classification and the establishment of relationships were based primarily on overall similarities. The basic stability of Linné's system of classification shows the strength of this methodology. Today, two conceptually distinct methods of establishing relationships and expressing them in systems of classification can be recognized. These are *evolutionary systematics* and *phylogenetic systematics*. Both endeavor to establish classification on the basis of evolutionary relationships, and both depend on recognition of homologous structures.

With the realization that all organisms ultimately share a common ancestry, evolutionists reasoned that similar structures observed in closely related organisms had evolved from a similar structure in their immediate common ancestor. Structures that are so related are termed homologous. Within vertebrates, the upper bone of the forearm, the humerus, is homologous among bats, whales, and primates. It may differ greatly in form and function among these animals, but they share a common ancestry among early mammals in which this bone was present. Homology can usually be recognized among living organisms by the relative position of the structure and by similarities in the pattern of its embryological development.

However, very similar structures may evolve independently in different groups. This frequently occurs through the process of evolutionary convergence in which similar selective forces act on unrelated organisms. For example, sharks and whales show convergent patterns in the evolution of a streamlined body form necessary for rapid swimming. Structures that evolve convergently are termed analogous or homeoplastic rather than homologous.

Establishing relationships depends on the recognition of homologous structures, which reflect common ancestry, and their distinction from homeoplastic structures which do not reflect close relationship.

Another concept that is important for both phylogenetic and evolutionary systematists is that of the monophyletic group. If several species can be shown to share advanced characters that are not present in other groups, it is assumed that they share a common ancestry, distinct from all other species. Since they have a single ancestry these species are said to belong to a monophyletic group.

Evolutionary Systematics:

Like Linné, evolutionary systematists depend primarily on overall similarity to establish relationships. Where possible, they rely heavily on the fossil record to establish the homology of structures. The writings of evolutionary systematists such as Ernst Mayr and George Gaylord Simpson indicate that they do not consider classification a strictly objective task, but one which involves a degree of judgment and creativity, in addition to a detailed knowledge of the organisms being classified.

Numerical taxonomy, elaborated by Peter Sneath and Robert Sokal, may be considered as an effort to quantify and make more objective a system of classification based on overall similarity. They have used computers to analyze large data sets which give indexes of similarity. These indexes can be used as a basis for classification. Numerical classification (also referred to as phenetics) differs from evolutionary systematics in that little attention is

given to establishing specific homologies. It is reasoned that overall similarity, measured by the summing of many different characteristics, is itself evidence of close genetic relationship.

To quote from Sneath and Sokal (1):

> A basic attitude of numerical taxonomists is the strict separation of phylogenetic speculation from taxonomic procedure. Taxonomic relationships are evaluated purely on the basis of the resemblances existing *now* in the material at hand. These phenetic relationships do not take into account the origin of the resemblance found nor the rate at which resemblances may have increased or decreased in the past.

Much has been written about numerical taxonomy but it has not been widely used among paleontologists.

Phylogenetic Systematics:

Within the past 25 years, a new methodology, phylogenetic systematics, has revolutionized concepts of the way in which relationships should be established and organisms classified. Phylogenetic systematics is based on the work of Willi Hennig (2). Much of his early research concentrated on the taxonomy of insects. Insects have a relatively incomplete fossil record, and most relationships must be established on the basis of the physiology and soft anatomy of living species. Hennig sought to develop an objective means of analyzing characters and placing organisms into a system of classification directly reflecting evolutionary relationships.

The most important concept stressed by Hennig was that relationships should be determined on the basis of advanced, or derived, characters rather than on the basis of overall similarity. For example, all fish groups share many characters, such as fins and gills. These characters are of no use in establishing specific relationships among the fish since they are possessed by all members of this assemblage. However, advanced, or derived, features shared by particular fish groups, such as the presence of a median rather than a paired opening for the external nostril in the lamprey and one group of Paleozoic fish (the Cephalaspidomorpha), suggests that they are more closely related to one another than are either to other groups of fish.

Hennig coined the term sister groups to describe two groups that uniquely share derived characters. For example, among mammals, placentals and marsupials are considered sister groups because both give birth to live young, as opposed to more primitive mammals, the monotremes, which lay eggs. Hennig also coined the terms plesiomorphic and apomorphic to describe, respectively, primitive and advanced (or derived) characters. A derived character that is possessed by a single group is termed an autapomorphy. An autapomorphy characterizes this single group, but is of no significance in establishing this group's relation to other groups, none of which have this character. A derived character that is shared by two groups is a synapomorphy. A shared primitive trait is a symplesiomorphy.

A particular character can be simultaneously an autapomorphy, a synapomorphy, and a symplesiomorphy, depending on the taxonomic level being discussed. The presence of fur was presumably an apomorphy or autapomorphy of a single lineage of early mammals, before this group began to differentiate. By itself, this character would have been of no value in establishing the relationships of this lineage. As mammals diverged into the lineages leading to marsupials and placentals, the presence of fur would be a synapomorphy reflecting the common ancestry of these two groups and differentiating them from all other groups of vertebrates. Within marsupials and placentals, fur is a plesiomorphic character which is of no value in establishing relationships among the many subgroups because it is common to all of them.

The use of these terms is becoming increasingly common in paleontology. Students wishing to understand the paleontological literature must be familiar with changes in the philosophy and practice of establishing relationships and systems of classification.

Because only characters that are derived at a particular taxonomic level can be used in determining relationships, a method must be developed to identify derived characters. Without some prior knowledge of the relationships of a species or its evolutionary history, a particular character cannot be identified as primitive or derived. For example, a reptile may have a particular number of teeth. Is this number a primitive or derived condition relative to other related reptiles? Did its ancestors have a smaller or a greater number of teeth? The direction of evolutionary change is referred to as the polarity of the character. A particular character may exist in either a primitive or a derived character state, or in several distinct derived conditions, all evolved from a single primitive character state. For

example, the primitive character state for a group of clams may be a smooth shell. The derived state may be an ornamented shell, but this ornamentation might take many different forms, such as ridges, grooves, or spines, each of which would be an alternative derived state of the character.

Polarity:

Since Hennig's own research concentrated on a group with a poor fossil record, he applied methods of establishing the primitive or derived nature of traits, and hence polarity, among contemporary species. These include outgroup comparison, commonality, and embryological development.

Since outgroup comparison is considered the most useful method, it will be discussed first. An outgroup includes taxa that are not part of the particular group under consideration, but do share a distant common ancestry. For example, if a paleontologist is considering relationships among primates, the outgroup might include all other mammals. The polarity of a character may be judged by its distribution within the group being studied and its outgroup. A character (or character state) that is widely distributed in both the outgroup and the group under consideration is probably primitive. A character that is found only in the group under study is probably a derived feature of this group.

Another method is commonality. If a character is universally present in a group, it is almost certainly a primitive feature of this group, for example, hair in the modern mammal groups. Conversely, if a character is only rarely present in the group being studied, it is likely to have evolved within this group. There are obvious exceptions, however. Egg laying is very rare among mammals, being restricted to the platypus and the echidna living in the Australian area. This is certainly not a derived character of these genera, but a primitive feature, as established through consideration of their outgroup, other terrestrial vertebrates—reptiles, birds and amphibians—almost all of which lay eggs.

Another method of establishing the polarity of alternative character states is the study of the development of individuals from their embryos. Derived character states should be recognizable by the fact that they appear later in development. For example, primitive vertebrates have a large number of major blood vessels, the aortic arches, extending from the heart through the gill region. Adults of birds and mammals have only two major vessels, one that goes to the lungs, and the second to the rest of the body. Both develop from paired vessels, one of which is lost. In birds, the major vessel to the body develops from the right side, whereas in mammals it develops from the left side. Embryological evidence confirms that the condition in mammals and bird was derived, as was suggested by the distribution of these vessels in adults. It also confirms that the particular pattern in these two groups was independently derived, rather than evolving from a single ancestral group that had already reduced the paired condition to a single vessel.

Identifying ancestors:

Finding the ancestral species for a modern or fossil species should, on superficial consideration, be easy. We should need only to look for a fossil species that is similar but shows more primitive characteristics in sedimentary deposits slightly older than the ones in which the descendant species is found. Because change in organisms, particularly simple organisms, has been slow when averaged over the length of geological time, we would not expect great differences in form to separate ancestor from descendant. Because, in the long perspective, life has become more complex with time, we might expect the ancestor species to show its primitiveness by simpler construction. However, the chances of finding such an ancestor are small and the recognition of its primitiveness is difficult.

The transition from ancestor to descendant is unlikely to be captured in the fossil record because the chance of preservation of any particular species is small (Chapter 1), and the transition may have taken place in a remote area of the world or one where deposition was not taking place. Sedimentary series are the products of deposition of a succession of different environments. Each environment is characterized by a type of sediment and its own suite of species. The sequence of species collected layer by layer commonly reflects the coming and going of species adapted to the different environments, not the change of one species into another. Problems of locating fossil ancestors in the sedimentary rock record are similar to problems of people seeking their roots. The ancestry of most North Americans cannot be determined by examining lo-

cal records of the last century because most of us are descended from immigrants from other countries, and in many of these countries records have been destroyed.

However, the earliest fossil record of a character may not accurately reflect its actual time of appearance. Evolution of particular characters occurs at different rates in different lineages, and some species (termed *living fossils*) retain many primitive features long after they have achieved the derived condition in other species within the same group. Use of the stratigraphic sequence to establish polarity is not infallible, but it is often effective in groups represented by a good fossil record.

Evolutionary systematists have long tried to discover ancestors of the major groups. Phylogenetic systematists argue that it is difficult, if not impossible, to demonstrate ancestor–descendent relationships, and unnecessary for phylogenetic analysis. Sister group relationships can be established on the basis of shared derived characters. Ancestors, conversely, can be identified only on the basis of the *absence* of one or more characters that are present in the descendant. It can be argued, however, that an ancestor can be recognized by shared derived characters that identify it as a member of the same monophyletic group as the putative descendant, along with the presence of one or more characters of a more primitive character state, and none of a more advanced state.

The basic philosophy of establishing relationships espoused by Willi Hennig, and more recently discussed by Peter Ax, (3) is not fundamentally different from that used by evolutionary systematists. Many systematists before Hennig did specify the use of derived, rather than primitive, characters in establishing relationships, but this was not elaborated as a distinct methodology. Phylogenetic systematics has provided a much more rigorous methodology in which the polarity of all variable characters should be established. The main problem with applying this methodology, as is the case with evolutionary systematics, is the difficulty of establishing polarity and homology.

As in the case of numerical taxonomy, phylogenetic systematics has attempted to apply computer technology in order to handle simultaneously large numbers of characters in many related groups. The results, however, still depend on the prior analysis of the polarity and homology of the characters chosen.

CLASSIFICATION

The great increase of interest in the methodology of establishing relationships has led to much more extensive and rigorous analysis of phylogenies of all taxonomic groups, fossil and living, in the past decade. Even greater changes are occurring in the overall methodology of classification. In retrospect, it seems strange that the basic system of classification proposed by Linné for a biological world without evolution could be accepted with almost no change by the followers of Darwin. Perhaps the slow and irregular growth in knowledge of the fossil record made this possible. Until relatively recently, many fossils were either classified directly with living groups, or recognized as members of extinct groups. Classification of extinct members of modern groups, such as molluscs, or lizards, could proceed much like classification of newly recognized species within the modern fauna. Extinct groups such as dinosaurs, however, could be classified independently of modern groups. In the past 20 years information linking fossil and modern groups has increased greatly, and many species that could be placed in true phylogenetic sequences have been discovered. With this new information, basic problems in the older methods of classification became evident.

One of the most important differences in classification between evolutionary systematics and phylogenetic systematics involves the concept of monophyletic groups. The term monophyletic was initially defined only in terms of the origin of a group. Evolutionary systematists defined a monophyletic group as one that had a single ancestor, rather than one that evolved from two or more ancestral groups. For example, the pinnipeds are a group of marine mammals including seals, sea lions, and walruses. If, as is frequently argued, seals evolved from a different family of terrestrial carnivores than did sea lions and walruses, the pinnipeds would be a polyphyletic group. Biologists frown on the recognition of polyphyletic groups as valid taxa.

Hennig and his followers argue that the term monophyletic should describe not only the ancestry of a group, but also its subsequent history. They contend that a monophyletic group should include both a single ancestral species and all its descendants. The term paraphyletic is applied to groups that have a common ancestry, but that do not in-

clude all their descendants. Hennig considered a monophyletic group as a logical and nonarbitrary assemblage of species. His definition, however, conflicts with many of the major taxonomic groups that are currently accepted. The most commonly discussed example of a paraphyletic group is the class Reptilia. This group includes the lizards, snakes, turtles, and crocodiles of the modern fauna, as well as the dinosaurs and many other extinct forms. Reptiles were defined on the basis of overall similarities in the structure and physiology of the modern species. As the fossil record became better known, both the birds and the mammals were recognized as ultimately evolved from animals whose skeletal anatomy resembled the pattern of living reptiles. We say that both birds and mammals evolved from reptiles. Clearly this concept of reptiles contradicts the definition of a monophyletic group proposed by Hennig; reptiles may have a single common ancestor, but they do not include all their descendants.

Both birds and mammals can be defined on the basis of unique derived characters, but reptiles must be defined on the basis of the absence of characters that distinguish their descendants. As the fossil record becomes better known, it is more and more difficult to formulate a point of distinction between reptiles (as currently defined) and birds, or reptiles and mammals, that is not arbitrary. This is evident if we look at the phylogentic relationships of the groups involved (Fig. 3–1). Among living groups, birds share a more recent common ancestry with crocodiles than that between crocodiles and lizards, or crocodiles and turtles. Birds also share a closer common ancestry with all these "reptile" groups than they do with the ancestors of mammals, which are also classified as reptiles.

In the case of reptiles, the generally accepted pattern of relationships is not reflected in the generally accepted classification. A natural classification, based on the relative recency of common descent, would group birds with crocodiles, and both of these groups with lizards and turtles, to the exclusion of mammals and their immediate ancestors.

The simplest solution would be to unite the mammals and their immediate (reptilelike) ancestors in one taxonomic group, and the birds and modern reptiles in a second group.

Both evolutionary and phylogenetic systematists recognize a single larger taxonomic group, the Amniota, which includes all the groups now termed reptiles along with birds and mammals. All share derived features that distinguish them from more primitive terrestrial vertebrates, the amphibians.

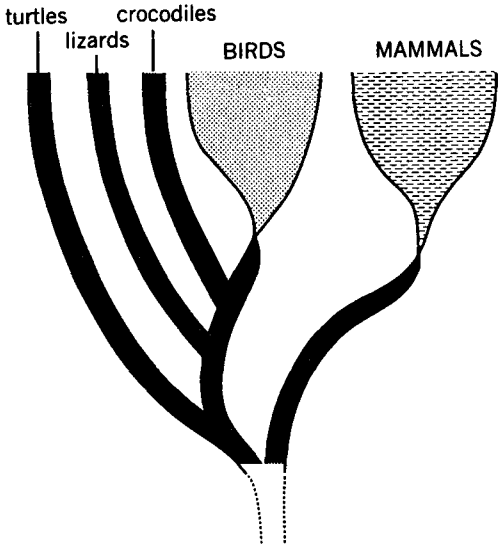

Figure 3-1 Simplified phylogeny of amniotes. The class Reptilia as customarily defined includes all the darkly stippled lineages. Reptiles have a common ancestry but are considered paraphyletic, because they do not include all their descendants. Birds and mammals can be defined on the basis of unique, shared derived characters. Reptiles can be defined as amniotes that lack the specialized characters of birds and mammals. From *Vertebrate Paleontology and Evolution* by Robert L. Carroll. Copyright © 1987 W. H. Freeman and Company. Reprinted with permission.

However, the term reptile is familiar to most scientists, whereas no commonly used word is available that refers to a group including dinosaurs, crocodiles and birds, or these groups together with lizards and turtles. It is also difficult to accept a group that includes both warm-blooded, furry mammals and a host of markedly more primitive Paleozoic and Triassic genera, many of which have none of the attributes usually associated with mammals. Popular names have been supplanted in the past, and a classification more closely reflecting their relationships will probably eventually be accepted for the animals now termed reptiles. The living and fossil genera now grouped as amphibians are probably also a paraphyletic group, as are the bony fish. These groups too will eventually be reclassified. Major changes will also occur in the classification of invertebrates and plants as their evolutionary relationships become better known.

A host of practical problems makes application of the principles of phylogenetic classification to large taxonomic groups difficult. Among these are the proliferation of a great many new taxonomic ranks suggested by some workers, or the abandonment of all ranks above the species, as proposed by others. Either of these solutions would make it very difficult to communicate and compare systems of classification. Neither of these major changes has yet achieved general acceptance. For this reason, names and taxonomic ranks used in this text will follow the familiar Linnean pattern.

Another striking difference between evolutionary and phylogenetic systematics is the way in which relationships are graphically represented. Relationships have long been represented as family trees, with modern species on the terminal branches, and older and possibly ancestral forms on the lower branches and trunks (Fig. 3–2). This is the pattern followed in this text. It accords well with paleontological practices, since such family trees usually include a geological time scale. The relative distance between species corresponds roughly with their morphological differences, or presumed evolutionary distances. The exact shape of the tree is at the discretion of the author.

Hennig and his followers, in contrast, have consistently used a different pattern, termed a cladogram, to represent relationships (Fig. 3–3). It consists of an angled axis, from which are drawn a number of parallel lines. Typically, taxa are represented only at the ends of the lines. Only sister groups, never ancestor–descendant relationships, are indicated. The sequence of origin of derived characters are listed along the main axis and the parallel lines. These show a nested hierarchy of derived charcters that can be used to form a nested, hierarchical system of classification (Fig. 3–4). Use of this system avoids the recognition of paraphyletic groups.

Cladograms are a very effective way to illustrate the distribution of derived characters. Typically, cladograms have lacked time scales, but there is no reason why this information cannot be incorporated. Phylogenetic systematics depends on determining the relative time of the divergence of sister groups and the appearance of derived characters. Establishment of either of these factors from the fossil record provides an important basis on which to test the accuracy of their determination by other means, such as outgroup comparison.

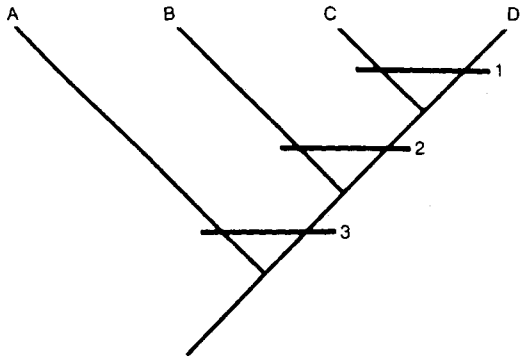

Figure 3-3 Cladogram showing the relationships between four species repesented by letters. The numbered bars represent shared derived characteristics (synapomorphies). Bar 1, joining species D and C, indicates that they share a derived characteristic that B does not. From this characteristic we deduce that D and C are more closely related than either is to B, because they share a more immediate common ancestor. The separation of the other three from A in the diagram is deduced from its lack of another derived characteristic (represented by bar 2) shared by B, C, and D. Its connection to a common ancestor must have been still more remote. All four will share many primitive characteristics (synplesiomorphies), but these are unimportant in the construction of the cladogram and in the determination of the relationships.

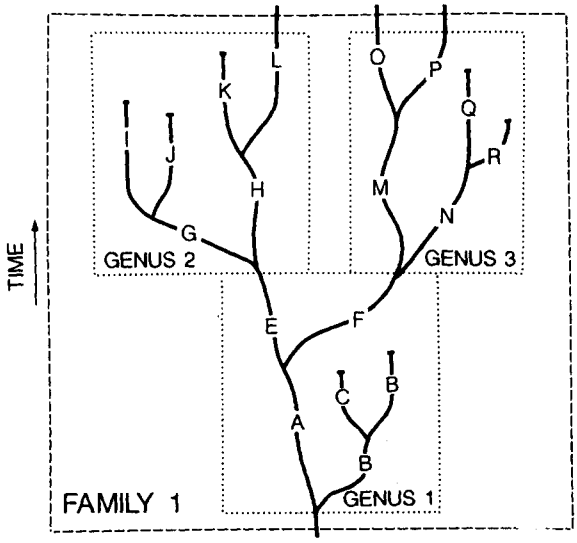

Figure 3-2 Hypothetical phylogeny showing the idealized relationship between species (A, B, C . . .), genera, and families.

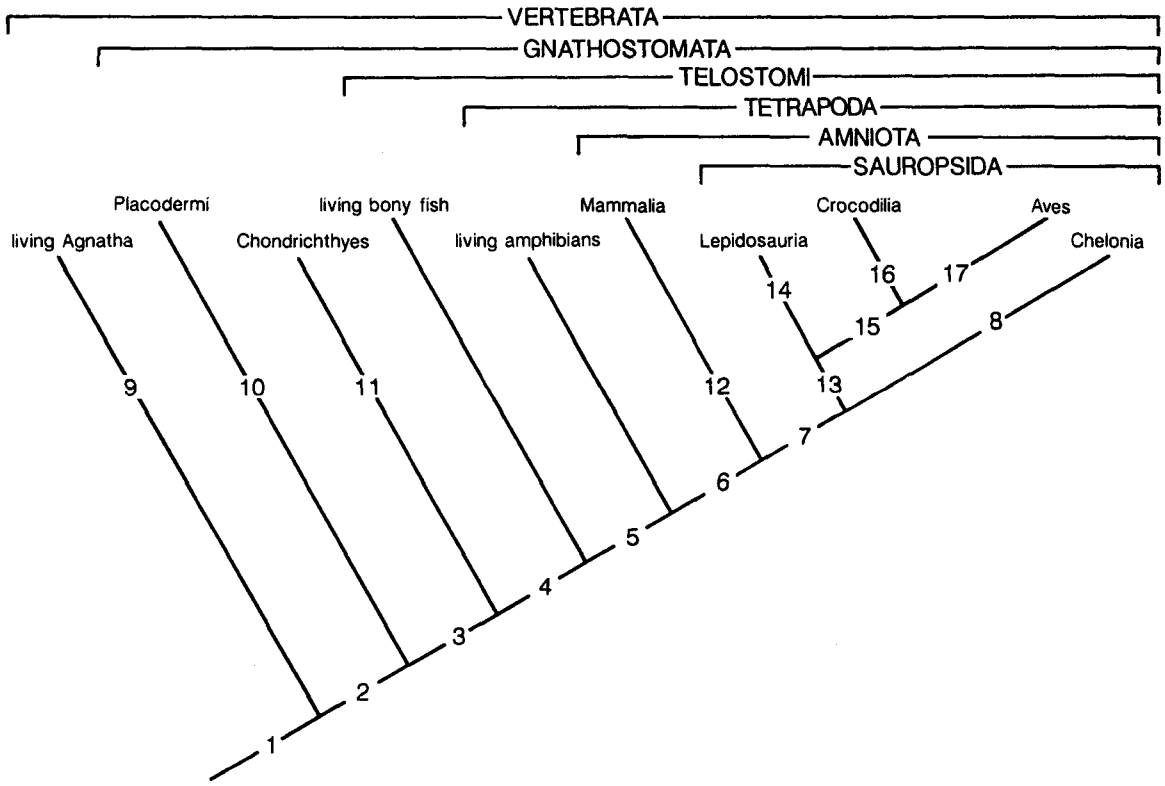

Figure 3-4 A cladogram showing a nested series of monophyletic groups among the vertebrates. The derived characteristics that define the nodes of the cladogram and characterize each group are as follows: 1, brain, specialized paired sense organs, ability to form bone; 2, jaws, gill filaments lateral to gill supports; 3, regular tooth replacement, palatoquadrate medial to adductor jaw musculature; 4, bone, a regular constituent of the endochondral skeleton. Swim bladder or lung; 5, paired limbs used for terrestrial locomotion; 6, extraembryonic membranes, allantois, chorion, and amnion, direct development without an aquatic larval stage; 7, loss of medial centrale of pes; 8, loss of ectopterygoid bone, closely integrated dorsal carapace, and ventral plastron; 9, gill filaments medial to gill supports; 10, palatoquadrate lateral to adductor jaw musculature; 11, prismatic cartilage; 12, fur, mammary glands; 13, dorsal and lateral temporal openings, suborbital fenestra; 14, large sternum on which the scapulocoracoid rotates; 15, hooked fifth metatarsal, foot directed forward for much of stride; 16, an akinetic skull with extensive pneumatization, elongate coracoid; 17, feathers. Neither osteichthyes nor modern amphibians can be defined on the basis of unique derived characteristics. From *Vertebrate Paleontology and Evolution* by Robert L. Carroll. Copyright © 1987 W. H. Freeman and Company. Reprinted with permission.

Molecular Phylogeny:

Comparisons of phylogenetic significance can be made at the molecular as well as at the morphologic level. The sequence of bases in chains of genetic material (DNA and RNA) and amino acid sequences of proteins are characteristic of each organism. Similar organisms have similar amino acid sequences, and the degree of genetic difference between organisms is reflected quantitatively in the differences of their proteins. The differences between amino acid sequences have been interpreted as a measure of the remoteness of a common ancestor. Most molecular comparisons have confirmed conclusions about relationships reached by morphologic comparisons (Fig. 3–5).

Although proteins are subject to bacterial attack and may be decomposed rapidly after the death of an organism, collagen persists in bones up to a million years old. This allows comparisons to be made of the amino acid sequences of animals that became extinct in the Pleistocene Epoch with those of modern mammals. Direct comparison of amino acid sequences of fossils older than a million years is not yet possible. Proteins have been detected in fossil shells hundreds of millions of years old, but the molecules have been greatly changed and their original configuration is difficult to reconstruct.

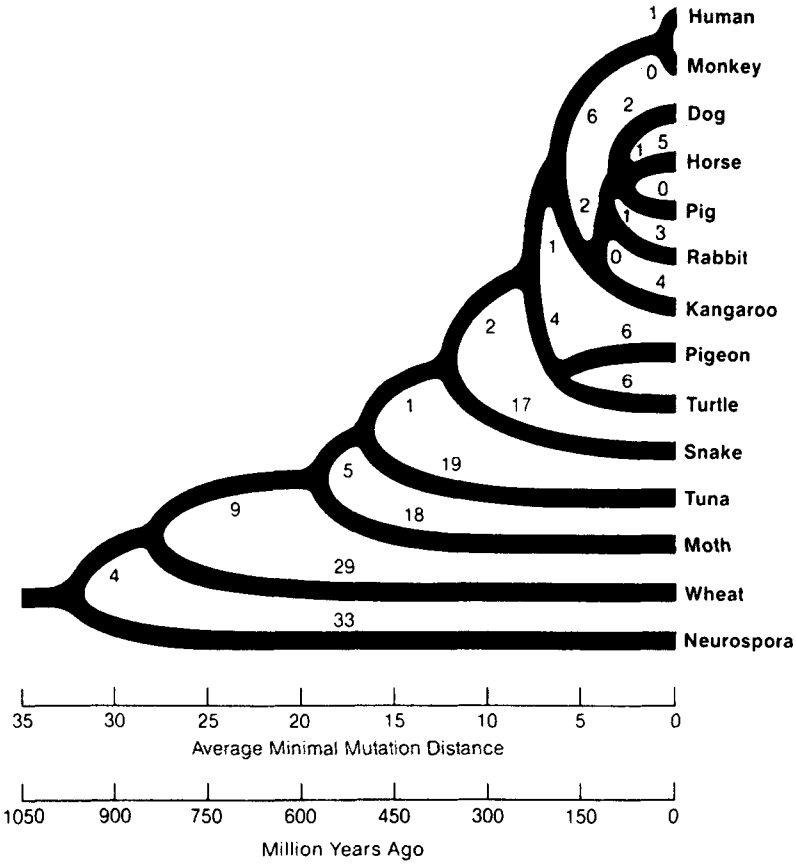

Figure 3-5 Relation between organisms based on the amino acid sequences in the protein cytochrome c in several mammals, a bird, two reptiles, a fish, an insect, a plant, and a yeast. The numbers on the figure are the mutational distances along the line of descent. If the divergence points are scaled against the fossil record, an average mutation rate of about one per 15 Ma for this protein of about 100 amino acids can be deduced. (Reproduced with permission, from *Annual Review of Earth and Planetary Sciences*, v. 14, © 1986 by Annual Reviews Inc.; courtesy of J. M. Lowenstein, modified from E. Margoliash.)

Although direct analysis of the amnio acid sequences in proteins is not possible in fossils older than one million years, phylogenetic analysis is possible by measuring the differences between the sequences in living groups, in the same way that relationships of living organisms were established on the basis of anatomical differences when little information was available from the fossil record.

Homologous proteins can be recognized, just as homologous anatomical structures can be recognized. For example, the oxygen-carrying globin proteins such as hemoglobin are common to all vertebrates. Particular globin proteins have similar numbers of amino acids in all vertebrate groups, but the specific amino acids differ from species to species. The total length of the molecule, its geometry, and some segments may be under stringent selection pressure to maintain an optimal pattern necessary for carrying oxygen, but some segments of the molecule can apparently function with any of a great variety of amino acid sequences. Through random mutations different amino acids are substituted in the ancestral sequence. The extent of substitution is thought to be more or less directly proportional to time. Although we can never directly establish the ancestral sequence, the amount of difference between any contemporary species is a good measure of the time that has passed since they diverged. This provides a measure of the relative time of divergence of a series of related species. Information from the fossil record helps to provide an absolute time scale. For example, we know that there has been a substitution of approximately 50 percent of the amino acids of particular globin molecules since the divergence of the ancestors of the modern reptile and mammal groups in the Late Carboniferous, 300 million years ago, and a 93 percent substitution since the divergence of sharks from the primitive vertebrate stock, 430 million years ago. This information suggests a substitution rate of 1 percent per 5 to 6 million years. The rate of change can then be applied to measure the time of divergence of groups for which the fossil record is less completely known. In human paleontology, this method has indicated humans diverged from apes only 5 or 6 million years ago. When this calculation was first published, it strongly contradicted estimates based on the fossil record which

then suggested a time of divergence close to 20 million years ago. Fossils discovered more recently show that humans and living African apes might have diverged between 6 and 14 million years ago.

WHAT IS A SPECIES?

Whatever method is used to establish relationships and to classify organisms, the species is accepted as a fundamental biological unit. Biologists use two definitions or concepts to recognize species: one based primarily on morphology—form, size and proportions—and the other based on distribution and potential for interbreeding.

The Biogeographic–Genetic Approach to Species Definition:

Within the last 50 years biologists have formulated an approach to species definition based on the spatial distribution of organisms and their interbreeding. When the habitats of animals and plants are established, biologists find that groups of organisms that have been recognized as species on a morphologic basis occupy areas from which similar species of the same, or related, genera are commonly excluded. At the boundaries of their home range, species compete with related species for space and resources but do not interbreed with them or grade morphologically into them. The spatial boundaries of species are marked by morphologic and reproductive discontinuities. Within the boundaries, the individuals of the species interbreed and thus maintain a homogeneous population with a continuous range of variation. The boundaries of the species may be physical barriers to interbreeding, such as rivers, lakes, or mountains, or they may be more subtle. At the boundaries of their ranges two related species may be in contact but never interbreed because, for example, one mates in May and the other in June. A pair of insect species may never interbreed, even though their ranges overlap geographically, because one lives exclusively on one type of vegetation and the other on another type. The species in these examples are said to be genetically isolated from one another. The biogeographic–genetic definition of species is that they are populations of interbreeding individuals that are spatially segregated and genetically isolated from similar adjacent groups.

The morphology of organisms is controlled by the genetic material handed down from parents to offspring, that is, the genes. By interchanging genes in random interbreeding within a species population, the group maintains homogeneity. This does not mean that all individuals are alike, but that variation is continuous and within certain limits. The species can be considered either a collection of individuals or the totality of the genes that these individuals possess. This totality of genes is called the gene pool and individuals of the species can be thought of as determined by selections of sets of genes from this pool. The pool is kept homogeneous by the continual gene flow among the individuals of the species as they interbreed.

Within the geographic range of most species, the morphologic variation is continuous, but specific morphologies are clumped together rather than uniformly distributed. The environmental features of a species range are rarely uniform. Through natural selection, individuals adapting to local conditions separate into microgeographic races. This can be illustrated by a hypothetical example of mouse populations living in a range including highlands and plains. Suppose that a population of brown mice have genes giving them a temperature tolerance that favors their survival in the highlands, whereas black mice have genetically dictated features that favor survival in the plains. If black mice straying into the highlands did not mate as effectively in the cold nights there, and brown mice straying into the plains were debilitated by the hot noon-day sun, the resulting local populations would break the morphologic continuity of the species. Interbreeding between the brown and black mice would still take place on the boundaries of the highland and the variation between them would remain continuous, but the populations would have different proportions of the color phases as long as each type of mouse was at a disadvantage in the other's territory.

With further differentiation of interbreeding groups (typically on the basis of geographical distance) populations are recognized as subspecies, and the addition of a third Latin name to the standard genus and species names. The western bullfrog, *Bufo woodhousei woodhousei*, lives in the prairie states and is larger than the forest-dwelling eastern subspecies, *Bufo woodhousei fowleri*. However, they grade into and breed with one another over a belt that reaches a width of 300 km in Texas. Some populations recognized as subspecies are separated by physical barriers and cannot interbreed in nature.

For example, the salamander *Plethodon vandykei* is divided into a subspecies (*P. vandykei vandykei*) that lives in western Washington state and a subspecies (*P. vandykei idahoensis.*) that lives in the mountains of Idaho. The two are separated by the drylands of central Washington. They differ morphologically in skin markings.

The distinction between microgeographic races, subspecies, and species is sometimes unclear even after living populations have been intensely studied. Subspecies names have been used by some paleontologists for subdivisions of a species separated by morphologic differences smaller than those considered to be of specific rank.

The biogeographic–genetic approach to species definition is important in understanding the origin of species. Unfortunately, paleontologists cannot examine the breeding behavior of organisms that have been dead for millions of years, and they have no precise idea about the position or nature of the range boundaries for most fossil species. Fortunately, most modern species can be distinguished by morphological differences which reflect their genetic isolation. By studying the variation found in modern species, defined on the basis of interbreeding criteria, the paleontologist can estimate the range of morphological variation in fossil species.

Linnean Species:

Linné distinguished various species of organisms on the basis of their form. This species concept used by Linné, and still used by biologists and paleontologists for many groups of organisms, is therefore a morphologic definition. No two individuals of any species are exactly alike when examined critically, although to a casual observer the birds in a flock may appear to be identical. The various species could be distinguished by Linné because, despite the range of variation within each species, in nature one kind of animal or plant does not grade continuously in form into other kinds. That is, the Linnean system of identifying species is based on discontinuities in the range of variation in form of organisms. It is these discontinuities that are used to draw boundaries between species.

The morphologic discontinuities between species may be subtle and difficult to detect. The form of each individual of a species may be described by the proportions—such as length, height, width, and weight—of the whole organism and of each of its constituent parts. For species of simple organisms consisting of a single cell, the number of measurements or characters completely describing its morphology would be small, perhaps less than 20. But for a complex animal like a dog, the number of characters would be in the millions. However, biologists, in defining such complex species, must demonstrate only that the diagnostic characters are sufficiently different from those of similar species to make objective recognition of the new species possible.

A paleontologist must often decide whether a collection of fossils contains only a single species of a particular genus, or two or more species. The paleontologist then looks for morphologic discontinuities that separate species in the collection. A similar problem, which must be approached in much the same way, is whether the characteristics of the

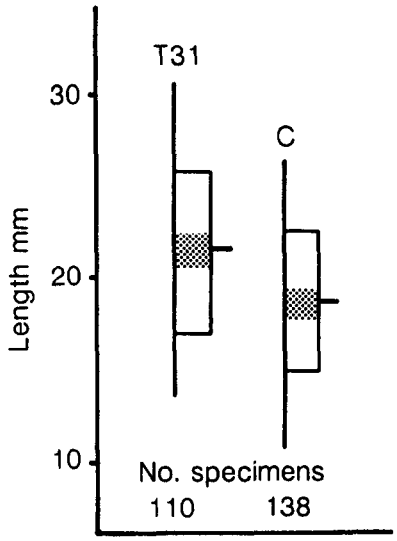

Figure 3-6 Dice diagram comparing the variation between two collections of the brachiopod *Atrypella phoca*. The vertical line represents the total range of length in the specimens collected. The empty box is two standard deviations long. The standard deviation can be calculated by taking the differences between each measurement and the average value (mean), squaring them to eliminate their positive or negative sign, summing them, taking their square root, and dividing by the number of measurements. This procedure yields a value that represents an averaging of the differences of values from the mean without regard to sign. The length of the filled box is ±1 standard error of the mean and the horizontal line is the mean value. Note the considerable difference in the range and mean of two samples of the same species. (Courtesy of Brian Jones, The Paleontological Society, and *Journal of Paleontology*, v. 51, p. 466.)

group of fossils to be identified are within the range of previously described species variations. If they are not, the fossils may represent a new species. To solve these problems, the range of variation in species must be assessed.

Nature of Variation in Fossil Species:

In everyday life we are confronted with a wide range of variation in form of some species, such as *Homo sapiens* or *Canis familiaris*. The extent of variation can be expressed by measuring various dimensions of the species and quoting the range of values. For example, the variation in length of the brachiopod *Atrypella phoca* from a single locality is from 6 to 19 mm. Because the range in values is so large, some of the specimens in the collection are probably juveniles. A more accurate idea of the extent of variation can be obtained by calculating the mean (average) (14 mm) and standard deviation (1 mm) of the measurements that have been made, and plotting them on a Dice diagram (Fig. 3–6)(See an elementary statistics textbook and the figure caption for methods of calculation). The set of measurements can also be plotted as a histogram to illustrate graphically the extent of variation in this single character (Fig 3–7). The frequency distribution of the measurements shown in the diagram suggests that the few specimens represented by measurements of low value on the left are juveniles and that the many on the right are adults. Differentiation of juveniles also allows the paleontologist to estimate the average adult size.

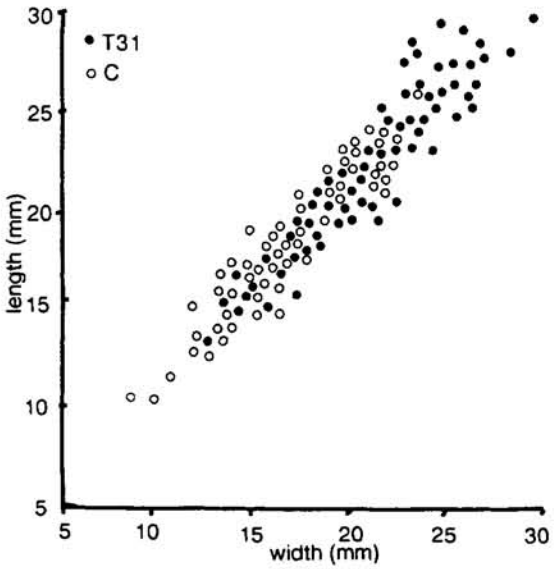

Figure 3-8 Scatter diagram showing the relationship between length and width in the specimens in two collections of the brachiopod *Atrypella phoca*. Although the diagram shows a large area of overlap, it also shows that some specimens from collection T31 are longer and wider than any from collection C. (Courtesy of Brian Jones, The Paleontological Society, and *Journal of Paleontology*, v. 51, p. 468.)

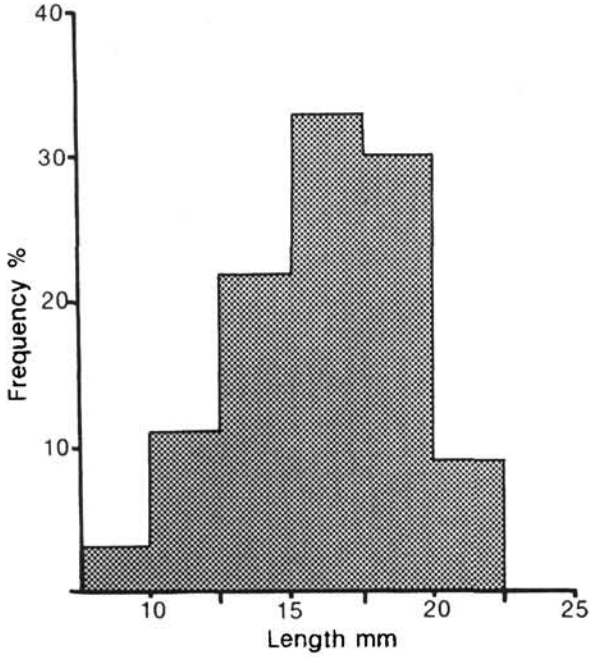

Figure 3-7 Histogram showing the frequency distribution of lengths of the brachiopod *Atrypella phoca*. (Courtesy of Brian Jones, The Paleontological Society, and *Journal of Paleontology*, v. 51, p. 476.)

Paleontologists illustrate the variation in a species and the discontinuities that separate it from similar species by means of diagrams such as Figure 3–8, in which the width and length of two collections of the brachiopod *Atrypella phoca* are plotted. Each dot on the diagram represents the width and length of an individual shell. Immature shells plot on the lower left; large adults on the upper right. In Figure 3–9 the proportions of a related species, *Atrypella foxi*, are compared with those of *Atrypella phoca*. The morphologic discontinuity between the two species is clearly illustrated. The proportional relation between three characters can be plotted on a two-dimensional graph, but the relation between more than three characters is almost impossible to illustrate graphically. However, mathematically, 10 or

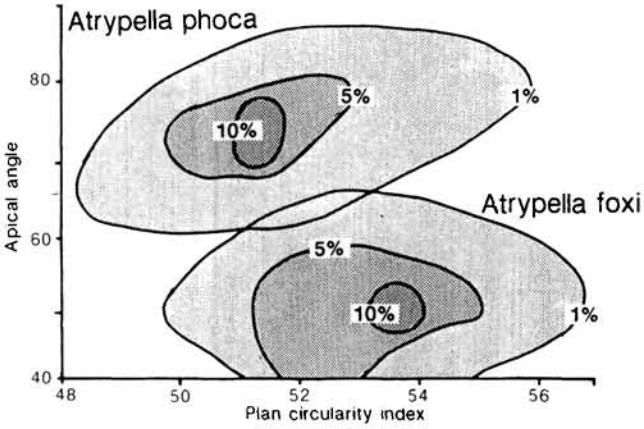

Figure 3-9 Bivariate plot of the dimensions of two species of the Silurian brachiopod *Atrypella*. The density of points of each specimen measured has been contoured. The plan circularity index is defined as 100 times the length divided by the sum of the length and width. Note that the two species can be separated clearly on the basis of these proportions. (Courtesy of Brian Jones, The Paleontological Society, and *Journal of Paleontology*, v. 51, p. 462.)

20 characters can be compared simultaneously in order to separate individuals of species that are morphologically close. Because each character is considered a dimension in the comparison, the ranges of variation of the groups are then multidimensional solids. Although multidimensional space and the solids that occupy it are difficult to imagine and impossible to illustrate, the comparison of many characters can be treated mathematically, with the aid of a computer, by various techniques.

In assessing the extent of variation within a species of living organisms, the biologist can relatively easily determine that the species sample consists only of adults. If the sample contained both juveniles and adults it would include a wide range of dimensions that change with growth, which would misrepresent the adult variation. In many animals, and some plants, species exist in male and female forms which have size differences greater than those between related species. Species which exist in two different forms are said to be dimorphic. Obviously, when collections are being compared to determine morphologic discontinuities, the biologist must be sure that adults are being compared with adults and males with males, or females with females.

In dealing with a collection of fossils, the paleontologist may have difficulty in defining the variation of a species because it is far more difficult to identify juveniles and dimorphism from skeletal parts than from living organisms. Specimens of ammonites (fossil shells described in Chapter 8) now believed to be male and female forms of the same species, were once described as belonging to different genera (Fig. 3–10). Many species of foraminiferans (single-celled organisms also described in Chapter 8) exist in two forms (microspheric and megalospheric) which are much different in overall size and size of the embryonic chamber. This is the result of an alternation in the animal's life history between sexual and asexual reproduction modes.

Despite such difficulties paleontologists can usually find characteristics to measure that are not age

Figure 3-10 Dimorphic forms (macroconch and microconch) of the Jurassic ammonite *Eliganticeras elegantulum*. (Courtesy of Ulrich Lehmann, *Ammonites and Their World*, Cambridge University Press.)

dependent, can differentiate adults from juvenile specimens, and can identify dimorphism.

Types:

When, through a search of the literature and possibly through statistical comparisons, a paleontologist or a biologist is convinced that an undescribed species has been found and prepares to describe it as a new species, he or she sets aside in a museum a single specimen that is a typical example of the morphology of the species. This specimen is called the holotype of the new species and is conserved by the museum so that future paleontologists who wish to compare their specimens with the new species have a sample of what was defined as typical by the original describer. As a single specimen cannot illustrate the range of variation of the new species, the describer may designate several other specimens as paratypes and include them in the museum's collection. It has been suggested that the use of holotypes is misleading, as no single specimen can represent the range of variation found in a species, and later workers may assume that their specimens must be identical with the holotype in order to be recognized as members of the species. This is a misrepresentation of the purpose of the holotype. The holotype merely assures that, if the description or illustration of the new species is inadequate, there is on record a concrete expression of what the author of that species had in mind.

Paleontological Species Concept:

The biogeographic–genetic species concept has had a marginal effect on the practice of species identification and discovery by paleontologists and biologists. An essentially Linnean species concept is still used; that is, species are defined as the lowest grouping of morphologically similar individuals. Although statistical analysis of measurements may help the paleontologist to reveal morphological discontinuities separating species, the identification of a group of specimens as a new species is largely a subjective one, based by the specialist on long experience with the range of variation commonly found in the group of fossils studied and the range found in modern species of related organisms. Nevertheless, the biogeographic–genetic species concept has had a profound influence on our understanding of how species originate, evolve, and are distributed. It provides a theoretical foundation on which practical methods of species recognition can be based.

In this chapter, species have been treated largely as though they existed only in space, instead of in both time and space. The variation of species in time is the subject of evolution, and a species definition cannot be fully formulated without reference to the fact that organisms change from one species to another in time. Before we examine the problems of defining species in time, we will examine the history of life as preserved in the geological record.

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PART TWO

THE FOSSIL RECORD

Chapter 4

The Time of Microscopic Life

For most of geological time, organisms have lived in the earth's surface environments playing an essential part in the formation of the atmosphere and the seas, the erosion of the land, and the deposition of the sedimentary record. But living things were not always present on earth; there was a time when the earth's surface was lifeless. We now know that within the solar system, life is a unique feature of our planet and that even the nearest planets, Mars and Venus, probably never supported life.

Geologists and biologists have extended our knowledge of life history 3.5 billion years, almost back to the beginnings of the rock record. They have formulated hypotheses to explain the stages by which life could have formed from nonliving matter and evolved from the first living cells to the complex invertebrates of the beginning of the Paleozoic Era. At present, scientists are uncertain of the specific time when life began, and of the conditions on earth at that time. Nor have they have they been able to document in the fossil record the steps that led from complex carbon compounds to the first self-replicating, energy-regulating cells.

This chapter is concerned with the evolution of organisms that are capable of carrying on all of life's functions within a single cell. Some of them form colonies seen easily with the naked eye, but most noncolonial forms can be studied only under the magnification available in light and electron microscopes. These primitive organisms evolved slowly, and some that live today have almost identical ancestors in rocks 3500 million years old (Fig. 4–1). The record of their increasing complexity, adaptation to new environments and modification of environments by their life processes is contained in rocks of Archean and Proterozoic age. Three-quarters of the time span of life history is preserved in these rocks.

Pre-Paleozoic time can be divided into seven intervals (Table 4–1).

These divisions have not been standardized, nor have they been universally accepted. The eras are those recommended by the Decade of North American Geology Scale of 1983 (1), and the United States Geological Survey, who prefer the term pre-Archean for the Hadean Eon. A recent subcommission report recommends that the Early, Middle, and Late Proterozoic eras be called Proterozoic I, II, and III, respectively.

In the Hadean Eon, the crust of the earth was forming and the atmosphere and oceans appeared, setting the stage for the origin of life. The record of these events has not yet been found. They occurred prior to 3800 million years ago, the age of

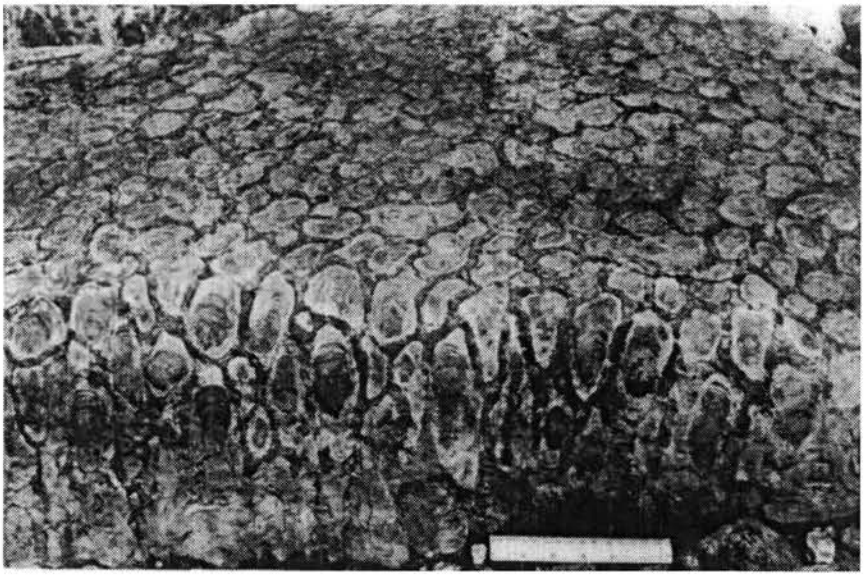

Figure 4-1 The columnar stromatolite *Mistassinia wabassiuon* from the Early Proterozoic Mistassini Group, Lake Mistassini, Quebec. (Courtesy of Hans Hofmann.)

the oldest earth rocks so far discovered. Our only evidence of this earlier period consists of mineral grains, dated as 4200 million years old, that have been incorporated as sedimentary particles in younger rocks. Our reconstruction of geological processes that occurred prior to 3800 million years ago must therefore be based solely on indirect evidence.

THE HADEAN AND EARLY ARCHEAN EARTH

Earth Origin and Hadean Environment:

The theory that the planets formed from a rotating disk of hydrogen and helium gases, water, ammonia, methane ices, and solid particles of iron and silicate minerals has been accepted by astronomers for about 40 years. The earth formed from solids and gases of the dust cloud at low temperature, but early in its history it passed through a hot stage. The heating of the embryonic earth was probably caused partly by the accumulation of energy from impact of solid bodies during the accretion process, and partly by the energy released by radioactive isotopes that were abundant at this early stage but have since decayed to extinction. The whole earth may not have reached a liquid state during this hot phase, but it became hot enough for iron to be mobilized and drain toward the center of the planet to form the core. At the same time much of the gaseous material trapped in the accretion process escaped into space.

TABLE 4-1 DIVISIONS OF PRE-PALEOZOIC TIME

EON	ERA	MILLION YEARS
	Late Proterozoic	900 to 675
PROTEROZOIC	Middle Proterozoic	1600 to 900
	Early Proterozoic	2500 to 1600
	Late Archean	3000 to 2500
ARCHEAN	Middle Archean	3400 to 3000
	Early Archean	3900 to 3400
HADEAN		4600 to 3900

The only direct evidence of the nature of the Hadean environment in the vicinity of the earth comes from the moon (Fig. 4–2). The astronauts who visited the moon in the seventies brought back rocks from the highlands that have been dated as between 4200 and 4400 million years old. These rocks indicate that frequent collisions of solids from the dust cloud were still taking place in mid-Hadean time. The uppermost layers of the earth are believed to have been accreted in late Hadean time, following the hot phase.

The first atmosphere of light gases that the Hadean earth inherited from the dust cloud is believed to have been lost in early Hadean time. The second atmosphere, in late Hadean and Archean time, was probably formed of the gases that were trapped in the earth during the final phase of accretion and

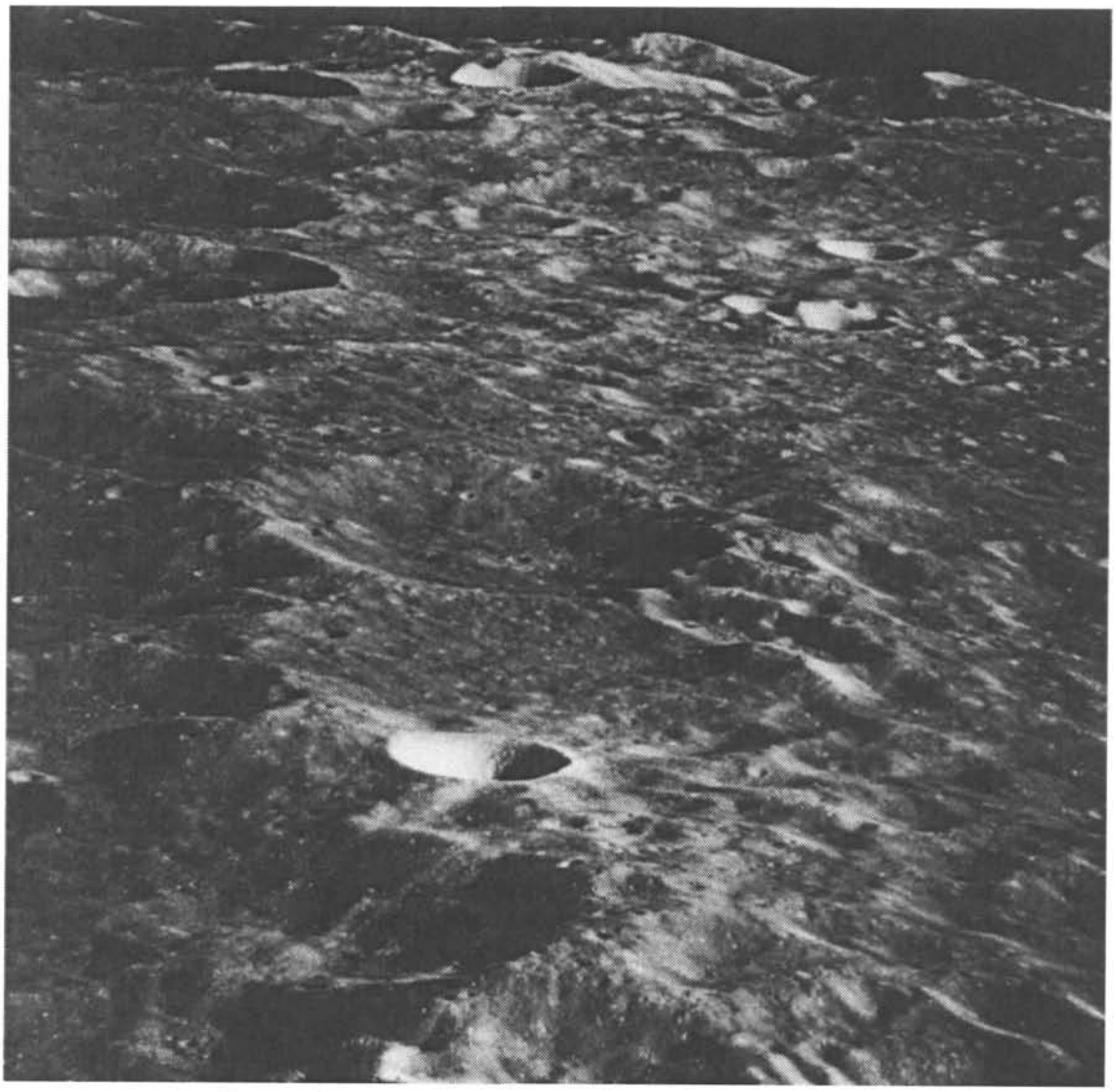

Figure 4-2 Cratered topography of the moon as photographed by the orbiting Apollo 10 astronauts. (Courtesy of NASA.)

subsequently leaked out. The escape of gases from the earth's interior, which is called degassing, must have been rapid then, but it still continues at lower rates as volcanoes and submarine fissures release water vapor, carbon dioxide, methane, hydrogen, and other gases, all of which are contributed to the atmosphere. Geologists do not agree on the specific composition of the second atmosphere.

The Early Archean Environment:

The first direct evidence of the environment of the earth's surface comes from the oldest rocks so far dated, the 3800-million-year-old Isua Group of western Greenland. They are composed of metamorphosed sediments such as cherts, conglomerates, shales, and carbonate rocks. The sediments were deposited in water and some are composed of particles eroded from a continental source area. They indicate that by this time the earth was cool enough for water in liquid form to exist in a large body, and that continental masses rose above the surface of this primitive ocean. The presence of carbonates in the sediments shows that carbon dioxide was present in the atmosphere. Unfortunately, the rocks have been considerably changed by me-

tamorphism and do not give additional definitive evidence of the nature of that atmosphere.

Scientists deduce the composition of the late Hadean atmosphere according to their assumptions about the timing of the hot phase, the formation of the core, and the availability of hydrogen at that time. One set of assumptions leads to the conclusion that the atmosphere was largely ammonia, methane, and hydrogen sulfide; another, that it was largely carbon dioxide, nitrogen, and water vapor. We know that by Early Archean time, water vapor derived from degassing had condensed into the original ocean. Space probes to both Mars and Venus have shown that their atmospheres are largely composed of carbon dioxide. This suggests that an atmosphere rich in carbon dioxide existed early in the history of all the inner planets and persists today in those planets where it was not subsequently modified by life processes.

Formation of Complex Carbon Compounds:

Compounds of carbon, hydrogen, nitrogen, and oxygen are the building blocks of life. The compounds that we recognize as necessary for life are complex polymers whose origin from simpler compounds must have taken place in Hadean time. Spectroscopic analysis of the light from interstellar gas tells us that some of these simple compounds, such as formic acid (HCOOH), methylacetylene (CH_3C_2H), and methylamine (CH_3NH_2), exist in space and were probably constituents of the primeval dust cloud trapped in the accreting earth. Simple organic compounds can be produced by the application of energy that would have been available from the sun, from lightning, or from thunder shock waves to the various gas mixtures that are possible models of Hadean and Early Archean atmospheres. Experiments in which such gas mixtures are subjected to electrical discharges and radiation show that such simple compounds as formic acid (HCOOH), formaldehyde (HCHO), alcohols (such as ethanol, CH_3CH_2OH), simple sugars, amino acids, and nitrogenous bases could have been formed under Hadean and Early Archean conditions. We conclude that the ocean of Early Archean time contained a variety of the simpler organic compounds left over from the dust cloud and produced by inorganic processes. However, biologists can only speculate on the path, or paths, by which simple carbon compounds passed to more complex polymers and eventually formed a cell that, through its properties of replication (reproduction of itself) and energy intake and regulation, is defined as being alive. A. Graham Cairns-Smith (2) has speculated that clay crystals, on which inorganic ions were replaced by simple organic compounds, may have been intermediates between living and nonliving systems. However, fossils of intermediate forms have not been found, nor have intermediate compounds been identified in rocks of Early Archean age.

The accumulation of complex carbon compounds could only have taken place in an atmosphere in which oxygen was either absent, or in very short supply. Although scientists are in doubt about the composition of that atmosphere, they are sure that it lacked oxygen. Some idea of the nature of early life-forms may be obtained by examination of modern unicellular organisms living in oxygen-deficient environments. Deep in ocean sediments, in soil, or in marshy ground, removed from the present oxygen-rich atmosphere, environments still exist that duplicate the oxygen-deficient atmosphere of the early earth. In these areas unicellular organisms similar to those of the Archean persist.

TYPES OF UNICELLULAR LIFE

Organisms that live in environments devoid of oxygen are called anaerobes, or are said to be anaerobic. Organisms that live in oxygen-rich atmospheres are aerobes, and those that live in both are amphiaerobes.

Eukaryotes and Prokaryotes:

All organisms are either eukaryotes or prokaryotes. The differences between the two are so profound that the prokaryotes have been considered to constitute a kingdom separate from all other organisms, the kingdom Monera (Fig. 4–3).

Eukaryotic cells have a nucleus bounded by a well-defined membrane, and prokaryotic cells have no nuclear membrane. The eukaryotes enclose in the nucleus two copies of the genetic code which separate into sex cells in reproduction; the prokaryotes have a single copy of the code within the cell body which duplicates when the cell divides in asexual reproduction. Eukaryotic cells oxidize sugars as a source of energy, whereas many prokaryotic cells are anaerobes. Eukaryotic cells are usually considerably larger than prokaryotic cells, and this is one

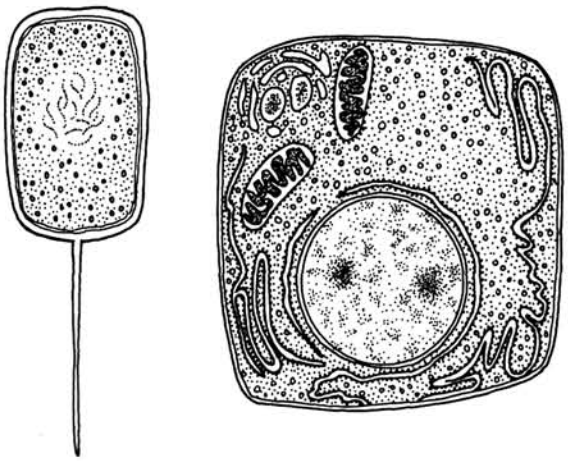

Figure 4-3 Major features of living prokaryotic and eukaryotic cells. Diagrammatic. Note the vague nucleoid in the prokaryotic cell and the membrane-bounded nucleus in the eukaryote. (*Source:* L. Margulis, *Early Life*.)

of the few criteria that can be used to distinguish them in the fossil record. Prokaryotes range in diameter from 0.3 to 20 micrometers and eukaryotes from 3 micrometers to several millimeters. The other differences either are behavioral or have not been preserved in the fossil record.

Unicellular Metabolism:

Modern unicellular organisms can be separated into six groups on the basis of their methods of obtaining energy. These methods probably evolved as life adapted to the earth's changing environments, but unfortunately direct evidence of metabolic pathways cannot be preserved.

Type 1—Anaerobic cells that obtain energy by assimilating complex carbon compounds. Examples are the bacteria that exist in the guts of most advanced animals and aid in the digestive process. The reaction used is that of fermentation.

Type 2—Anaerobic cells that use carbon dioxide to produce their own carbon compounds without the use of light. These bacteria are called methanogens because they produce methane from carbon dioxide.

Type 3—Anaerobic cells that use light to make carbon compounds from carbon dioxide, but use elemental hydrogen, or hydrogen sulfide, rather than water to supply the hydrogen for these carbohydrates. These bacteria use what is called photosystem-I in their photosynthesis, which is represented in highly simplified form by the equation: $CO_2 + 2H_2S + \text{light} = 2SO_2 + H_2O + CH_2O$ (organic compounds).

Type 4—Amphiaerobic bacteria that are capable of living in oxygen-rich or oxygen-deficient environments. These exist at present in sediments near the seafloor in which the oxygen level fluctuates.

Type 5—Aerobic cells containing chlorophyll which use light, carbon dioxide and water in what is called photosystem-II. This can be simplified in the equation: $CO_2 + 2H_2O + \text{light} = O_2 + H_2O + CH_2O$ (organic compounds).

Type 6—Aerobic cells that depend for energy on the oxidation of sugars. This process is called respiration.

The closeness of the relationship of one type of prokaryote to another is investigated by comparison of their amino acid sequences (Chapter 3). The biochemistry of these groups suggests that each did not give rise to the next most complex type in succession, but that the groups are stages in evolution reached in several lines of descent. Biochemistry confirms that the methanogens are a very primitive group that separated from the bacteria soon after the origin of life. To some, this justifies the formation of a separate kingdom, the Archaebacteria, which would also include sulfur- and sulfate-using bacteria. Photosynthesis apparently developed in many lines of bacterial descent and aerobic respiration did not develop once and spread but was a level of metabolism attained by different lineages (3,4).

DIRECT EVIDENCE OF PRE-PALEOZOIC LIFE

Some unicellular organisms secrete shells of mineral matter that are commonly preserved as fossils, but the primitive organisms that lived in Archean and Proterozoic time were completely soft-bodied and only rarely preserved. Until about 25 years ago they were almost unknown. Then the examination of black cherts in thin section showed minute cells preserved as organic residues in three dimensions. Since that time black cherts throughout the pre-

Figure 4-4 Tangle of algal filaments and spores from the Gunflint chert of Early Proterozoic age (approximate magnification ×800). (Courtesy of E. S. Barghoorn.)

Paleozoic succession have been examined (Fig. 4–4).

Black Chert Microfossils:

Many subspherical bodies the size of bacteria occur in pre-Paleozoic cherts but most of these were formed inorganically. Of the 22 reported occurrences of Archean microfossils, William Schopf and Malcolm Walter (5) recognize only two as including true microfossils. Two other collections include objects of doubtful significance and the rest contain only inorganic spheres and filaments. Because living bacteria are everywhere in the modern world, they can easily be included in samples collected for the purpose of finding pre-Paleozoic fossils and are easily mistaken for such fossils. Modern bacteria have undergone little evolutionary change since pre-Paleozoic times and still closely resemble their ancient ancestors in form. Therefore, great care must be taken to minimize contamination and to identify misleading bacteria that have entered cracks and pores of the samples after the rock was deposited. To qualify for acceptance as microfossils, the cells must be shown to be embedded in the rock and to have been deposited at the same time as the rock was formed. Although authenticated fossil localities of Archean age are extremely rare, 24 localities are known to yield early Proterozoic microfossils.

The oldest fossils come from the Warrawoona Group in the region of western Australia called North Pole because of its remoteness (6,7). The rocks bearing the black cherts are dated as between 3300 and 3500 million years old by interbedded volcanic flows. The fossils include long sinuous threads with diameters ranging from a fraction of

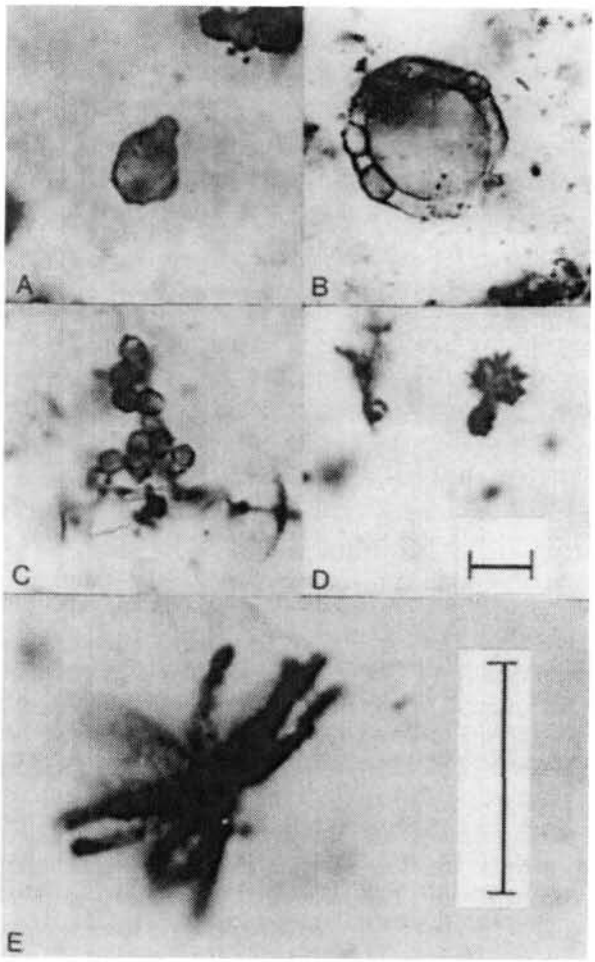

Figure 4-5 Microfossils from the Early Proterozoic Gunflint Formation, Lake Superior, Ontario. The scale bars are 10 micrometers long and that in Figure D applies to Figures A–D. A. *Huroniospora* showing budding. B. *Eosphaera tyleri*. C. *Huroniospora* in a cluster. D. *Kakabekia umbellata*, E. *Eoastrion simplex*. (Courtesy of Hans Hofmann and Geological Survey of Canada [neg. 140940] from *Iron Formations Facts and Problems*. Elsevier Science Publishers.)

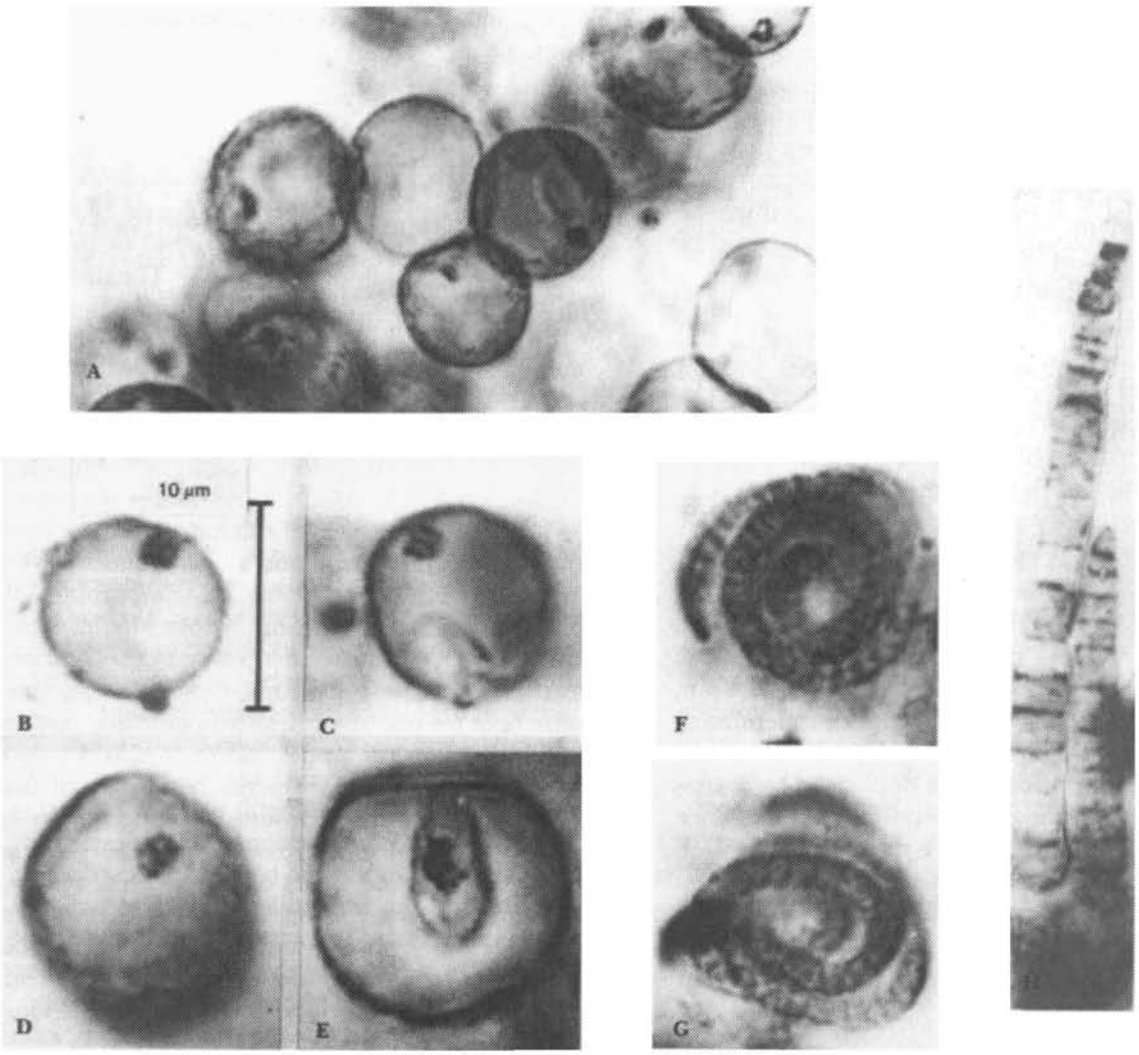

Figure 4-6 Microfossils from the Late Proterozoic Bitter Springs chert, Australia, magnified about 2500 times.
A. Green alga *Glenobotrydion aenigmatis* showing spots suggestive of intracellular structures. B–E. Single cells with internal granular areas suggestive of organelles and membranes. F, G. Coiled cyanobacterium *Contortothrix vermiformis*. H. Filamentous cyanobacterium *Cephalophytarion grande*. (Courtesy of J. W. Schopf, The Paleontological Society, *Journal of Paleontology*, and Kluiver Academic Publishers)

a micrometer to several micrometers, and globular groups of cells enclosed in a sheath. The largest filaments are divided by cross partitions and represent linear colonies of cells. These cellular filaments are similar in form to many modern prokaryotes and closest to cyanobacteria. The cyanobacteria (sometimes called blue-green algae) are photosynthetic bacteria of type 5. Isolated cells in the deposit have been identified as methanogens.

Black chert microfossils, from the Gunflint chert (8), were first described in detail by E. S. Barghoorn and S. A. Tyler in 1965. The fossils of Early Proterozoic age (1900 million years old) were found on the north shore of Lake Superior in western Ontario (Fig. 4–6). Most are long filaments consisting of cells similar to those that are today are characteristic of the cyanobacteria. Some of the filaments look like strung beads (Fig. 4–5). Other fossils in the Gunflint chert are more complex. Some large spherical cells have daughter cells arranged around them (*Eosphaera*); others are starlike in form (*Eoastrion*). The most complex fossil, which is called *Kakabekia umbellata*, consists of a bulbous cell joined by a shaft to a disk supported by radial arms, so

that it looks like a tiny umbrella. The affinities of this form are problematic, but very similar anaerobic bacteria have been found in modern ammonia-rich soils. *Kakabekia* is unlikely to be indicative of an atmosphere in which ammonia was a principal constituent, for other geochemical indicators suggest that by early Proterozoic time oxygen was becoming abundant, and ammonia would be unstable unless separated in some way from the oxygen.

The microfossils of the black chert of the Bitter Springs Formation in Australia are typical of Late Proterozoic assemblages. They are about 900 million years old. A large variety of cyanobacterial filaments have been found accompanied by the fossils of advanced eukaryotic algae. Among the most interesting fossils are those showing cell division (Fig. 4–6). In Bitter Springs cells, and in cells of other collections as old as 1800 million years, dark aggregates of matter appear that look like nuclei, or other intracellular structures typical of eukaryotic cells. The origin of these dark masses is controversial. When either eukaryotic or prokaryotic cells dry out, the cell contents shrink inside the cell membrane into a dark mass (Fig. 4–7). The dark structures of the Bitter Springs cells can be duplicated by drying modern prokaryotic cells; therefore their presence is not incontrovertible evidence that eukaryotes were present in Bitter Springs time. However, the large size of the cells is independent evidence of their eukaryotic nature.

Many black cherts containing microfossils occur within and around layered, domed structures called stromatolites.

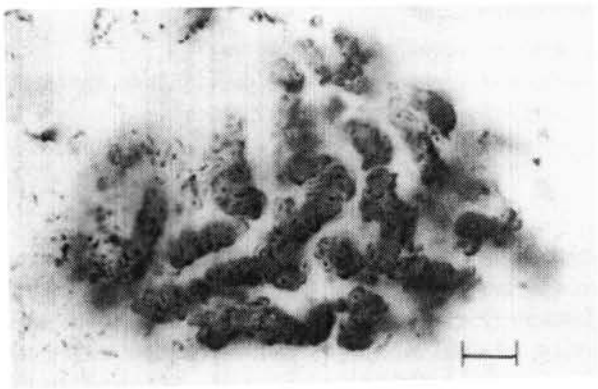

Figure 4-7 Coccoid cyanobacteria (*Eosynechococcus moorei*) showing pseudonuclei. From Early Proterozoic rocks 1900 million years old in the Belcher Islands, Canada. Scale bar 10 micrometers. (Courtesy of Hans Hofmann, The Paleontological Society, and *Journal of Paleontology*, v. 50, p. 1056.)

Stromatolites:

Finely laminated structures called stromatolites are built up of layer upon layer of mineral particles, commonly calcium carbonate, trapped or precipitated by bacteria or cyanobacteria (9). The thickness of the individual layers is usually a few millimeters, or fractions of a millimeter, but the layers can accumulate into structures many meters high (Fig. 4–8). In some stromatolites the layers are planar and build a tabular structure, but in most they are convex upward and build hemispherical, bulbous, or columnar forms. Modern freshwater stromatolites are formed of layers of calcium carbonate precipitated around the filaments of cyanobacteria. Modern marine stromatolites are communities of prokaryotic microorganisms whose surficial organic layers are stratified according to the light requirements of the organisms. Cyanobacteria that utilize light for photosynthesis and produce oxygen commonly form the upper layers; anaerobes that do not require light live in the basal part of the living layer. The sticky filaments of the bacteria trap a thin layer of calcium carbonate particles settling out of the water and, when covered with sediment, move through the accumulated layer to produce another sticky surface and trap the next layer. The layering may be a product of daily, monthly, or yearly cycles in the environment. Living stromatolites are uncommon but may be studied in western Australia at Shark Bay (Fig. 4–9), at Andros Island in the Bahamas, and in some lakes. When the microorganisms that form the stromatolite die and decay, little trace of their presence remains, except molds of the filaments. Stromatolites are identified on the basis of their growth form and microstructure. A single stromatolite may be formed by a community of several different bacteria, but the predominant builders are the cyanobacteria. Because most cyanobacteria are photosynthetic type 5 bacteria, the occurrence of stromatolites in ancient rocks suggests that photosynthesis was taking place at the time of their deposition and that oxygen was being produced.

Because many structures produced by microbes are not laminated, many paleontologists have expressed dissatisfaction with the term stromatolite. Robert Burne and Linda Moore (10) have suggested that the term microbiolite be used for all

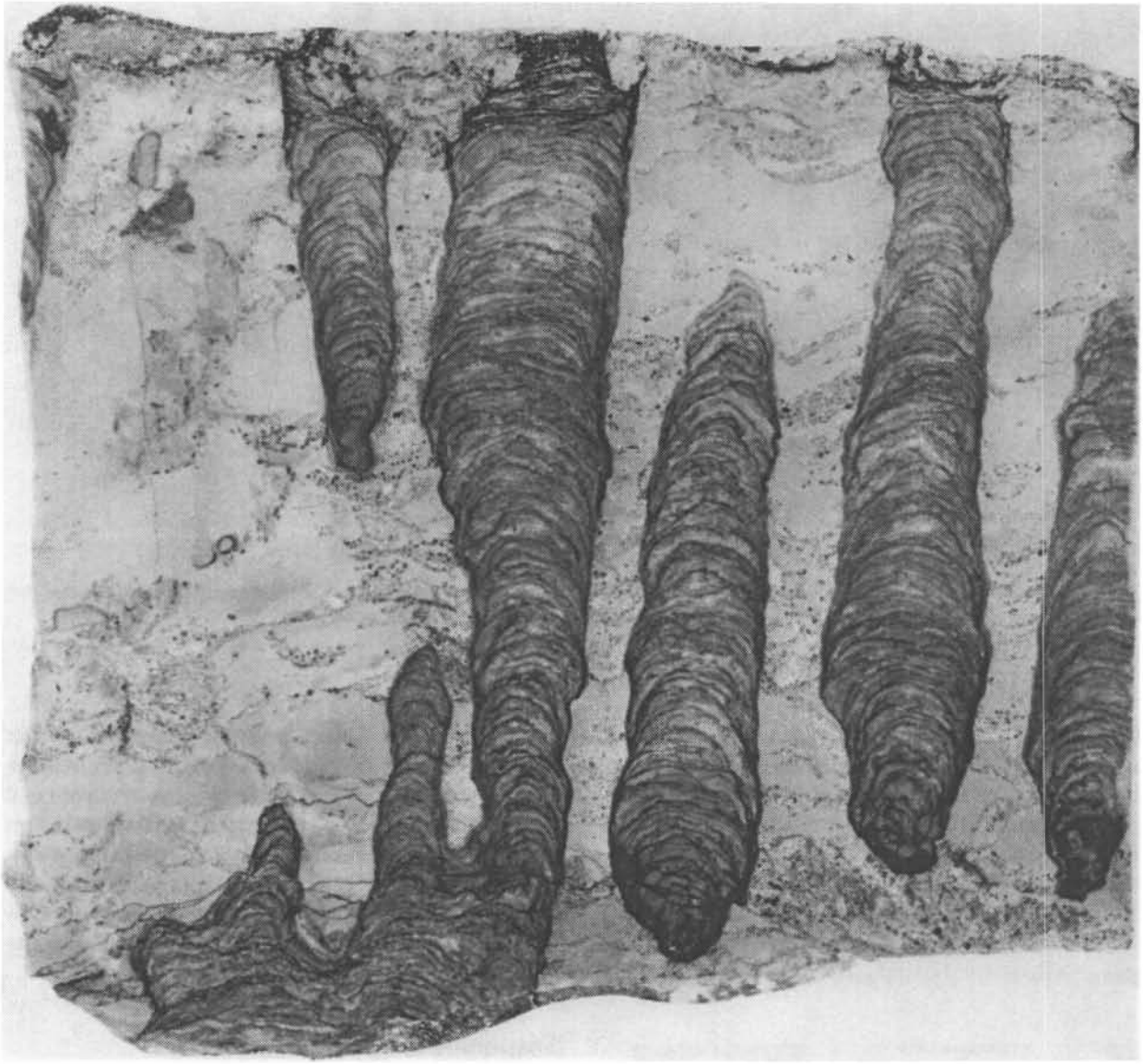

Figure 4-8 Stromatolites from Manitounuk Island, Hudson Bay; the columns are about 2 cm across. (Courtesy of Hans Hofmann and Geological Survey of Canada.)

structures that formed from microbial community action in trapping, binding, and causing mineral precipitation, whether laminated or not.

The oldest stromatolites are found in the same beds with the oldest microfossils in the Warrawoona Group of western Australia. These are nodular, bulbous, and columnar forms much like those produced later by cyanobacteria (Fig. 4–10). A possible conclusion from this similarity is that oxygen-producing photosynthesizers were already present at this early date. However, some cyanobacteria can switch from photosystem II to photosystem I, which does not produce oxygen, when conditions change. Possibly these Archean stromatolite builders used photosystem I, and therefore the presence of stomatolites need not imply oxygen production. At least 12 other occurrences of stromatolites in Archean rocks are known. These fossils become increasingly abundant in Late Archean time.

During the Proterozoic Eon stromatolites reached their greatest abundance and diversity. During early Proterozoic time stromatolites in a host of different

Figure 4-9 Underwater photograph of living subtidal stromatolites about 40 cm high at Shark Bay, Western Australia. (Courtesy of A. E. Cockbain, Geological Survey of Western Australia, and Elsevier Science Publishers.)

growth forms constructed carbonate barriers at the margin of the North American continental platform. Soon after the beginning of Paleozoic time stromatolites became less abundant and were restricted to very shallow water, usually intertidal environments. The youngest extensive stromatolitic limestones in the North American succession are of Early Ordovician age. The stromatolites called *Cryptozoon* form the Fossil Gardens that are a tourist attraction in the Late Cambrian limestones of the Saratoga Springs area of New York State. The mid-Ordovician decline of stromatolites may have been caused by competition for space in shallow-water environments from more complex and faster growing organisms such as corals, sponges, stromatoporoids, and advanced algae, or by predation by the rapidly expanding mollusc and arthropod population.

Figure 4-10 Oldest known stromatolite from Warrawoona Group, North Pole, Australia. Scale is 10 cm long. (Courtesy of M. R. Walter, reprinted by permission from *Nature*, v. 284, p. 444, © 1980, Macmillan Magazines Ltd.)

Dispersed Organic Matter:

Pre-Paleozoic rocks contain carbon and carbon compounds dispersed in small quantities. Geologists speculate that these are fragments and degradational products of primitive organisms that remained trapped in the sediment after the organism itself was destroyed. Organic matter in older rocks is referred to as kerogen. It is defined as the organic matter in rocks that is insoluble in organic solvents. It has no definite chemical composition and exists in various states of metamorphism. In extensively metamorphosed rocks, organic matter is reduced to the mineral graphite, a form of elemental carbon. It is difficult to determine whether the graphite that is widely distributed in Archean rocks is the remnant of organisms or whether it was produced

by metamorphic processes acting on carbonates. Biochemists can extract and analyse complex carbon compounds in small quantities and have discovered a wide range of compounds in pre-Paleozoic rocks that are at present produced only by organisms. These chemical fossils have been widely accepted as evidence of Archean life. Analyses of kerogen from the oldest rocks of the Isua Group have shown organic compounds, but these could have been produced either by primitive organisms or by inorganic processes acting in the primeval ocean as discussed earlier.

Stable Isotopes:

In order to distinguish compounds produced by life processes from those produced inorganically, biochemists have measured the proportions of the isotopes of carbon, nitrogen, sulfur, and oxygen that they contain. Nearly all the elements exist in various nuclear configurations called isotopes. Some isotopes are radioactive and can be used in dating rocks. The others are known as stable isotopes. Carbon has stable isotopes of atomic weights 12 and 13, which are symbolically represented as ^{12}C and ^{13}C. Oxygen has stable isotopes of atomic weights 16, 17, and 18; nitrogen, 14 and 15; and sulfur, 32, 33, 34, and 36. Although the isotopes of an element are identical chemically, they participate in reactions at slightly different rates owing to their different masses.

In chemical reactions that take place within organisms, the proportions between the isotopes in the organism and in the environment are changed, and the isotopes are said to be fractionated. A plot of the proportions of carbon isotopes of various organisms (Fig. 4–11) shows that organic carbons are enriched in ^{12}C over ^{13}C, compared to inorganic carbon of the atmosphere and oceans. However, the isotopic signatures overlap and a ratio is not specific to each organism.

The isotopic proportions of the kerogens in Archean rocks suggest, but do not prove, that they were produced by life. Kerogens 2000 to 3500 million years old have changes in ^{13}C values that range from −27 to −30 parts per thousand, in the range of many primitive organisms. Kerogens over 3500 million years old have values of about −16 parts per thousand, which may be interpreted as indicating that they are different and possibly inorganic in origin, although this value is within the range of the methanogens, cyanobacteria, and some plants.

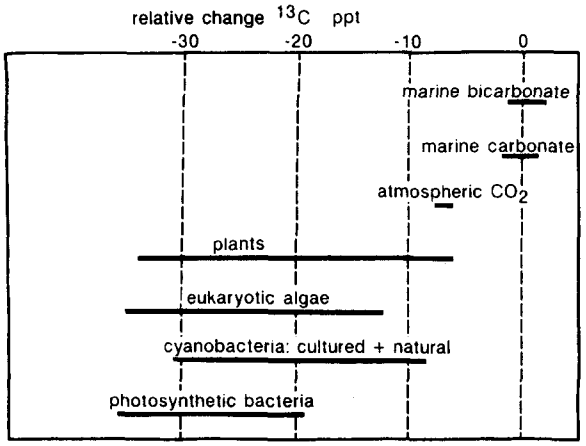

Figure 4-11 Carbon isotope composition of primitive organisms, the atmosphere, and the sea expressed as change of the carbon-13 isotope in parts per thousand (ppt) with respect to the carbon-12–carbon-13 ratio of a standard. Carbon-13 is depleted through fractionation by life processes.

OXYGEN LEVELS

Although oxygen is essential to cells that obtain energy by respiration, it is poisonous to anaerobes that are not equipped to use it. Eukaryotes have mechanisms for counteracting the deleterious effects of free oxygen but bacteria of types 1, 2, and 3 cannot live with it. In its presence no complex carbon compounds could have accumulated from inorganic processes before life began.

Although it could not have been generally available in the Early Archean atmosphere, oxygen may have been produced by photosynthesis or by the dissociation of water molecules by radiation from the sun. Some local, temporary concentrations, or oases, of oxygen could have existed where cyanobacteria formed stromatolites, but they would have been rapidly depleted in oxidizing organic matter and other compounds. Tracing the stages by which oxygen reached its present level of about 20 percent in the atmosphere has proved difficult, and geologists do not yet agree on what percentage was present at various times. Some evidence may be preserved in Archean and Proterozoic sedimentary rocks.

Evidence from Sedimentary Rocks:

In sediments that have been weathered from their parent rock and deposited under conditions where oxygen is present, the iron oxides are reddish

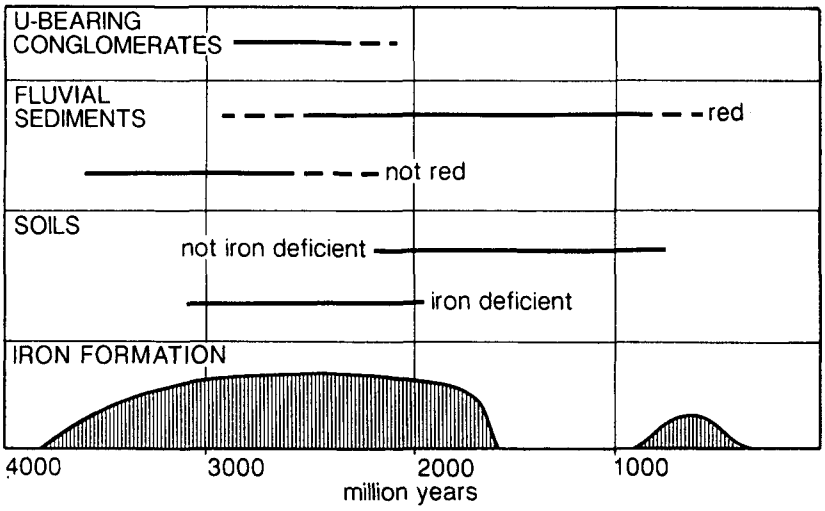

Figure 4-12 Sedimentary indicators of the oxidizing state of the atmosphere. The lines represent the range in time of the indicators; broken lines indicate uncertainty. Note that the indicators of oxidation (redbeds, iron-rich soils) overlap in time with those of a reducing atmosphere (uranium-bearing conglomerates, iron deficient soils) and a transition zone at about 2200 million years ago is suggested. (*Source:* Modified from J. W. Schopf and others, *Earth's Earliest Biosphere.*)

brown—they are in the oxidized, or ferric, state. Such sediments are called redbeds and they are common in Paleozoic and younger sedimentary successions. The oldest documented redbeds are between 2500 and 2000 million years old (Fig. 4–12). Red soils are also evidence that oxygen was available in the atmosphere when they were formed. The oldest red soils are about 2200 million years old. Banded iron formation (Fig 4.–13) is a sedimentary deposit that is confined to pre-Paleozoic rocks and is therefore believed to be a product of environmental conditions that disappeared at the end of Proterozoic time. Iron formation is composed of layers of iron oxides, such as hematite and magnetite, alternating with layers of iron silicates, iron-rich cherts, called jasper, and, locally, iron carbonate. The deposition of iron formation may have been controlled by periodic emissions from volcanic springs, by upwelling of deep iron-rich oceanic waters, or by blooming of microorganisms, but for all hypotheses ferric oxides in the deposits require that oxygen be available, at least locally, during deposition.

The oldest iron formation is found in the oldest rocks yet dated, the Isua Group of Greenland. Its presence suggests that this Early Archean atmosphere was not completely without oxygen. Deposits of this type reach their greatest abundance and widest distribution in rocks of Late Archean to Early Proterozoic age (3000 to 2000 million years old). Whether in their original state as silica-rich ores, or concentrated to nearly pure oxides by weathering, Early Proterozoic iron formations constitute nearly all the major iron ore deposits in the world.

Another sedimentary mineral deposit confined to the early part of Proterozoic time is uranium-bearing conglomerate. None is younger than 2200 million years. Commercially important deposits occur in the Elliot Lake mining area in Canada and in the Witwatersrand area of South Africa. The sedimentary particles of the mineral uraninite weather rapidly in the modern, oxygen-rich atmosphere, and their preservation through a cycle of erosion, transportation, and deposition in early Proterozoic time suggests an atmospheric oxygen level then of less than 1 percent of the present level. The restriction of these uranium ores to a particular time in the past suggests that deposition was terminated by a change in the worldwide environmental condition toward a more oxygen-rich atmosphere.

Eukaryotic Cells:

If eukaryotic cells could be easily recognized in the fossil record, their first occurrence would indicate when sufficient oxygen was available to support respiration. The oxygen level necessary to support respiration is about 1 percent of the present atmospheric level; this proportion is sometimes referred to as the Pasteur point. As already discussed, the identification of the first eukaryotes is a matter of disagreement, but William Schopf, one of the most experienced of pre-Paleozoic paleontologists, believes they can be recognized in rocks as old as 1500 million years.

These data suggest that progress toward the present oxygen-rich atmosphere was extremely slow. Some of the data seem contradictory. Oxygen was present only locally in the atmosphere and oceans

Figure 4-13 Contorted banded iron formation from Archean rocks, Beresford Lake, Manitoba. (Courtesy of Geological Survey of Canada.)

of Early Archean time. It was probably first produced in small amounts by photodissociation, but early photosynthesizers must have produced it in increasing quantities so that by Late Archean time when stromatolites and iron formation became widespread, oxygen oases were common. By mid-Proterozoic time when eukaryotes appeared, the oxygen level had reached about 1 percent of its present value. Some paleontologists have suggested that it did not reach its present value until the middle of the Paleozoic Era. From Hadean to Paleozoic time the atmosphere changed largely through the conversion of carbon dioxide to oxygen. The other major constituent, nitrogen, was derived either from early degassing or from oxidation of ammonia, and changed little in proportion after Hadean time.

Ozone Shield:

At present a layer of ozone (O_3 rather than the usual molecular form of oxygen, O_2) high in the atmosphere prevents much of the ultraviolet radiation of the sun from reaching the earth's surface. This radiation is lethal to many microorganisms. Before oxygen was an important constituent of the atmosphere, no ozone shield would have formed, and the full strength of the lethal radiation must have forced microorganisms to live beneath the sediment surface, or in deep water where the water column would provide some protection. The relative insensitivity of cyanobacteria to ultraviolet radiation may explain their early success. The evidence that Early Archean life developed in shallow water, however, has led some geologists to suggest that the ozone shield was in place at this time and that oxygen was more abundant than previously thought (11). The increasing availability of oxygen to form the ozone shield would have progressively opened new environments in the oceans' surface waters to more sensitive microorganisms.

DEVELOPMENT OF PRE-PALEOZOIC LIFE

On the basis of the evidence that has been reviewed, a plausible sequence of events, a scenario, or model, can be formulated as to how life evolved in the three-quarters of earth history that are the Proterozoic and Archean eons.

1. In Early Archean time the oceans were habitable. They contained a mixture of inorganically produced carbon compounds, a great deal of carbon dioxide, and only local traces of oxygen produced by dissociation.
2. Before 3500 million years ago living cells originated in the oceans by the joining of carbon compounds into complex molecules that characterize all life-forms. Consideration of current hypotheses of the origin of life is out of place here, for it requires a background knowledge of microbiology and biochemistry. These simple cells were capable of building stromatolites. The primary production for this first community was inorganic, or abiotic, that is, cells were anaerobes that obtained energy by absorbing inorganically produced carbon compounds from the primeval ocean and processing them by fermentation.
3. The next step was the development of methanogenic bacteria (type 2). With them came the first photosynthetic bacteria that used

photosystem-I to form organic compounds (type 3). Some cells did not separate when they divided and formed long filaments.

4. By Late Archean time stromatolites built by anaerobic microorganisms were abundant enough to make significant oxygen oases and some types of cells (type 4 amphiaerobes) developed mediating mechanisms so that they could live in both oxygen-bearing and oxygen-deficient environments.
5. Some time in the Late Archean Era microorganisms (type 5) began using photosystem-II. Through photosynthesis, oxygen in quantity became available. The cyanobacteria, probably the first organisms to use this mechanism, left a record of their flourishing in the abundant Late Archean and Early Proterozoic stromatolites. Some oxygen produced was immediately combined with ferrous salts to form the extensive deposits of sedimentary iron oxides. Preston Cloud has suggested that the potentially lethal oxygen produced by early photosyntheizers was removed from the sea as it oxidized the abundant iron salts in the ocean, precipitating them as iron formation (12,13).
6. The major step in the history of pre-Paleozoic life was the appearance of eukaryotic cells about 1500 million years ago, after 2 billion years of prokaryotic evolution. The step was so large that it was probably made through several intermediate stages. Many microbiologists believe that the intracellular organelles that characterize eukaryotes, such as the nucleus, plastids, mitochondria, and other organelles, were once independant prokaryotic cells that entered a large prokaryotic host cell for their mutual benefit (14). The organisms that resulted not only could use the rapidly increasing oxygen supply by oxidizing carbohydrates but also could reproduce sexually.

All prokaryotes reproduce by simple division: the one copy of the genetic code, which forms a ring within the protoplasm, is divided into two identical daughter cells. Because the daugther cells will be identical to their parent unless there is some serendipitous accident (mutation) which changes the composition of the genetic material itself, the rate of evolution of prokaryotes is extremely slow. Some bacteria are capable of exchanging genetic material through a thin bridge between them in a type of sexual process. In eukaryotes the genetic material is a sequence of genes arranged on paired chromosomes in the nucleus. In sexual reproduction the cells of both parents split into sex cells, or gametes, each of which takes one copy of the genetic material. The sex cells are dispersed and some eventually unite with sex cells from another individual of the same species to produce an individual that has some characteristics of each parent. By recombination of genes in sexual reproduction new variants of eukaryotic species are produced, some of which may be more advantageous to the survival of the species. Direct changes may also take place in the nature of the genes themselves through mutation. Innovations in the organism itself do not necessarily immediately follow mutation and recombination, as some of the new genes may be recessive, that is they are present in the chromosomes but not expressed in the body of the organism because their effect is overpowered by a dominant gene that determines the particular character or trait. The nature of dominant and recessive genes is discussed in elementary biology textbooks. The point to be made here is that sexually reproducing organisms can accumulate, in the form of recessive genes, a wealth of variation that only infrequently results in the character appearing in the body of the organism. However, this stored variability is available in the event of an environmental change that makes the common variant a less efficient competitor. The organism may have available a variant that can better cope with the changed circumstances and allow the species to persist in a modified form. Thus eukaryotes, in several ways, have potential for more rapid evolution than prokaryotes.

Despite this potential, the next step in the history of life—the appearance of many-celled organisms in which cells are specialized for various functions—did not take place for several hundred million years after the first appearance of the eukaryotes. The evolution of the first multicelled animals, called metazoans, took place at the close of the Proterozoic Eon.

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Chapter 5

Origin and Diversification of the Metazoa

METAZOANS AND PROTISTANS

Living organisms may be divided into five kingdoms (Fig. 5–1). The kingdom Monera consists of prokaryotic organisms, such as bacteria, considered in the last chapter. The eukaryotes that carry on all life processes within a single cell are placed in the kingdom Protista. Some of these single-celled organisms live by photosynthesis, like plants, some by digesting food particles, like animals, and some by both. Organisms consisting of many cooperating cells that live by photosynthesis constitute the Plantae. The primitive aquatic plants, generally known as algae, are placed by some in a kingdom with the Protista (the two together then constitute the kingdom Protoctista), by others in a kingdom of their own, and by still others (as in this book) in the plants. Fungi obtain food by absorbing organic matter through their cell walls, and the Animalia capture and digest organic matter produced by the other kingdoms. Some biologists recognize the viruses as a separate kingdom and others split the Monera into Archaebacteria (including the methanogens, sulfur-metabolizing and sulfate-reducing bacteria) and Eubacteria (or true bacteria). This chapter is concerned with the transition from single-celled eukaryotes (protistans) to animals composed of many cells that work together with specialized functions (metazoans).

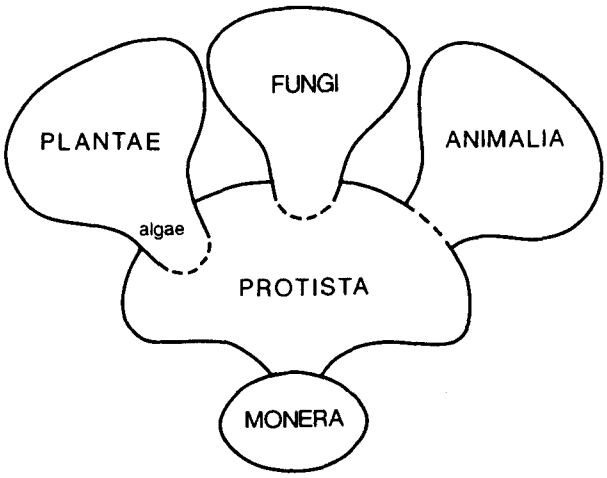

Figure 5-1 Relation between the five kingdoms of organisms recognized in this book.

Protistans are composed of single cells or colonies of cells, but in either case, each cell is capable of all of the life functions, such as ingestion, digestion, respiration, reproduction, and excretion. In the

Animalia, cells are specialized for various functions and cooperate for the good of the whole organism. The Animalia are said to have reached the metazoan stage of organization. The specialized cells of metazoans are united into tissues, such as the exterior membrane or skin of an animal formed of flattened protective cells, or the digestive surface formed by the cells that line the gut. Tissues are united into organs, such as the heart, kidneys, and lungs which facilitate the circulation of fluids, the excretion of wastes, and the exchange of gases with the water or air. The simplest animals are those without backbones, known as invertebrates.

ANIMAL PHYLA IN THE FOSSIL RECORD

The invertebrates are an informal division of the Animalia that includes animals only slightly more complex than colonial protistans, and others, such as insects and sea urchins, with many intricately interacting organ systems. Most invertebrates, and all primitive ones, live in water and a vast majority live in the sea. The bodies of the simplest animals are small and composed of only a few cell layers. As a result, few of the cells are more than a millimeter or so from the water in which they live. The cells can obtain food and oxygen, and excrete wastes by diffusion through the cell walls that are directly in contact with the water, or through a layer of adjacent cells. As animals become larger and more active, with thicker bodies, interior cells become so separated from sources of food (the digestive tissue) and waste disposal (the exterior of the animal) that a system of plumbing is needed to circulate fluid bearing food and oxygen, and to remove waste. A pump, or heart, is needed to maintain flow in the pipes. Excretory organs, such as kidneys, are needed to dispose of the wastes in the fluid. A liver is needed to clean the circulating fluid, the blood. A whole range of organs was developed in the invertebrates as they grew in size, increased their activity, and invaded new environments.

The simplest invertebrates do not have organ systems, only sets of specialized cells united into tissues. (Some biologists would not consider the cell layers of the sponges to be tissues.) They consist of a cavity lined with digestive cells which is enclosed in a sheet of protective cells. When organ systems developed, they were located in cavities, called coeloms, in the body between the gut and the protective cells (Fig. 5–2). The primitive invertebrates, because they do not have coeloms, are said to be acoelomate; the rest are said to be coelomate.

The number of invertebrate phyla that are recognized varies from reference book to reference book. The variations depend largely upon the status given to a varied group of worm-like animals that have scanty fossil records. As this group is rarely encountered by paleontologists, it is given little attention in this book. Of the 50 or so invertebrate phyla recognized by some biologists, only eight have significant fossil records. The Protozoa are not invertebrates but are commonly grouped with invertebrates, because they are their immediate ancestors. The Chordates are by definition not invertebrates but those chordates that have close affinities with invertebrates are described in the following chapters with the invertebrates (Table 5–1).

Protozoa:

The protozoans are animal-like protistans, that is, they obtain food by capturing other organisms. Some

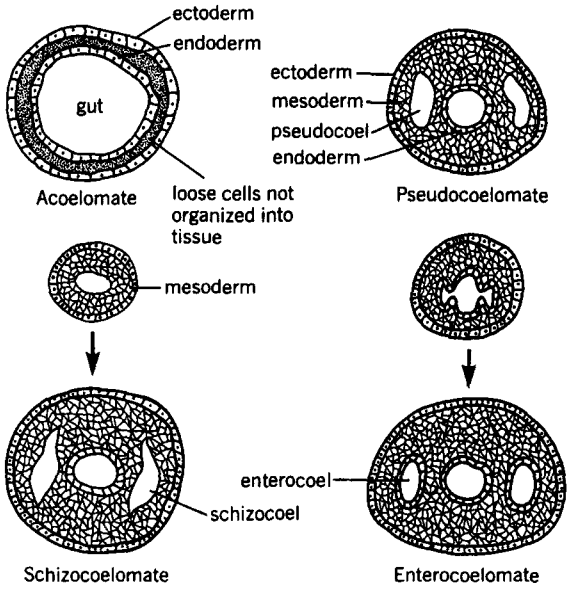

Figure 5-2 Diagrammatic representation of the development of the coelom in invertebrates. In acoelomates, there is no coelom in the unorganized cells between the endoderm and ectoderm. In pseudocoelomates, the pseudocoel is the space unfilled with mesoderm. The schizocoel develops by a split in the mesoderm. An enterocoel initially develops as pouches from the gut.

Table 5–1 PHYLA OF INVERTEBRATES AND PROTOCHORDATES WITH A MAJOR FOSSIL RECORD

	TISSUES AND ORGANS Tissues–T Organs–O	TISSUE LAYERS Endoderm–En Ectoderm–Ec Mesoderm–M	COELOM TYPE Acoelomate–A Coelomate–C Schizocoelomate–S Enterocoelomate–E	METAMERISM Oligomeric–O Metameric–M Pseudometameric–P	MOUTH Protostome–P Deuterostome–D
Protozoa	Neither	None	A	–	–
Porifera	?T	En, Ec	A	–	–
Cnidaria	T	En, Ec	A	–	–
Brachiopoda	T & O	En, Ec, M	C	O	P & D
Bryozoa	T & O	En, Ec, M	C	O	P & D
Mollusca	T & O	En, Ec, M	?	P	P
Annelida	T & O	En, Ec, M	S	M	P
Arthropoda	T & O	En, Ec, M	S	M	P
Echinodermata	T & O	En, Ec, M	E	O	D
Protochordata	T & O	En, Ec, M	E	O	D

of them secrete small shells of calcium carbonate or silica and have extensive fossil records. Since they are single-celled, they are neither metazoans nor invertebrates, but the more complex members reach organizational levels comparable to those of the Porifera.

Porifera:

The poriferans are the sponges. They probably developed from protozoans with whiplike extensions surrounded by a collar of fine hairlike processes. In the sponges, layers of these collar cells form digestive surfaces in internal cavities of the body through which water is impelled by the motion of the whips. Microorganisms in the circulating water are trapped by the collars and digested to produce food for the sponge.

Cnidaria:

This phylum comprises the corals, jellyfish, and their relatives. These animals are simple digestive sacks consisting of digestive tissue that lines the interior, protective tissue covering the outside of the animal, and a jellylike layer between the two. These animals capture small organisms in the water by means of tentacles equipped with stinging cells.

Brachiopoda:

The brachiopods are a small group of invertebrates enclosed in two shells. To feed they open their shells and filter micoorganisms and organic matter from the seawater with a comblike organ called a lophophore. They are more complex organisms than corals, and have organ systems for the circulation of fluids and the excretion of wastes. In brachiopods, and all more complex invertebrates, three layers of cells can be distinguished rather than the two of the lower invertebrates: the protective outer layers, called the ectoderm; the digestive surfaces, called the endoderm; and the cells between, which constitute the mesoderm.

Bryozoa:

Bryozoans are small colonial organisms that build a calcareous skeleton much like that of the corals. However, they have soft parts organized like those of the brachiopods. They have the same type of filtering apparatus for food gathering, the lophophore.

Mollusca:

The molluscs include the clams, squids, octopuses, and snails of the present day, their many fossil representatives, and several minor and extinct groups.

Many members of this phylum secrete a shell or pair of shells that enclose the soft parts. The molluscs have organs for respiration (gills), circulation (heart), digestion (digestive gland), etc., but do not have a well-developed body cavity or coelom.

Annelida:

The annelids are the segmented worms. In annelids the organ systems, appendages, and musculature are repeated in many almost identical segments along the axis of the body. As members of this phylum do not secrete skeletons, their fossil record is largely confined to their jaw parts, which are called scolecodonts, their burrows, the linings of the burrows, and their tracks in sediments.

Arthropoda:

This phylum includes not only the insects, spiders, and centipedes, but also the marine crabs, lobsters, and their minute floating and swimming relatives. The number of segments in the body is less than in the annelids, and different sets of segments are specialized for various functions, such as walking, swimming, or food handling. The segments have paired appendages that are modified to serve these functions. Arthropods secrete a rigid skeleton around the outside of the body (the exoskeleton) and therefore, to be efficient, these appendages must have flexible joints. The arthropods are among the most complex and successful of the invertebrate phyla.

Echinodermata:

Familiar members of this phylum of exclusively marine animals are the starfish and sea urchin. Other more obscure members of this group living today are the sea cucumber and sea lily (crinoid). Many members of the phylum secrete skeletons made up of plates of calcite fitted together, therefore they have a diverse and extensive fossil record. The echinoderms differ from other complex invertebrates in their fivefold symmetry and their intricate hydraulic water system that controls locomotion, food handling, and respiration.

Chordata:

By definition this phylum is not an invertebrate group because most of its members are characterized by a vertebral structure, a strengthening rod, or backbone. However, many of the primitive members, called protochordates, resemble invertebrates more than they do the advanced chordates called vertebrates. The modern representatives of the protochordates are marine organisms called sea squirts and acorn worms. The importance of the protochordates to the paleontologist lies in the information they give about the relations between the invertebrates and the vertebrates. The graptolites, a group of extinct, abundant fossils, probably were early protochordates.

All of these phyla, their living representatives as well as their fossil ones, are considered in greater detail in subsequent sections of this book.

RELATIONS BETWEEN THE PHYLA

One of the major unsolved problems of paleontology is the origin of the invertebrate phyla from advanced eukaryotic cells at the end of Proterozoic time. Two types of evidence provide information for the solution of this problem: the fossil record, and the comparative anatomy and embryology of living representatives. We will consider the latter first.

Development of the Coelom:

The relations between the invertebrate phyla are revealed by the origin of their coelomic cavities. The Cnidaria, Porifera, Protozoa, and Platyhelminthes (a group of flatworms that do not have a fossil record) are without a coelom and are said to be acoelomate. The molluscs have a poorly developed coelomic cavity and may be closely related to the acoelomates.

In coelomates the body cavity may form during the development of the embryo in various ways (Fig. 5–2). In the phyla grouped as the pseudocoelomates, it is the space between the gut (endoderm) and the external covering (ectoderm) that has not been filled with mesodermal cells during development. The phyla within this group (e.g., the rotifers and nematodes) are wormlike in form. Many are parasitic in habit, small in numbers, and most do not have a fossil record.

In embryos of echinoderms and chordates the coelom is formed when pouches from the gut ex-

tend into the mesodermal cells and are pinched off. These cavities are called enterocoels.

In the annelids and arthropods the coelom forms first as a split in the mesodermal tissue and is therefore called a schizocoel.

The way in which the coelom is formed (or not formed) divides the invertebrates into four groups: acoelomates, pseudocoelomates, enterocoelomates, and schizocoelomates (Table 5–1).

Metamerism:

Metamerism is a term zoologists prefer to the term *segmentation*. The phyla, such as the annelids and the arthropods, in which segmentation of the coelom and organs divides the whole body, are said to be metameric. In most of the other phyla the body cavity is divided into three parts from head to tail; these phyla are said to be oligomeric. In the Mollusca, the musculature of one of the primitive classes is repeated down the axis of the organism, but segmentation is not comparable to that of the annelids or arthropods. This condition is said to be pseudometameric. On the basis of segmentation the arthropods and annelids are separated from the rest of the phyla and the molluscs are distinct from both groups.

Location of the Embryonic Mouth:

In the early stages in the development of most invertebrates, the embryo is a hollow ball formed of a single layer of cells. One side of the ball pushes inward, is said to invaginate, to form a primitive digestive cavity and the cells that line the invaginated part become the digestive surface, or endoderm (Fig. 5–3). In the group of invertebrates that includes the molluscs, annelids, and arthropods, the entrance to this cavity becomes the mouth of the digestive system and the exit for the digestive tract (anus) develops by another infolding of the external cell layer that joins the opposite end of the digestive cavity. This group of phyla are called protostomes (Greek, *protos* = first, *stoma* = mouth). In the echinoderms and chordates, as the embryo develops beyond the invaginated ball stage, a new mouth forms opposite the aperture and the first aperture becomes the anus. These phyla constitute the deuterostomes (Greek, *deuteros* = second).

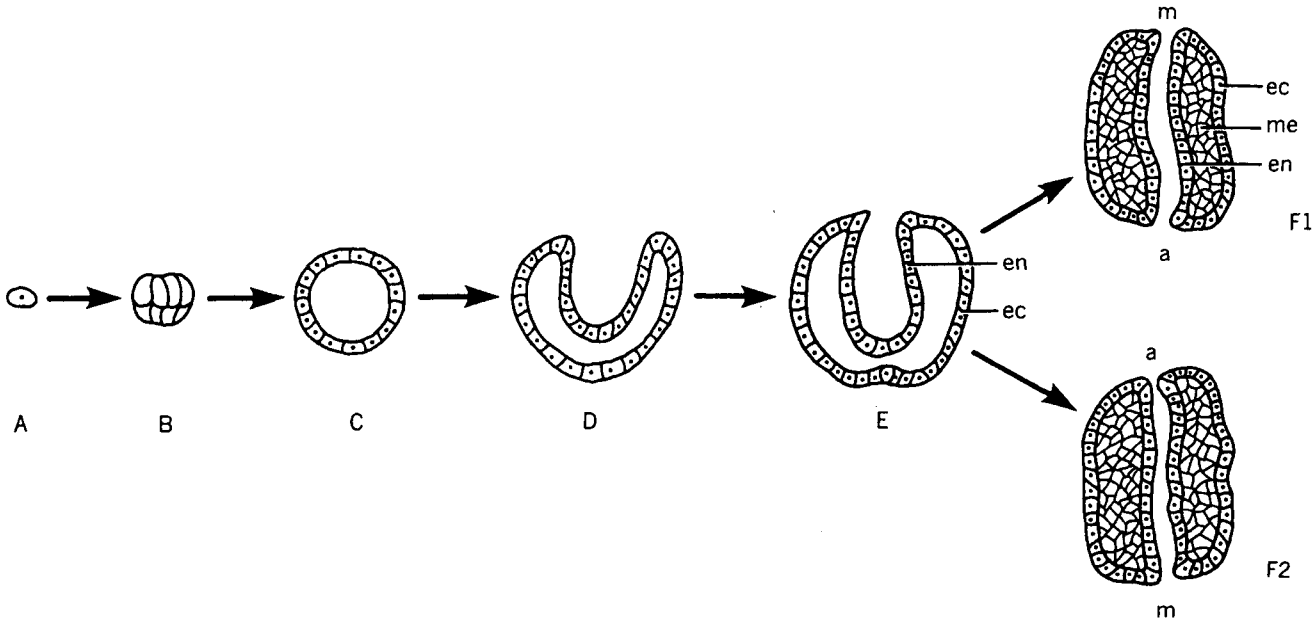

Figure 5-3 Diagrammatic representation of the early stages in the development of invertebrates. The diagrams are not to scale. A. Fertilized cell, B. Multiplication of cells by cleavage, C. Formation of a hollow ball of cells, D. Invagination of the hollow ball to form a digestive cavity, E. Differentiation of the lining of the cavity into endoderm (en) and the outer covering into ectoderm (ec), F. Filling of space between the endoderm and ectoderm with mesoderm. In protostomes (F1), the mouth (m) is at the site of the invagination; in deuterostomes (F2), the anus is in this position and a new mouth is formed.

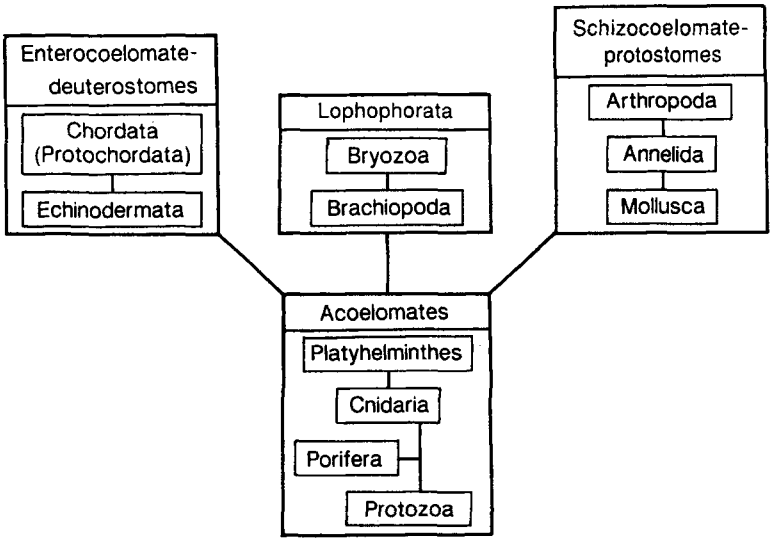

Figure 5-4 The major groups of invertebrate phyla. The lines joining the boxes suggest that the acoelomates are ancestral to the other groups.

Lophophorates:

The position of the embryonic mouth and the origin of the coelom separate the echinoderm–chordate group of phyla (deuterostomes, enterocoelomates) from the annelid–mollusc–arthropod group (protostomes, schizocoelomates). However, the brachiopods and the bryozoans do not separate neatly into these divisions. These phyla have characteristics in their embryonic development that suggest affinities with both the deuterostomes and the protostomes, and with both the schizocoelomates and the enterocoelomates. For this reason, when the relations between the phyla are expressed in a diagram (Fig. 5–4), these two phyla are commonly placed between the annelid–mollusc–arthropod group and the echinoderm–chordate group. Because both the bryozoans and the brachiopods possess a lophophore, the term lophophorates is used to refer to these phyla.

Embryology and Historical Relationships:

Why is the embryonic development of invertebrates so important to those who try to find relationships between phyla and the sequence in which they were derived from one another? The similarities between animals may not be obvious from a comparison of their adult forms, but the relations between them appear more clearly in their embryos. The principle that the embryos of animals resemble the embryos of other related animals much more than do adult forms was first recognized by the German biologist Karl Ernst von Baer (1792–1876). The pathways by which the fertilized cells of an invertebrate grow into an adult are relatively few. Some of the major differences in these pathways, such as the development of the coelom or the mouth, have been described above. The branchings of the developmental pathways are believed to preserve in the life history of the individual different adaptive choices made by ancestors at the time when the phyla were diversifying. For example, segementation may have developed in primitive invertebrates to produce efficient burrowing movements, but many annelids that acquired segmentation early in their embryonic development are no longer burrowers. As the individual develops from the fertilized cell, the structures that are basic to the organization of its phylum, such as coelomic configuration, segmentation, and organ systems, are modified by the development of structures related to the specialized adaptations of that particular species. Therefore the structures that are essential to membership in a phylum are more clearly seen in embryos, and the relations between phyla are more clearly revealed by a comparison of embryos. We will return to this subject in Chapter 15 and discuss its relationship to the mechanisms of evolution.

By comparison of adult and embryonic anatomy of living invertebrates, the phyla can be placed in an organizational diagram (Fig. 5–4). The diagram represents the structural similarity between the invertebrates that are common in the fossil record and suggests how one might have been derived in time from another, but to produce a model of the course of differentiation of the phyla at the end of the Late Proterozoic Era, we must determine whether

the conclusions from these comparative studies are supported by the fossil record.

PALEONTOLOGICAL RECORD OF THE EARLY METAZOA

The interval of earth history during which the diversification of the metazoans took place, at the end of the Proterozoic Eon, has been given various names, none of which has as yet received the approval of stratigraphic commissions or international acceptance. This interval lies between the end of the Late Proterozoic glaciation (approximately 680 million years ago) and the beginning of the Paleozoic Era, marked by the appearance of fossils of animals with hard skeletons. In this book, the term Ediacaran as defined by Preston Cloud and Martin Glaessner (1) is used, but the interval is considered to be part of the Late Proterozoic Era, not of the Paleozoic Era as they propose.

Tracks and Burrows:

The fossils of the earliest metazoans are not their shells nor the impressions of their bodies, but burrows that they have left in soft sediments. The oldest undisputed metazoan traces come from rocks of early Ediacaran age. Structures that have been described as metazoan traces have been recorded from older Late Proterozoic rocks (680 to 900 million years old) but the interpretation of these older structures is controversial. The oldest structures that may be metazoan burrows have been described by Erle Kauffman and James Steidtmann (2) from rocks as old as 2000 million years. A famous fossil of doubtful significance is *Brooksella canyonensis* (Fig. 5–5) from the middle Proterozoic beds of the Grand Canyon (1100 to 1300 million years old). It was originally described as a jellyfish impression and given the name of a jellyfish genus, but has now been interpreted as either the trace of a burrowing complex metazoan (3) or as a deformed sedimentary blister (4). Many paleontologists ascribe all pre–Ediacaran metazoan fossils to inorganic processes such as the escape of water or gas from consolidating sediments. The most convincing evidence for pre–Edicaran metazoan fossils are carbonaceous, transversely ridged tubes found below late Proterozoic tillites in China, but the affinity of these has also been questioned (5). At the beginning of the Ediacaran successions, indisputable traces of

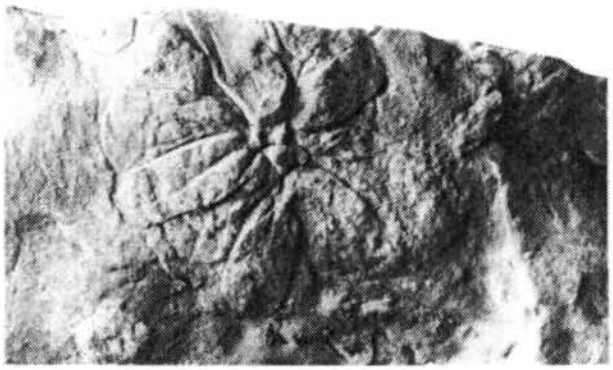

Figure 5-5 A Middle Proterozoic structure of doubtful significance, *Brooksella canyonensis*, from the Grand Canyon. It has been interpreted as a jellyfish, a sedimentary blister, and a trace fossil. (Courtesy of Smithsonian Institution.)

metazoans that burrowed subhorizontally to shallow depths in the mud and sand appear in abundance. They are joined in late Ediacaran strata by the traces of animals that crawled along the surface, including traces that could only have been formed by such complex invertebrates as arthropods. Until the close of the Proterozoic, burrows were less than 2 cm deep but at that time deeper vertical burrows become common, possibly in response to the appearance of predators. The sequence from simple, shallow, horizontal burrows to horizontal, transversely annulated burrows, to horizontal burrows with upward prolongations, to vertical burrows, and finally to arthropod traces may be the key to biostratigraphic zonation of Ediacaran strata.

The Ediacaran Fauna:

A fauna of early metazoan body fossils (as opposed to trace fossils) is preserved in the Pound Quartzite in the Flinders Range of South Australia. The rock is a sandstone formed from sands on which the organisms were impressed as they lay on the seafloor. The soft bodies of the organisms themselves have decayed. The impressions have not preserved fine details of the animals' surfaces because the sand that has taken the impressions is relatively coarse (Fig. 5–6). In all, 28 genera of metazoans have been described from the Pound Quartzite.

Most of the organisms preserved are what are commonly known as jellyfish and more technically

Figure 5-6 Fossils of metazoans from the latest Proterozoic Ediacaran interval. A. *Spriggina floundersi* (×2), B. *Tribrachidium heraldicum* (×1.5), C. *Charniodiscus arboreus* (×0.25), D. *Dickinsonia costata* (×1), E. *Cyclomedusa radiata* (×0.7). (Courtesy of R. Jenkins, M. F. Glaessner and *Science*, v. 217, p. 783, © 1982 by the AAAS.)

as medusoids. They have been assigned to several classes of the Cnidaria, but some are difficult to place in any living group. In all, 12 genera of medusoids have been described so far. Some of the more common forms are illustrated in Figures 5–6 and 5–9. The second largest group of Ediacaran fossils are leaflike organisms as long as 1 m that were anchored to the seafloor (Fig. 5–6, 5–9). They are considered to be colonial cnidarians that were composed of many polyps housed in depressions on the leaflike structures. Modern relatives of these cnidarians are the sea pens and sea fans, which are referred to as the soft corals because they do not secrete a solid skeleton. Three genera have been referred to the Annelida and two to the Arthropoda. *Tribrachidium* (Fig. 5–6) is a disklike impression with three symmetrical bent arms on its surface. Its resemblance to some primitive, pancakelike echinoderms of the early Paleozoic called edrioasteroids has suggested that it is an early representative of the phylum Echinodermata. However, the echinoderms characteristically have a fivefold symmetry; no other invertebrate has the threefold symmetry of *Tribrachidium*. A discoidal Ediacaran fossil with five radial grooves on the surface (*Arkarua*) has also been described as an ancestral edrioasteroid.

Since this remarkable fauna was found in the Flinders Range in the mid-1940s, similar fossils have

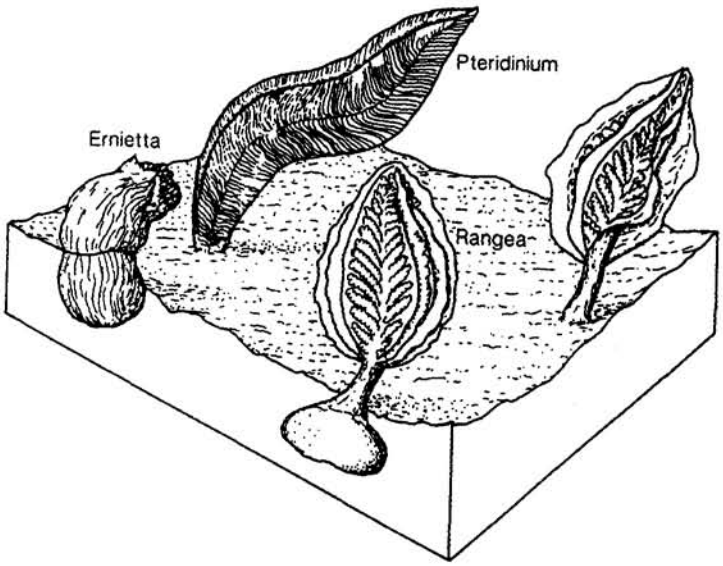

Figure 5-7 Reconstruction of primitive attached cnidarians (Petalonamae) from the late Proterozoic of Namibia, Africa. (*Source:* Based on reconstruction by Richard Jenkins.)

been found in beds of Ediacaran age in many places around the world. About 25 localities have been found and more are discovered every year. One of the richest faunas comes from the Nama Group of South Africa which overlies the Numees tillite, a deposit of the Late Proterozoic glaciation. This fauna was first described in the early years of this century. The tubular worm fossil, *Cloudina*, occurs at the base and in the middle of the group. In the middle part a diverse group of medusoids have been found, and many genera of leaflike colonial cnidarians including *Rangea* and *Petridinium* (Fig. 5–7). So widespread and varied are the attached cnidarians that H. D. Pflug (6) has suggested that they be recognized as a special order, the Petalonamae. Many genera of the Australian Ediacaran fauna occur in the Soviet Union where equivalent beds constitute the upper part of the Vendian System. Particularly rich finds have been made along the coast of the White Sea in arctic Russia and in the Ukraine. Other important Ediacaran faunas have been reported from England and China.

In North America the fauna appears in the Conception Group of eastern Newfoundland. It includes an enigmatic spindle-shaped organism (Fig. 5–8) whose surface is like the colonies of *Rangea*. The fossil impressions in Newfoundland are on beds below volcanic ash beds. Apparently the floating, fragile animals were killed and buried on the seafloor during eruptions of nearby volcanoes.

Figure 5-8 Spindle-shaped metazoan fossil from the latest Proterozoic Conception Group, eastern Newfoundland. (Courtesy of M. A. Anderson and S. B. Misra.)

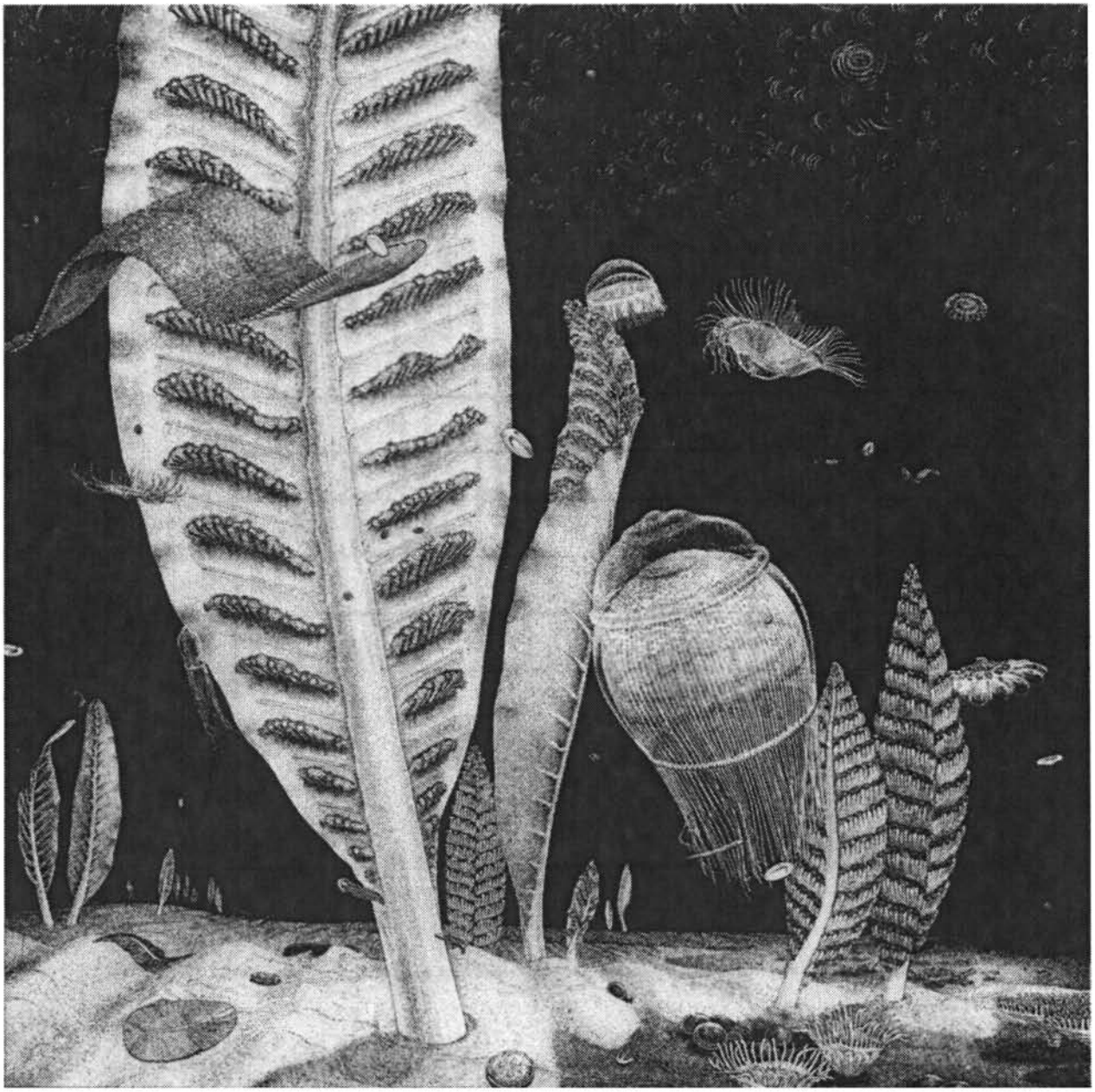

Figure 5-9 Reconstruction of some components of the Ediacara fauna. The large leaflike organism in the foreground is *Charniodiscus*. Various medusoids are reconstructed in the water. A large *Dickinsonia* undulates through the water while another lies on the sediment surface near a *Tribrachidium*. (Courtesy of Mary Wade, Robert Allen, and the Queensland Museum, Brisbane.)

The soft-bodied fauna of medusoids, colonial cnidarians, annelids, arthropods, and enigmatic forms disappears before the end of the Late Proterozoic Era, and youngest Ediacaran rocks contain only trace fossils. In this fauna we glimpse a fleeting stage in the diversification of the metazoa, a record of animals that may have given rise to the more diverse and abundant invertebrates of the Cambrian and later periods, but which became extinct before the end of the era.

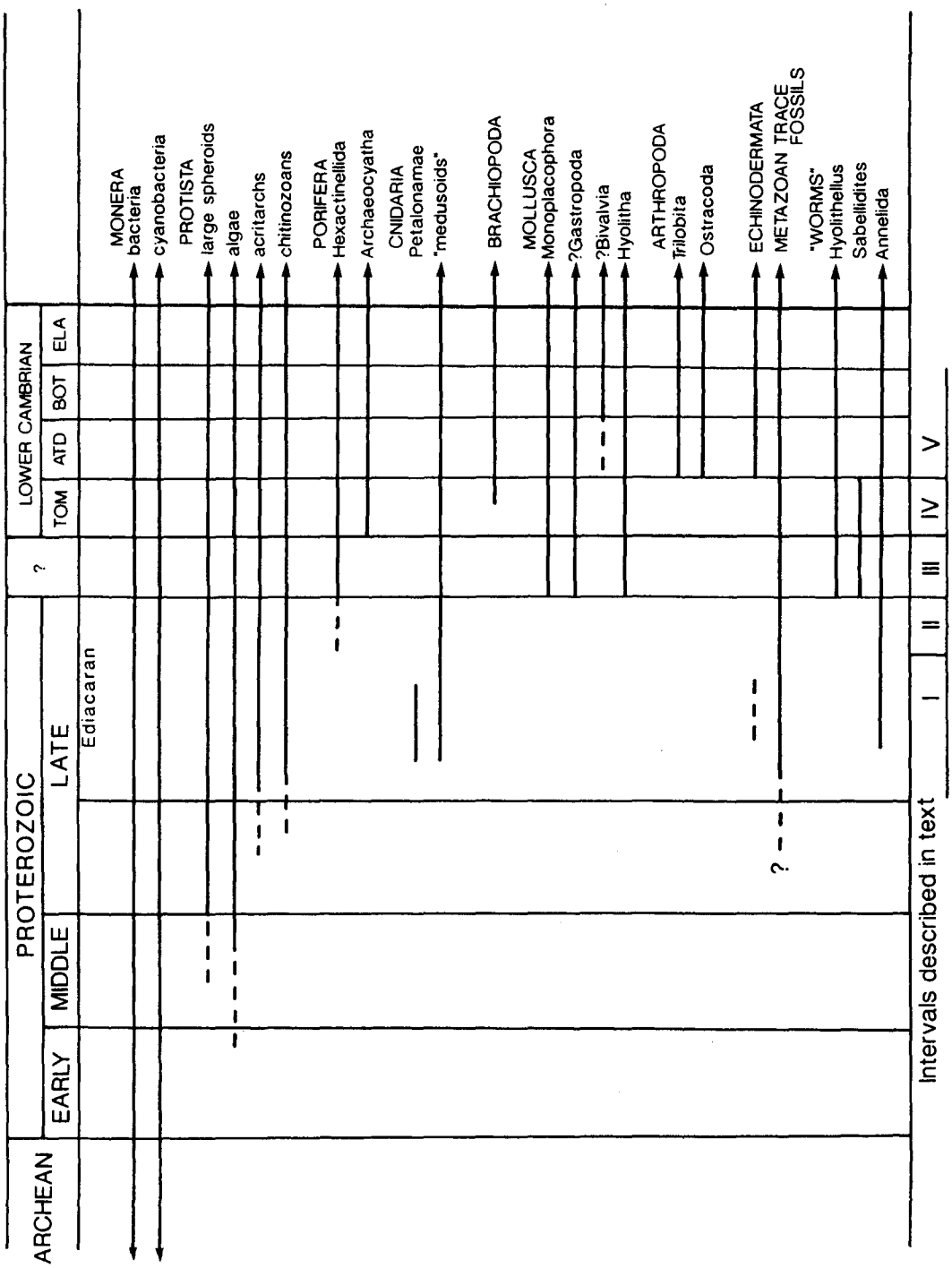

Figure 5-10 Ranges of major organisms across the Proterozoic–Cambrian boundary. The intervals described in the text are indicated at the bottom of the chart. The four stages of the Lower Cambrian recognized in the U.S.S.R. are abbreviated. (*Source:* Modified from Martin F. Brasier.)

Chapter 6

The Invertebrates Dominate the Seas:

ACOELOMATES AND LOPHOPHORATES

By the end of Early Cambrian time all the major groups of invertebrates were represented in the marine fauna, and the exponential increase in diversity that characterized the early Paleozoic was well under way. Many of these groups had acquired carbonate or phosphate skeletons. They had radiated into the major ecological roles, such as suspension feeder, deposit feeder, scavenger, and predator. In this and the following chapter each of the invertebrate groups that are important to the paleontologist is described, and its history in the Paleozoic summarized. A large number of these groups were decimated by events that ended the era, and Mesozoic and Cenozoic marine faunas are much different from those of the Paleozoic. For this reason the story of this second wave of invertebrates is reserved for Chapter 10, after the consideration of the plants and vertebrates of the Paleozoic Era.

Protistans and animals secrete calcium carbonate skeletons of two different minerals: calcite and aragonite. These minerals have the same chemical composition but the calcium, carbon, and oxygen atoms are arranged in different ways so that the minerals have different physical properties. How organisms control the nature of the carbonate mineral deposited is not clear, and many deposit both minerals at the same time in different locations. The pearly inner layer of a clam shell is made of aragonite, the chalky outer part of calcite. Aragonite is less stable and more soluble than calcite under conditions at the earth's surface. Fossils (or parts of fossils) that were made of aragonite tend to dissolve or be replaced by calcite when the shell is buried. Only under extraordinary conditions has aragonite resisted replacement or dissolution in fossils of Paleozoic age.

PROTOZOA

Protozoan Biology:

The protozoans are members of the single-celled kingdom, the Protista, that obtain energy by ingesting other cells. Like all protistans, they are capable of all life functions within a single cell, but the independant cells may be united into large colonies. The phylum contains many groups of great diversity and astronomical numbers of individuals that are important in the modern environment, many as parasites on people and animals. However, such

protozoans as the flagellates, ciliates, and sporozoans are of little importance to the paleontologist as they do not secrete preservable hard parts, and have little or no fossil record. The two groups that are well represented in the record, the Foraminiferida and the Radiolaria, belong to the subphylum Sarcodina, which is characterized by extensions from the body called pseudopods. The radiolarians have stiff pseudopods extending radially from the body and secrete a delicate skeleton of opaline silica (Fig. 10–7). Because their skeletal material is relatively soluble, they have a poor Paleozoic record, but are important for dating deep sea deposits in Cenozoic sediments and contribute their fragile tests to make extensive deposits of siliceous ooze in equatorial belts of the modern Pacific Ocean. They are further described in Chapter 10.

Biology of Foraminiferida:

These are the most abundant and diverse group of unicellular organisms that secrete preservable hard parts. In modern seas they are abundant, although rarely conspicuous, floating in the water or living on and in the bottom sediment at all water depths. Nearly all foraminiferans are marine. Distinctive features of the forams, as they are commonly called, are the skeletons called tests they secrete or construct from particles, and the nature of the thread-like pseudopods. Unlike those of other protozoans, the pseudopods of the foraminiferans form a net around the cell and are full of granules which stream up one side of the threads and down the other (Fig. 6–1). Food particles, such as algal and bacterial cells, are trapped in the net, transported towards the center, broken up, and digested.

The foraminiferan test may be a single chamber or a series of chambers that are added as the cell grows. The test has an aperture where most of the pseudopods are concentrated but also may be perforated by pores (the *foramina* that give the group its name). The function of these pores is problematic. In some recent foraminiferans, the pores are covered with a membrane. A considerable part of the cell is outside the test, and in certain planktonic species the pseudopod net is ten times the diameter of the test. When the cell has grown too large for the test a new chamber is formed. The pseudopods first extend far out from the aperture, and their ends form a protective cyst consisting of a thin membrane with debris cemented to it. The protoplasm of the central cell then bulges out of the aperture within the protective cyst to the shape of the next chamber. This bulge is bounded by another membrane. Small crystals of calcium carbonate appear on its surface and eventually fuse to form a new chamber wall. The series of chambers formed by the repetition of this process may be linear, biserial, coiled planispirally, coiled in a trochoid spiral, or in a variety of complex forms (Fig. 6–2).

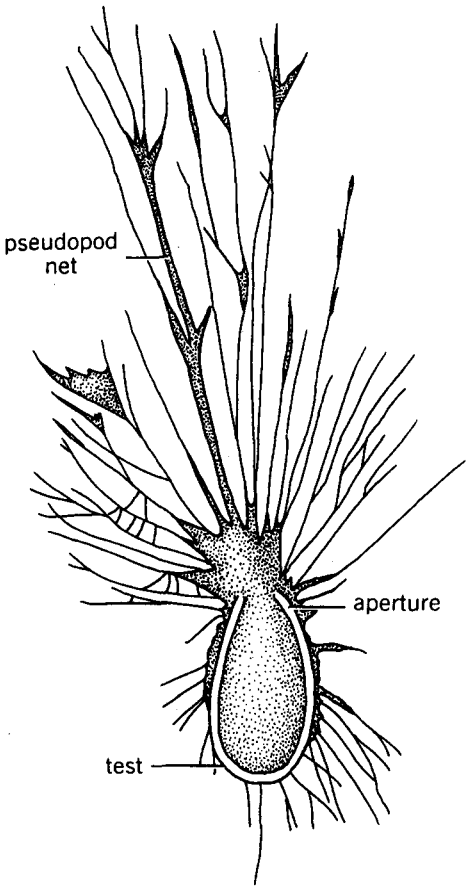

Figure 6-1 The simple living foraminiferan *Allogromia*, showing the relation between the soft tissue and the test. The cell is about 0.5 mm in width.

The reproductive cycle is important to the paleontologist because it results in dimorphism in the tests of many species. Unfortunately, the life cycle of only about 20 of the approximately 4000 living species is known. Although these cycles differ in detail, they all involve alternation of sexual and asexual reproductive phases (Fig. 6–3). In the asexual phase an individual completely divides into many smaller foraminiferans that leave the old test and start independent lives. This process may be re-

peated several times without the intervention of the sexual phase, whose onset may be triggered by environmental conditions such as increase in temperature. Then an individual cell breaks down completely into gametes that may be released freely into the water or may be exchanged when two individuals come together. The union of the gametes produces an individual that grows to adult size and then reproduces asexually. The initial chamber of the sexually produced foram is usually smaller than that of the asexually produced one although the test of the sexually produced foram may be larger. The dimorphic forms are referred to as microspheric (small initial chamber) and megalospheric (large initial chamber) tests. Because several asexual generations may intervene between sexual ones, megalospheric tests usually far outnumber microspheric ones.

The division of the order Foraminiferida into suborders is based on the nature of the wall of the test. In the most primitive suborder, the Allogromiina, the test is an uncalcified sack formed of proteins. The members of the second suborder, the Textulariina, form a test of particles of sediment, usually silt, held together by an organic or mineral cement. Such tests are said to be agglutinated. They are granular in appearance, and may incorporate such particles as mica flakes, sponge spicules, and carbonate grains. Forams of the suborder Fusulinina have walls composed of microgranular calcite. The wall of the Miliolina is calcite that has a matte surface like unglazed porcelain and, in adult tests,

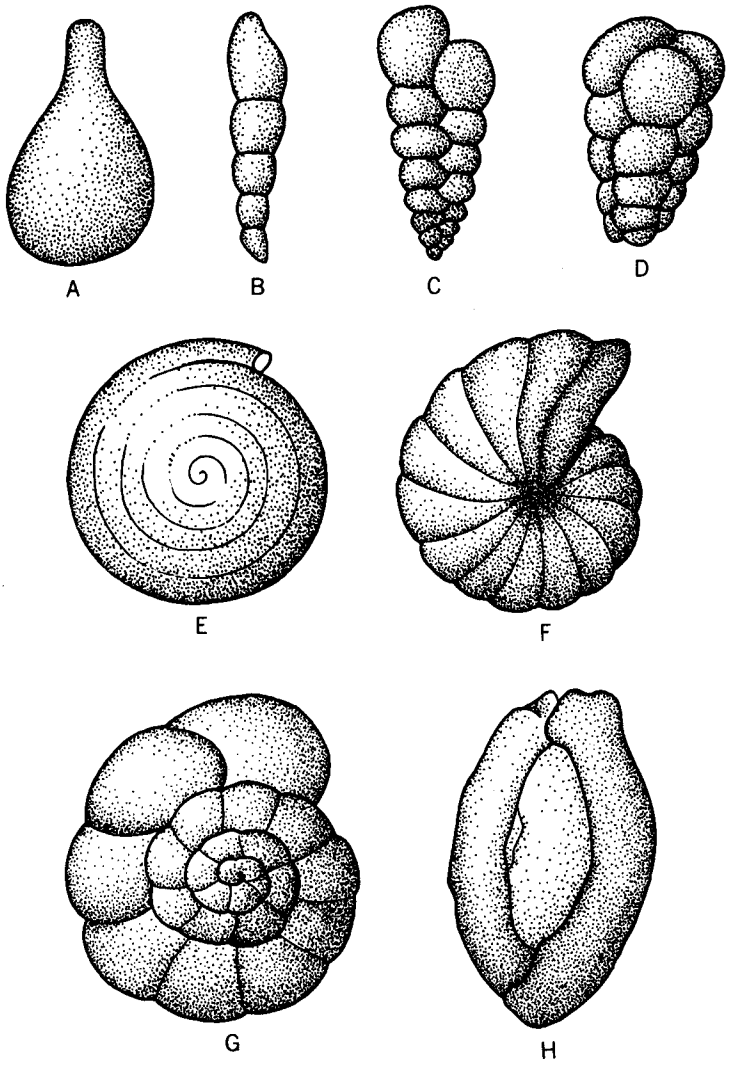

Figure 6-2 Patterns of foraminiferan tests. The tests are all less than 1 mm in length. A. *Lagena*, flask-shaped, B. *Dentalina*, uniserial, C. *Textularia*, biserial; D. *Eggerella*, triserial. E. *Ammodiscus*, simple coiled tube, F. *Cyclammina*, planispiral, inner chambers covered by outer, G. *Strebulus*, planispiral, inner chambers visible, H. *Quinqueloculina*, elongate chambers formed in five positions around a long axis.

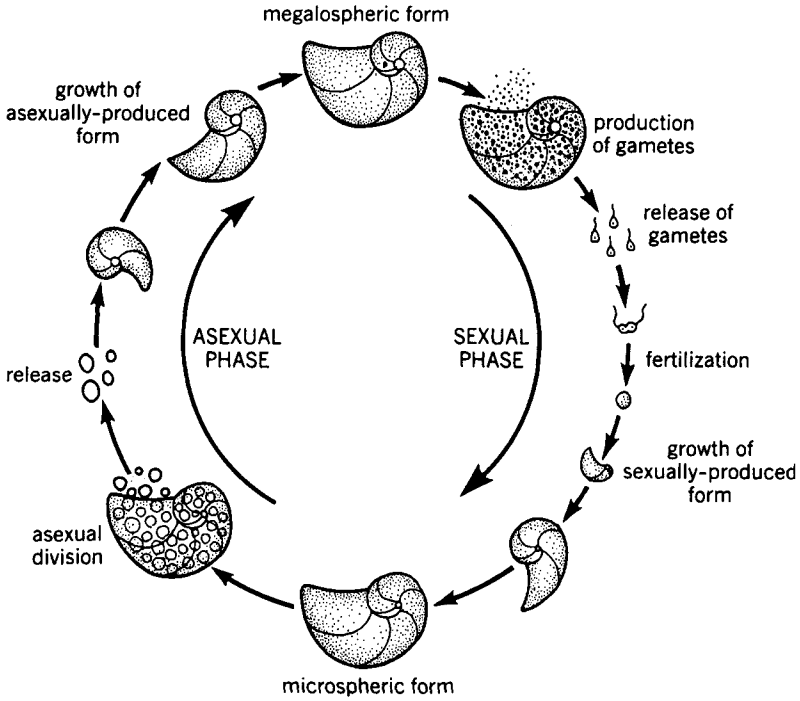

Figure 6-3 Diagrammatic representation of the reproductive cycle of foraminiferans.

is imperforate. The Lagenina have walls that are a single layer of radially arranged calcite crystals. The largest suborder, the Rotaliina, have walls that appear to be glassy (hyaline) and are perforated by many pores. Nearly all foram tests are composed of calcite, but a few are aragonite and one minor group secretes silica.

Kingdom—Protista
- Phylum—Sarcomastigophora
  - Subphylum—Sarcodina
    - Class—Granuloreticulosa
      - Order—Foraminiferida
        - Suborder—Allogromiina
        - Suborder—Textulariina
        - Suborder—Fusulinina
        - Suborder—Miliolina
        - Suborder—Lagenina
        - Suborder—Globigerinina
        - Suborder—Rotaliina + 5 minor suborders

The Paleozoic history of the foraminiferans is dominated by the agglutinated Textulariina and the calcareous Fusulinina. The suborders Miliolina, Lagenina, and Rotaliina, which dominate modern seas, become abundant in Mesozoic times. Their expansion is described in chapter 10.

Paleozoic Foraminiferida:

Because the Foraminiferida are the protozoans with the best fossil record, nineteenth century paleontologists expected that their fossils would be the first to appear in the paleontological record. Some pre-Paleozoic organic structures were then identified as foraminiferans, not because they resembled living ones, but because foraminiferans were expected to be the oldest fossils. Since that time many Proterozoic unicellular fossils have been discovered but none has been a foraminiferan.

The oldest foraminiferans are straight or coiled agglutinated tubes associated with archaeocyathids in Lower Cambrian rocks of the southwestern states. Members of the order without agglutinated or calcareous tests may have existed earlier, but their organic capsules have not yet been discovered. Most of the approximately 15 Ordovician genera that have been described consist of a single subspherical, or tubular, chamber, or of a few connected chambers, and have been discovered by examination of insoluble residues of limestones dissolved in acid. By Silurian time more complex genera of irregularly, planispirally, and trochoidally coiled single

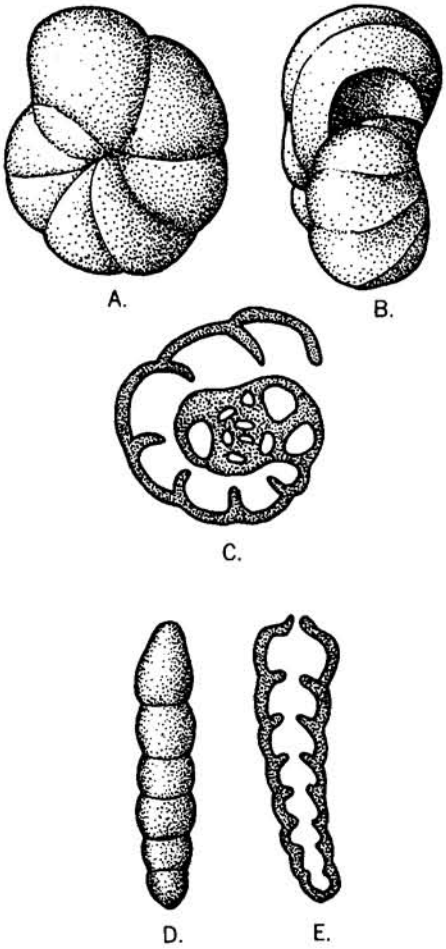

Figure 6-4 Mid-Paleozoic calcareous foraminiferans. A, B, C. *Endothyra* (0.4 mm), side and apertural views and cross section. D, E. *Nodosinella* (2 mm long), side view and cross section.

chambers had appeared (such as *Ammodiscus*, Fig. 6–2E) and the number of species had tripled. By Carboniferous time a great variety of coiled, uniserial, biserial, and triserial tests were being secreted by the Textulariina (Fig. 6–2C) and this variety of form persists today.

The oldest calcareous foraminiferans have been found in Ordovician rocks, but calcareous tests were not abundant until the Devonian Period. Many of the early members of the suborder Fusulinina, which includes the primitive calcareous forams, secreted a linear series of chambers (Fig. 6–4D, E). By Devonian time multiple-chambered tests coiled in a single plane were becoming prominent. By Early Carboniferous time (Mississippian) these minute calcareous tests, typified by the genus *Endothyra* (Fig. 6–4A, B, C), became so abundant that they were important contributors to limestones in the upper Mississippi valley. These granular limestones are extensively quarried in Indiana and Illinois for building stone. The stone is suitable for carvings and facing of buildings because it is uniform in texture and available in large blocks from very thick beds. Late in the Early Carboniferous the discoidal endothyrids gave rise to spindle-shaped foraminiferans that dominated the rest of the Paleozoic Era, the fusulines. These became so abundant that many late Paleozoic limestones are composed almost entirely of their remains (Fig. 6–5).

Fusulines are externally similar and must be thin sectioned along two planes at right angles to reveal their internal structure. Externally the tests are shaped like footballs or grains of wheat, but are usually less than 5 mm long. However, some members of this group grew to be giants up to 10 cm

Figure 6-5 Thin section of fusuline limestone from Permian rocks of Texas. The scale bar is 2 mm. (Courtesy of C. W. Stearn.)

long. The group evolved rapidly and spread widely and is therefore useful for correlating late Paleozoic limestones around the world.

The test consists of chambers arranged in a planispiral coil, but, unlike the endothyrids in which the axis of coiling is the smallest dimension, in the fusulines the axis is the largest dimension. The chambers are bounded above and below by a spiral wall that is wrapped around the axis of coiling and they are separated laterally by septa, which are partitions that run from pole to pole (Fig. 6–6). The continuity of the spiral wall is best shown by sections through the initial chamber at right angles to the axis of coiling. Sections parallel to the axis are also parallel to the septa but repeatedly cut the spiral wall as it winds around the axis. Evolutionary trends in the fusulines include the folding of the septa, the filling of the test with secondary deposits, the resorption of spiral passages (tunnels) through the septa, changes in the nature and thickness of the chamber walls, and changes in the shape of the test and the height of the chambers.

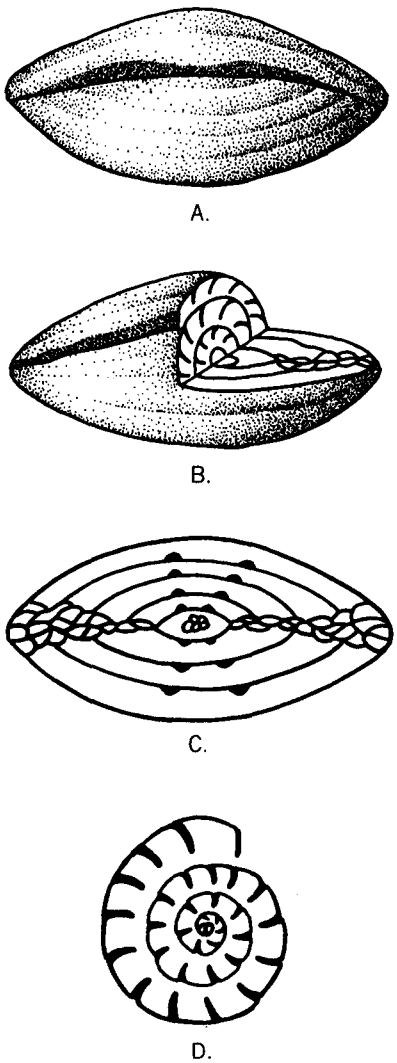

Figure 6-6 Late Carboniferous fusulinids. A, B. *Triticites*, view of the aperture and a specimen cut away to show the internal structure, C. *Profusulinella*, longitudinal section showing the initial chamber, spiral wall, and folded septa, D. *Profusulinella*, a saggital section across the coiling axis showing the spiral wall and septa.

Although they were extraordinarily abundant in Permian seas and reached their greatest size in this period, fusulines became extinct at the close of the Permian, a time of crisis for many invertebrate groups.

Fusulines lived in shallow, warm seas as part of the bottom fauna. They appear to have been confined to tropical waters.

SPONGES: THE PHYLUM PORIFERA

Biology of Living Sponges:

Sponges have no organs and the body is composed of only two layers of cells separated by a jellylike substance containing amoeboid cells. These mobile cells are capable of many functions including digestion, transfer of nutrients and waste products, reproduction, and secretion of the skeleton (Fig. 6–7).

Nearly all sponges are marine but a few genera live in fresh water, and encrust rocks and vegetation in lakes. A typical sponge is shaped like a vase, jar, cylinder, or chimney attached to the seafloor, but many form irregular incrustations on rocks and other organisms. The living tissue of a typical sponge surrounds a central cavity called the spongocoel. Both tissues and skeleton are highly porous and penetrated by numerous canals. The sponge draws water from outside the body cylinder through fine pores on its surface into internal cavities where the fine organic particles, mostly bacteria, are trapped and digested. The filtered water follows canals through the cylinder wall into the spongocoel and flows out through its orifice which is called the osculum (Fig. 6–7C). In encrusting sponges, the small pores through which water is admitted (incurrent pores) and the larger pores through which it is released (excurrent pores) share the upper surface.

The filtering and feeding processes take place in

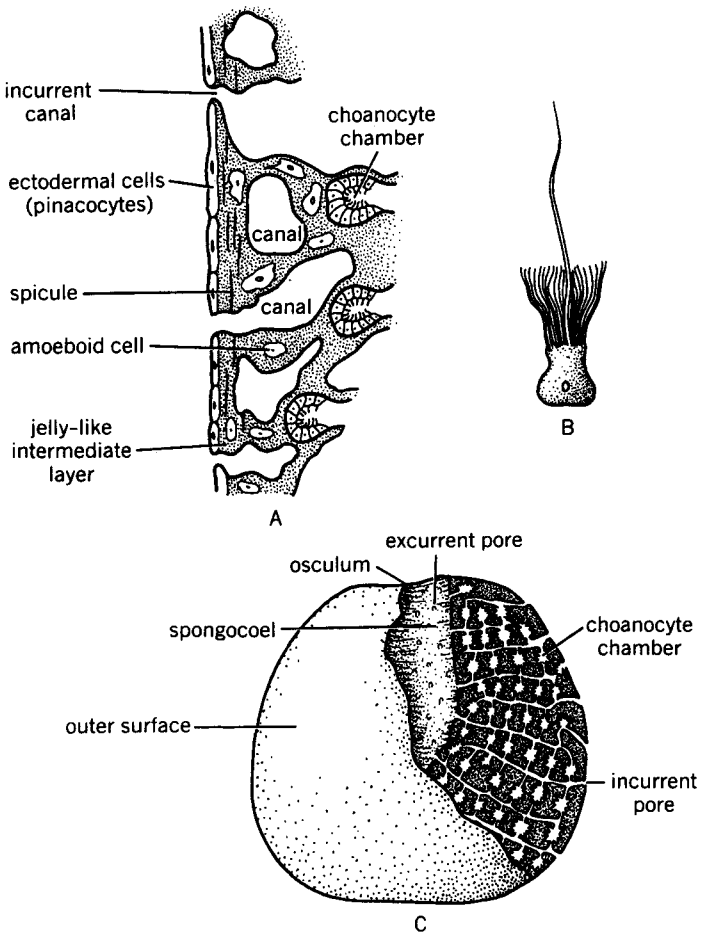

Figure 6-7 Anatomy of living sponges. A. Diagrammatic cross section of the outer surface showing the cell layers and canals. The cells are a few micrometers across, B. An isolated choanocyte showing its flagellum and collar of fine cilia, C. Small typical demosponge cut away to show the canal systems and choanocyte chambers. These are much enlarged for clarity.

internal chambers connected to the incurrent and excurrent canal systems. These minute chambers are lined with collar cells. Each collar cell has a single flagellum (a whiplike extension) pointing toward the exit from the cavity. The flagellum is surrounded at its base by a ring of very fine, hairlike tentacles which form the collar. The motion of the flagellum generates a current which draws water and its suspended microorganisms through the collar, where the bacteria are trapped and passed into the interior of the cell for digestion. The collar cells pass particles to the amoeboid cells for further digestion and distribution of the nutrients throughout the body. Large thick-walled sponges have hundreds of thousands of chambers lined with collar cells and connected by canal systems of great complexity. The flow of water through the sponge is maintained by the action of all the flagella. Some of the food requirements of sponges are also met by absorption of dissolved organic matter in seawater.

Sponges secrete skeletons of (1) organic fibers, (2) individual elements of mineral matter called spicules, and (3) layers and plates of calcium carbonate. The organic fibers are a type of collagen. Collagen is an important fibrous protein of both invertebrates and vertebrates and forms the connective tissue outside the cells. In mammals the thick inner skin is largely composed of this polymer. Sponges strengthened only by organic fibers are relatively soft and flexible and some are sold for cleaning. Paleontologists are more interested in sponge skeletons formed of mineral matter because these are more likely to be preserved. Each spicule of the sponge skeleton is secreted by a single cell, or a group of cells, in the jellylike intermediate layer. Most such spicules are formed of hydrous silica (Fig. 6–8), but in one class of sponges they are calcite. The simplest spicules are needlelike and lie unconnected to one another in the soft tissue, then fall apart on the death of the sponge. More complex spicules have several radiating shafts or axes (Fig. 6–9). Many are shaped like tuning forks; others have highly irregular forms. Complex spi-

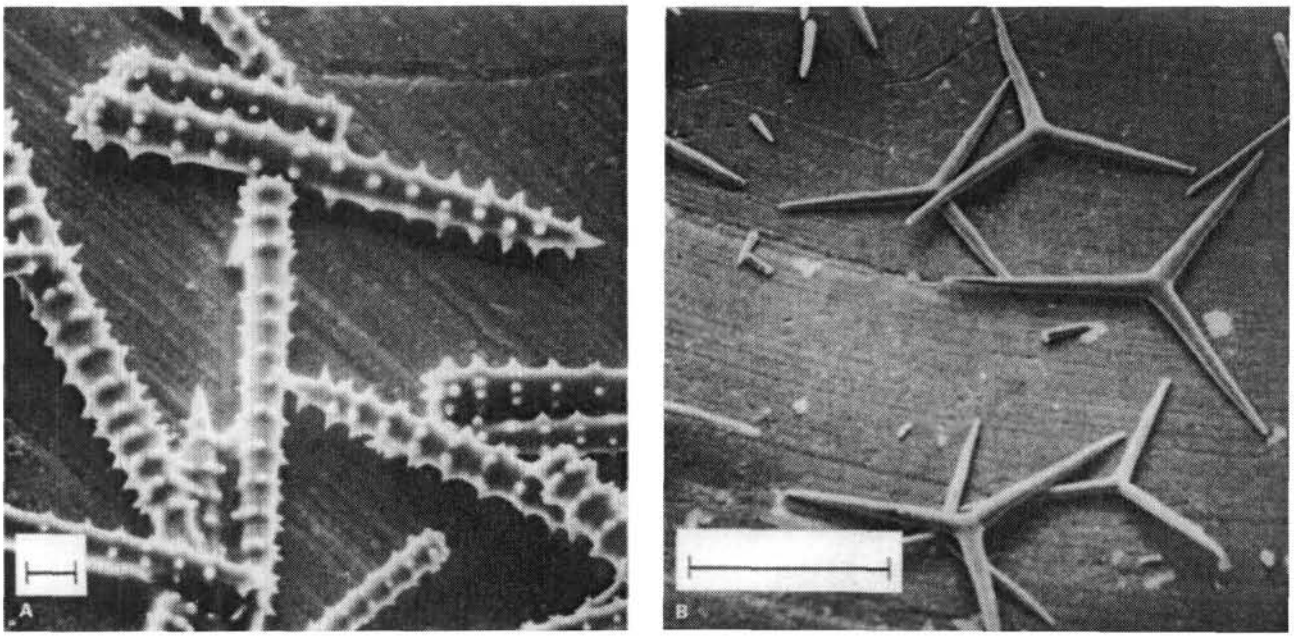

Figure 6-8 Scanning electron micrographs of the spicules of two living demosponges. The scale bars are 10 micrometers. A. *Agelas*. B. *Leucetta*. (Courtesy of C. W. Stearn.)

cules may interlock with adjacent ones to produce a rigid framework that may be preserved in the fossil record. In place of or in addition to a spicular skeleton, some living and many fossil sponges secrete (or secreted) a solid, continuous skeleton of either calcite or aragonite laid down by ectodermal cells at the base of the animal.

Phylum—Porifera
- Subphylum—Symplasma
  - Class—Hexactinellida
- Subphylum—Cellularia
  - Class—Calcarea
    - Order—Pharetronida
    - Order—Heteractinida
    - + others
  - Class—Stromatoporoidea*
  - Class—Archaeocyathida*
  - Class—Chaetetida*
  - Class—Demospongia
    - Order—Lithistida
    - Order—Sclerospongea
    - Order—Sphinctozoa
    - Order—Keratosa
    - + others

*These fossil groups may belong in the Demospongia or Calcarea

The Hexactinellida are placed in a subphyllum separate from the rest of the Porifera because the boundaries between their cells are poorly defined, unlike those of other sponges. Members of this group secrete delicate skeletons of siliceous spicules of six rays which may interlock to produce a three-dimenional grid. They are commonly known as glass sponges and are now largely confined to deep-water environments.

The Demosponges secrete skeletons of siliceous spicules and include about 95 percent of all sponges. Those demosponges in which the spicules have complex processes that interlock to form a semicontinuous skeleton are known as lithistid sponges and have the most extensive fossil record. Some demosponges have only organic fibers as skeletons (the Keratosa). The sclerosponges secrete a basal calcareous skeleton of aragonite or calcite. Modern sclerosponges are rare but are closely related to the fossil chaetetids and stromatoporoids.

The Calcarea secrete calcite spicules that are basically three-rayed but are usually complex in shape.

The Stromatoporoidea are an extinct group of Paleozoic reef-building sponges that secreted a continuous basal skeleton of calcium carbonate.

The archaeocyathids are another extinct group that are now placed in this phylum.

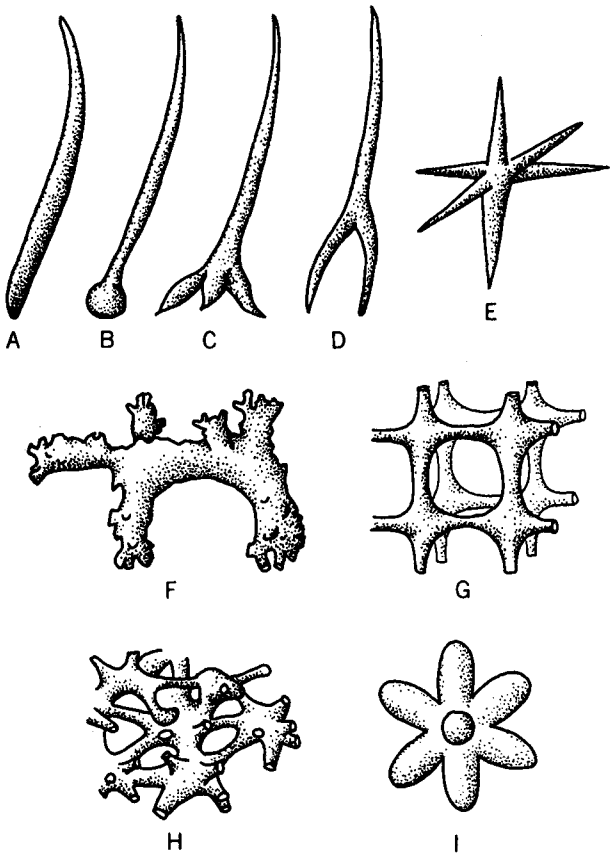

Figure 6-9 Typical sponge spicules and spicule networks. A, B. Simple needlelike spicules called monaxons, C. Four-rayed spicule called a tetraxon, D. Tuning fork spicule, E. Six-rayed spicule typical of hexactinellids, F. Isolated irregular spicule of a lithistid, G. Interlocking spicule network of a lithistid, H. Spicule network of a hexactinellid, I. Heteractine spicule.

Archaeocyathida:

Archaeocyathids formed a skeleton composed of two cones, one inside the other, separated by radial partitions or septa (Fig. 6–10). The space between the cones was usually divided by horizontal plates called tabulae. The cones, partitions, and tabulae were perforated by pores, tubules, or slits of various shapes and sizes. The animal grew up from the seafloor like a vase from its point, which was embedded in the sediment. Many secreted skeletal tissue consisting of overlapping curved plates called cysts outside the cone at the base to stabilize themselves or to cement themselves to other skeletons. Most of the conical animals were solitary, but some stayed together after budding from a parent to produce colonies. In the *Treatise on Invertebrate Paleontology* published in 1972, about 250 genera of archaeocyathids are listed; probably several tens of additional genera have been described since then.

The living tissue of the animal is believed to have occupied the space between the cones, leaving the central cavity empty like the spongocoel of a modern sponge. The porosity of the whole skeleton suggests that the archaeocyathid lived like a sponge, filtering seawater that passed through the body from outer to inner cone. However, no soft parts have been found with these fossil skeletons to confirm that this was their way of life. Because the shape, radial partitions, tabulae, and lack of spicules of archaeocyathids also suggest a relationship with corals, paleontologists have commonly placed them between the phyla Porifera and Cnidaria in a phylum of their own. The recent discovery of many living sponges that secrete a solid, non-spicular, calcareous skeleton like that of the archaeocyathids has removed most of the objections to uniting them with the Porifera (1).

In Early Cambrian time the archaeocyathids joined forces with an enigmatic, calcium carbonate secreting organism called *Renalcis* (Fig. 8–2), which was probably an alga, to build mounds tens of me-

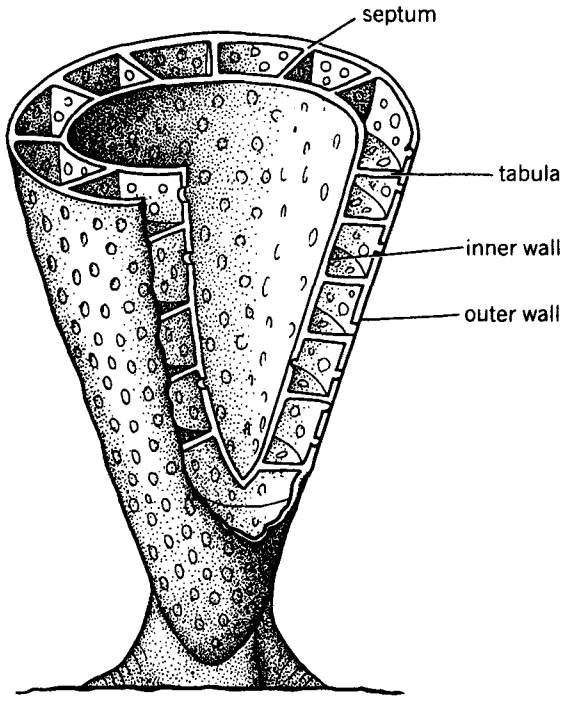

Figure 6-10 Diagrammatic reconstruction of a simple archaeocyathid.

ters high (Fig. 6–11). These are the first reefs built by metazoans. Some of the great carbonate masses found in Proterozoic rocks can also be described as reefs, but they were formed by cyanobacteria, not metazoans. Archaeocyathids are found in all continents but are particularly abundant and widespread in Siberia, southern Australia, and the Appalachian and Rocky Mountain regions of North America.

The archaeocyathids were the first metazoans to use calcium carbonate extensively to secrete skeletons. Their time of greatest success lasted for 30 million years. With the exception of a few genera that survived into Middle Cambrian, and one that may have survived into Late Cambrian time, the group became extinct at the end of the Early Cambrian Epoch (Fig. 6–12). They make excellent index fossils because they are restricted to a narrow time slot and can be easily recognized by the geologist in the field.

Hexactinellida

These sponges have six-rayed spicules which, in more advanced forms, fuse to make a three-dimensional rectilinear network (Fig. 6–13) like the steel framework of a modern office building. Isolated spicules of these sponges occur in Lower Cambrian rocks, but the oldest complete fossils are of Middle Cambrian age. These were shaped like a vase formed of a single sheet of spicules and were attached to the seafloor by a long tuft of straight spicules. By Middle Ordovician time they had a

Figure 6-11 Small archaeocyathid reef in Lower Cambrian rocks of southern Labrador, photographed from above. Note that the unbedded limestone of the reef in the center is more resistant that the surrounding bedded rocks and as the overlying sedimentary beds have been removed by erosion, the original relief of the reef has been revealed. (Courtesy of N. P. James and *Sedimentology*, v. 25, p. 7.)

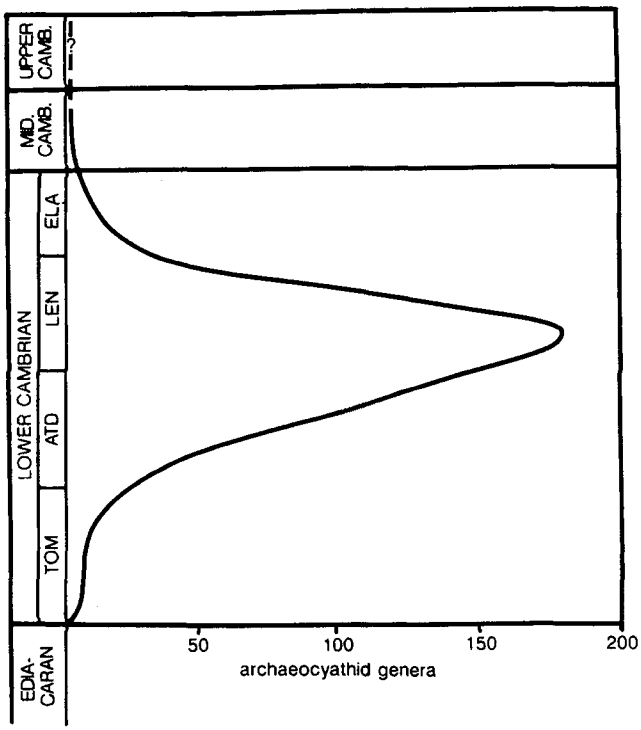

Figure 6-12 Generic diversity of the archaeocyathids. The names of the stages of the Lower Cambrian are abbreviated. (*Source:* Modified from M. F. Glaessner, *The Dawn of Animal Life.*)

double layer of spicules. The class became abundant and diverse in Middle Devonian time. Some beds in the Devonian sandstones of central New York State are famous for the many well-preserved hexactinellid sponge fossils they contain (Fig. 6–14). The class was again abundant in Jurassic and Cretaceous time. The sponges appear to have lived then in shallow water, but today their survivors have retreated into parts of the ocean deeper than 100 meters.

Demospongia:

Most complete demosponge fossils belong to the order Lithistida (Fig. 6–15) and have complex knobby siliceous spicules fused to one another. Scattered demosponge spicules are also preserved. The oldest demosponges occur in Middle Cambrian rocks. In Ordovician time the lithistids increased greatly in numbers and diversity and became prominent members of shallow-water marine communities. Important families in this period and the following Silurian Period are the astylospongiids and hindiids (Fig. 6–15A). Like the hexactinellids, the demosponges were not as widespread in the late Paleozoic and early Mesozoic as they were in early Paleozoic and late Mesozoic time. Mesozoic demosponges are more abundant in Europe than in North America. Although the Cenozoic record of this group is not good, they thrive today in many environments.

Calcarea:

The Calcarea comprise those sponges that secrete calcium carbonate spicules and, like the demosponges, they include one group, the pharetronids, that built rigid skeletons and are therefore much better represented in the fossil record than the others. The first pharetronids, from Lower Permian rocks, are part of a reef fauna, and succeeding members of the group continued to prefer the reef environment. In Triassic reef limestones of the Cassian Formation of northern Italy, the calcareous sponges are so faithfully preserved that the spherulitic microstructure and aragonite mineralogy of their skeletons is still intact. Pharetronids thrived in Jurassic and Cretaceous reefs of central Europe where they are represented by such genera as *Stellispongia* and *Peronidella* (Fig. 6–16). Although only a few genera of the Pharetronida persist to the present, other

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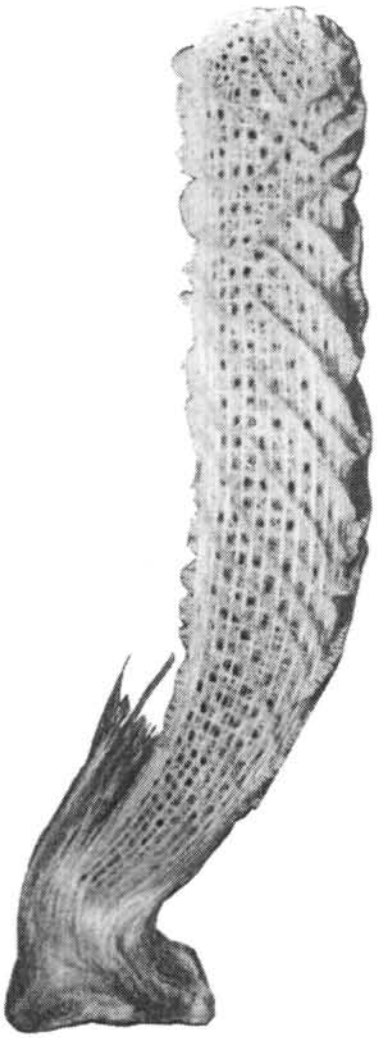


Figure 6-13 The modern hexactinellid sponge *Euplectella*, called Venus' flower basket. The sponge is attached by the fine, hairlike spicules at the base. The specimen is about 35 cm long. (Courtesy of H. Reiswig and C. W. Stearn.)

orders of the Calcarea are more abundant.

Two other groups of sponges that secreted calcareous skeletons but are excluded from the Calcarea by some paleontologists are of importance geologically. The Heteractinida secreted spicules that typically have six rays in one plane and two shorter rays at right angles to these (Fig. 6–9I). They are confined to Paleozoic rocks. The best-known North American genus is *Astraeospongium*, a saucer-shaped sponge with star-shaped spicules common in Middle Silurian rocks of the eastern states (Fig. 6–16D).

The second group, the Sphinctozoa (sometimes placed in the Calcarea but here considered demosponges), secreted a calcite skeleton that was not composed of spicules but consisted of a line of chambers arranged vertically and connected axially by a canal (Fig. 6–16A). The chamber walls were pierced by many pores through which water reached the axial canal and flowed out the osculum at the top. The sphinctozoans first appear in Cambrian rocks and persist as a single genus, *Vaceletia*, to the present. They were important contributors to the

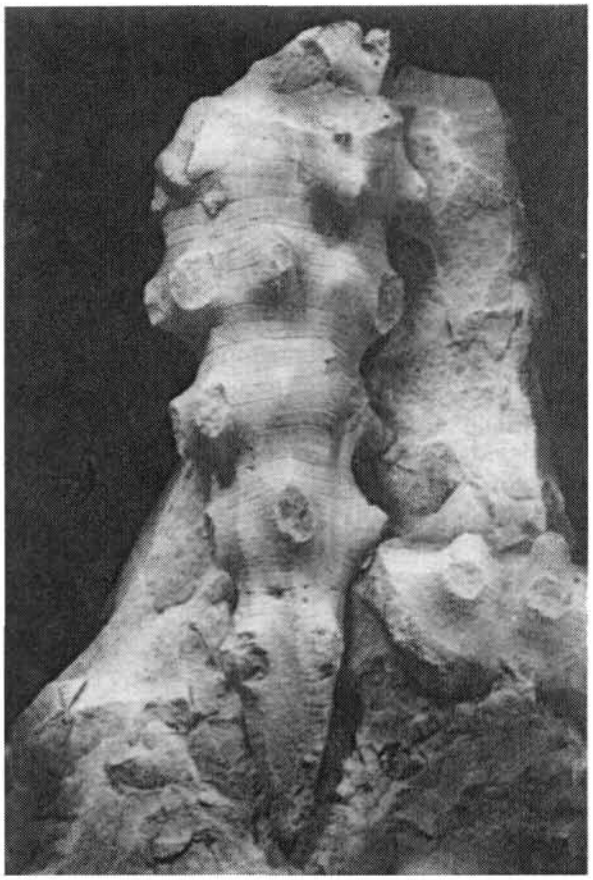


Figure 6-14 The fossil hexactinellid sponge *Hydnoceras* from Upper Devonian rocks of New York. The specimen is about 20 cm long. (Courtesy of C. W. Stearn and Redpath Museum, McGill University.)

Chapter 7

The Invertebrates Dominate the Seas II:

SCHIZOCOELOMATES AND ENTEROCOELOMATES

BIOLOGY OF LIVING MOLLUSCS

In modern seas, molluscs are the most conspicuous shell-bearing animals and are outnumbered only by the forams. Many molluscs secrete calcareous shells suitable for preservation, but many do not. The fossil record of the phylum extends back to the beginning of the Cambrian Period. The molluscan architecture of the soft body enclosed in one or two hard shells proved to be adaptive not only to marine, but also to freshwater and terrestrial environments.

Molluscs are unsegmented (or pseudosegmented), coelomate metazoans. The repetition of gills and/or muscle scars in the Monoplacophora and Polyplacophora, two minor groups, suggests that primitive molluscs shared a segmented ancestor with annelids and arthropods, but opinion is divided on the significance of these features. In molluscs, a muscular extension of the body, commonly referred to as a foot, was modified for burrowing, creeping, and grasping food. Molluscs have well-developed digestive, circulatory, reproductive, nervous, and sensory systems. In all groups except the bivalves, scaphopods, and some cephalopods, the food is torn into pieces for digestion by a unique rasplike ribbon behind the mouth called a radula.

The phylum is usually divided into eight classes, five of which are of minor importance to the paleontologist, although all but one have a fossil record. The minor classes are: (1) the Polyplacophora (chitons, most of which cling to rocks in the surf zone and secrete spicules and a covering of eight plates); (2) the Monoplacophora (single saucer-shaped shell, possibly segmented); (3) the Rostroconchia (bivalved shells joined permanently across the top); (4) the Scaphopoda (tooth or tusk shells), and (5) the Aplacophora (without shells). Small conical fossils such as *Hyolithes* and *Tentaculites* may represent a ninth class (Chapter 5), but some paleontologists regard them as a separate phylum. Only the three large classes are described separately in the following discussion.

Phylum—Mollusca
- Class—Aplacophora
- Class—Polyplacophora
- Class—Rostroconchia
- Class—Scaphopoda
- Class—Bivalvia
- Class—Monoplacophora
- Class—Gastropoda
- Class—Cephalopoda

The first molluscs probably evolved from flatworm (phylum Platyhelminthes) ancestors in Ediacaran time. Three of the six classes of molluscs with readily preservable shells appear in earliest Cambrian (Tommotian) beds, but all their shells are minute. Runnegar (1) believes that the Ediacaran ancestors of molluscs were a millimeter or less across and of very simple structure. The first shelled molluscs may have been simple conical monoplacophorans (Fig. 7–15), and these gave rise rapidly at the beginning of Cambrian time to the Rostroconchia and Gastropoda, and slightly later to the Bivalvia. High conical monoplacophorans with septa across the apex probably evolved into the cephalopods in Late Cambrian time.

Class Bivalvia:

This class includes the clams, mussels, scallops, and oysters. As the name implies, the Bivalvia have two valves, but they are not the only invertebrates with two valves. Other scientific names that have been applied to them include Lamellibranchia and Pelecypoda. The two shells, or valves, are mirror images of each other laterally placed on either side of the body. Like brachiopod shells, they have a bluntly pointed apex called the beak. This is the position of the larval shell where growth begins. Subsequent shell growth usually produces growth lines parallel to the margin of the larval shell (Fig. 7–1A). A single valve is not bilaterally symmetrical like that of a brachiopod, but the area of maximum curvature of the shell near the beak, called the umbo, is usually inclined forward. Just below the beak the valves usually interlock where the teeth in one valve fit into sockets in the opposite one (Fig. 7–1C). The teeth are at the hinge line along which the valves pivot to open the lower edge. The valves are drawn together by adductor muscles that leave scars on each valve (Fig. 7–1C). Oysters and scallops have only one muscle; most bivalves have two. When these muscles relax, the valves spring apart by the action of organic ligaments. These ligaments are located either above the hinge line, in which case the ligament is under tension when the valves close, or in a triangular cup inside the hinge line, in which case it is under compression.

The valves are secreted by the mantle that lines them. The mantle is usually attached to the shell at a scar near the shell's edge called the pallial line. The pallial line usually connects the two muscle scars (Fig. 7–1C). At the back the mantle lobes may be joined to produce two tubes, or siphons, one of which brings water into the shells and the other expells it. These siphons may be short, extending only to the edge of the valves, or they may be several times the length of the valves in species that burrow deep into the sediment. Small siphons can be retracted into a pocket when the valves close but larger ones cannot and the valves must gape at the back when closed to accomodate them. The existence of a pocket for retraction of the siphons is indicated by a bend in the pallial line (Fig. 7–1C).

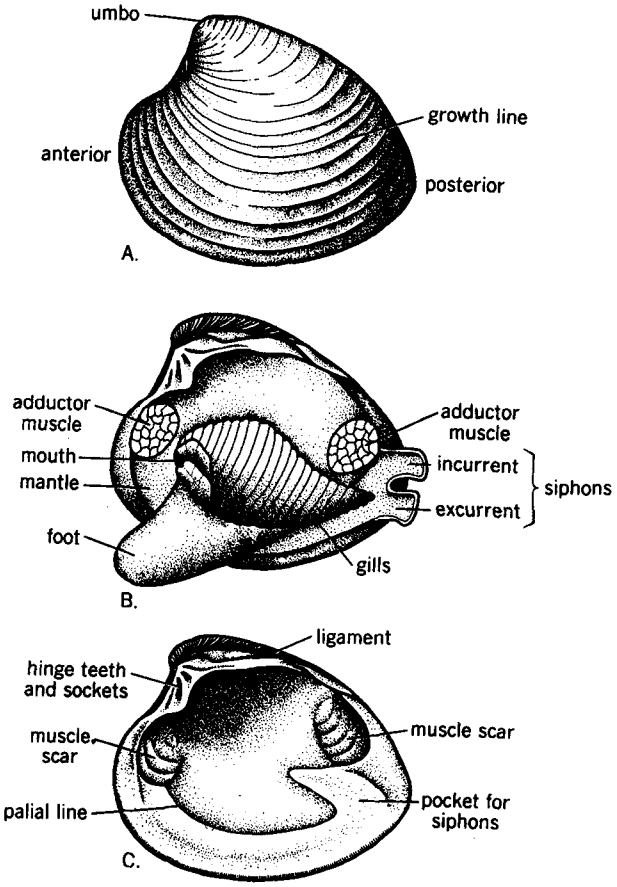


Figure 7-1 Anatomy of the living bivalve *Mercenaria*, about 10 cm long. A. Exterior of the left valve. B. Left valve and mantle removed to show the internal organs. C. Interior of the right valve.

Most bivalves are filter feeders and the water delivered by the siphon brings microorganisms for food. Between the viscera and the mantle lobes hang the gills, which filter water for food and extract oxygen for respiration. Small food particles collected on the gills are moved forward by cilia to the mouth which lies just below the front adductor muscle (Fig. 7–1B). Waste is extruded into the outgoing water stream. Bivalves do not have a head.

The heart surrounds the gut and pumps a fluid into open cavities in the body which act as a hydrostatic skeleton. The lower part of the body is a wedge-shaped foot that contains one of these large cavities. Most bivalves live partly or wholly within sediment. When they move forward, the valves are opened, and the foot is thrust forward into the sediment and expanded by fluid which is pumped into its cavity. When the foot is anchored, the muscles in it can then drag the valves toward it. The foot–anchor is then deflated by withdrawal of fluid, and thrust forward again. Progress is slow. Not all bivalves push through sediment; some stay in one place, some are cemented to hard objects, some attach to objects by threads, some bore into rock or wood, others swim through the water. The basic pattern of soft and hard parts previously described was much modified as bivalves adapted to these varied ways of life.

Class Gastropoda:

Gastropods are snails and slugs. They are presently the most diverse and abundant of the mollusc classes and successfully occupy marine, terrestrial, and freshwater environments in large numbers. The vast majority secrete a single shell, usually coiled in a conispiral, like a conical corkscrew. The shell is basically a cone translated down the axis of coiling as it turns. If the young, pointed part of the shell is oriented upward (Fig. 7–2C), in most gastropods the aperture is to the right of the axis of coiling. These shells are called dextral. Those few in which the opening is to the left are sinistral.

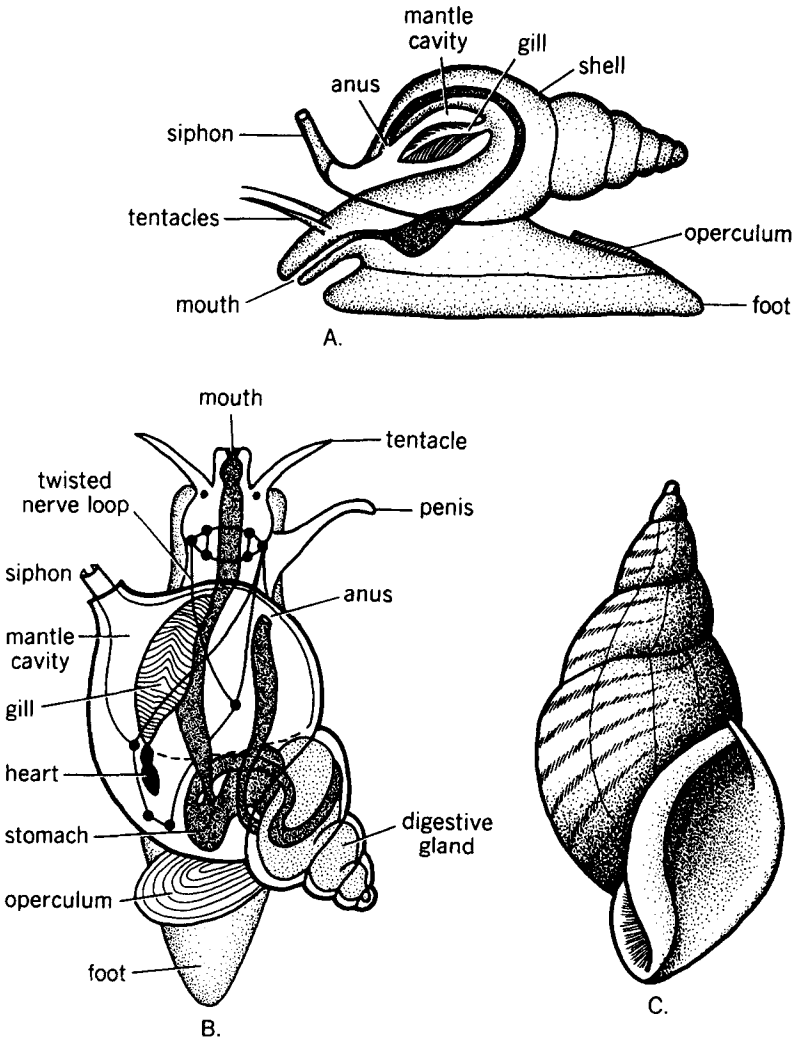


Figure 7-2 Gastropod anatomy. A. Side view of a typical gastropod in cross section. B. Top view of a mesogastropod with the shell made transparent. C. Dextral gastropod as conventionally oriented in illustrations (*Calicantharus*, Pleistocene).

Snails have distinct heads commonly equipped with eyes and feelers (Fig. 7–2A). They creep on a muscular foot. The body and foot can be retracted into the shell of most snails and many secrete a plate, or operculum, that closes the opening. During embryological development most snails undergo torsion, that is, the back of the embryo twists 180 degrees so that it comes to lie above the head. Both the end of the digestive tract and the mantle cavity containing the gills are twisted into this position. In this manoeuver, most snails lose one of the two gills and one of the two kidneys, and the nerve loop is twisted into a figure eight. In one subclass of gastropods, detorsion brings the mantle cavity and the anus to the back again but with only one gill and kidney. Although several theories have been proposed to explain the advantages of torsion to gastropods, no one theory is widely accepted. The gastropods that left the sea to live on land dispense with the remaining gill and use the mantle cavity as a lung by multiplying the number of blood vessels on its surface to absorb oxygen. Those that live in fresh water must rise to the surface periodically to trap air in order to supply the respiratory needs of their lung.

Many gastropods feed by scraping organic films and algae off the bottom. Others are deposit feeders and filter feeders. Some are parasitic and many are predatory. Some members of five different families drill neat holes in the shells of bivalves and other gastropods to feed on the soft tissue inside.

Gastropod classification is based largely on features of the soft parts, and paleontologists are forced to infer the nature of the anatomical features that are critical for classification from a study of their influence on the shell. Three subclasses are generally recognized: (1) the Prosobranchia, which are largely marine gastropods with viscera twisted by torsion; (2) the Opisthobranchia, in which detorsion has taken place and the viscera are no longer twisted; and (3) the Pulmonata, which are snails in which the mantle cavity is modified into a lung and the gill is lost. Opisthobranch gastropods with shells sufficiently thick for preservation are rare in the fossil record. An order of this subclass, the Pteropoda, reduced the shell to a thin semitransparent envelope, modified the foot into a pair of beating "wings", and joined the plankton floating near the surface of the sea. Their insubstantial shells accumulate on modern oceans floors locally to form pteropod oozes.

Class Cephalopoda:

The approximately 400 living species of cephalopods are a small fraction of the thousands that lived in the past and are known to us through their fossils. All living, and we suspect all fossil, cephalopods are, or were, marine. Bivalves and gastropods are basically adapted to living in and crawling on top of the sediment respectively, but cephalopods are adapted to swimming. The living squid, octopuses, cuttlefish, and their fossil representatives, the belemnites, are members of the subclass Coleoidea. *Nautilus* is the last living genus of the subclass Nautiloidea which has many fossil members. A vast number of fossils are included in the extinct subclass Ammonoidea. In each of these the head is equipped with tentacles for grasping food and bringing it to the mouth. The cephalopods are predators and scavengers and the largest are capable of defending themselves against sperm whales. Below the tentacles the mantle margin is shaped into a tube through which the water in the mantle cavity can be jetted by rapid muscular contraction (Fig. 7–3B). In reaction to this jet the cephalopod moves in the direction opposite to that in which the jet is directed. In *Nautilus* the backward motion is relatively slow but in the streamlined squid the repeated jetting of water from the mantle may be powerful enough to lift the body from the sea and meters into the air. The squid (Fig. 7–4) and octopus have largely dispensed with skeletons but *Nautilus* secretes an external shell made buoyant by the gas that fills its chambers (Fig. 7–3A,B). Although the shell is coiled, it differs fundamentally from gastropod shells in its division by partitions, or septa, with a central canal. The septa mark successive back walls of the body chamber secreted as the animal enlarges its shell, abandoning and sealing off the early sections. The animal removes liquid from these chambers and substitutes gas through a thread of soft tissue containing veins and arteries that passes in a tube through each septum and chamber to the initial one.

PALEOZOIC BIVALVES

John Pojeta and Bruce Runnegar (2) have presented evidence that *Fordilla* and *Pojetaia* from Early Cambrian rocks are the first bivalves (Fig. 7–5). They believe they are descended from the primitive

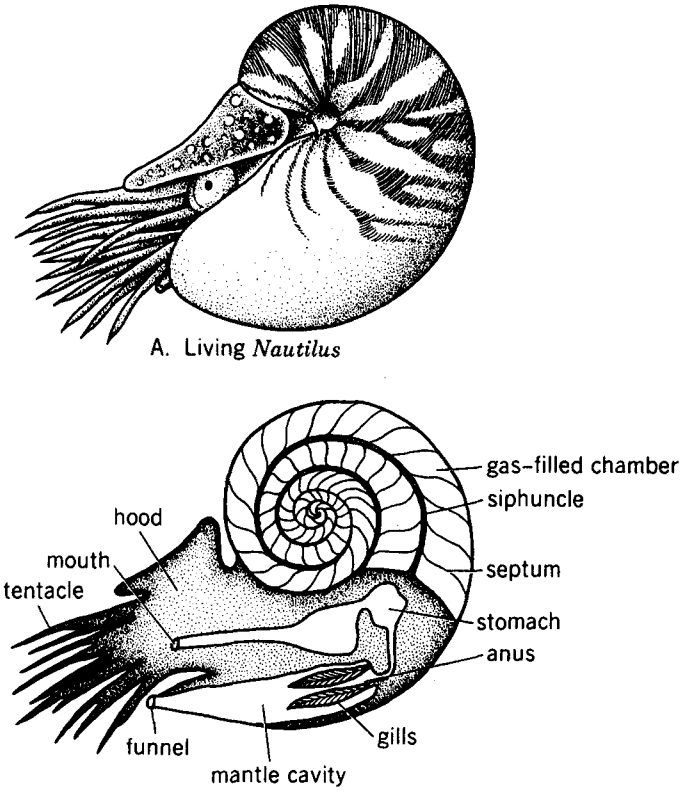


Figure 7-3 *Nautilus* (about 1.2 cm in diameter). A. Side view of exterior of the animal in living position. B. Cross section to show the relationship of the internal organs to the shell.

molluscan class Rostroconchia. The rostroconchs have two valves that gape at the front and back and are joined rigidly along the top by calcareous layers, so that they do not open and close as bivalves do. They lived from Cambrian to Permian time and in certain places were sufficiently abundant to form shell beds. The transition from rostroconchs to bivalves required the replacement of the rigid calcareous bridge between the valves by a flexible protein ligament and development of shell closing muscles. The diversification of bivalves, like that of several other groups secreting heavy calcareous skeletons, did not occur immediately after their appearance; in fact, no Middle or Upper Cambrian bivalves have yet been found. However, by Middle Ordovician time, all major subclasses of the bivalves had appeared.

Bivalves and other molluscs are not as well preserved in most Paleozoic sediments as are brachiopods. Usually bivalve fossils are molds of the interiors or exteriors of single valves. Possibly their shells contained a higher proportion of the less stable carbonate, aragonite, than those of later bivalves which are better preserved. When bivalves die and the adductor muscles relax, the ligaments spring the valves open and they are usually preserved sep-

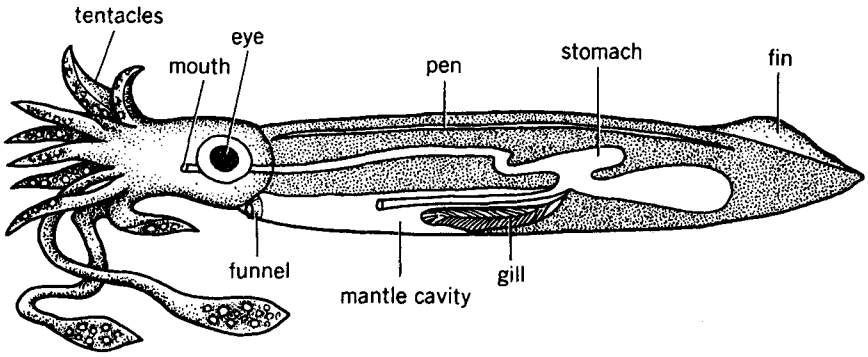


Figure 7-4 The living squid *Loligo* cut away to show some of the internal organs.

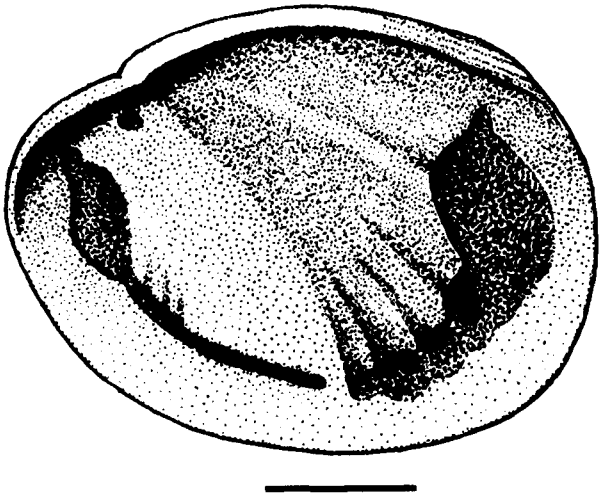


Figure 7-5 Reconstruction of the interior of the right valve of one of the first bivalves, *Fordilla*, from the Lower Cambrian rocks of New York. The two adductor muscle scale are more darkly shaded than the rest of the shell. The scar bar is 1 mm. (Courtesy of J. Pojeta and *Science*, v. 180, p. 867, © 1973, by the AAAS.)

arately whereas brachiopods, which are not spring loaded, are most often preserved with the valves in the closed position. Bivalves did not compete directly with brachiopods but many lived in nearshore, shallow environments and were capable of tolerating much suspended sediment (3). As a result they are commonly found in siltstones and fine sandstones deposited in estuarine environments. Through the Paleozoic they expanded into offshore environments and developed forms that could burrow deeper into soft sediment.

Classification of bivalves by zoologists is based on features that are not preserved in fossils, such as gill structure. Paleontologists use a classification that combines features of fossil shell, such as teeth and sockets at the hinge line, ligaments, shell microstructure, and shape. The close relation between bivalve shape and habitat in modern bivalves allows paleontologists to deduce habitats of fossil species (Fig. 7–6).

Many early Paleozoic bivalves moved about within, or on top of, soft sediment in the sea and fed by filtering microorganisms from the water or eating dead organic matter on the seafloor. Some stayed buried in one place; others attached themselves to hard substrates with horny threads, called a byssus, secreted by a gland in the foot. Because shells of early Paleozoic bivalves show no evidence that they had long siphons, paleontologists deduce that they were unable to burrow deep in sediments. Efficient burrowers are characterized not only by extensive siphons, but also by streamlined shells. Later Paleozoic rocks contain fossils of the forerunners of

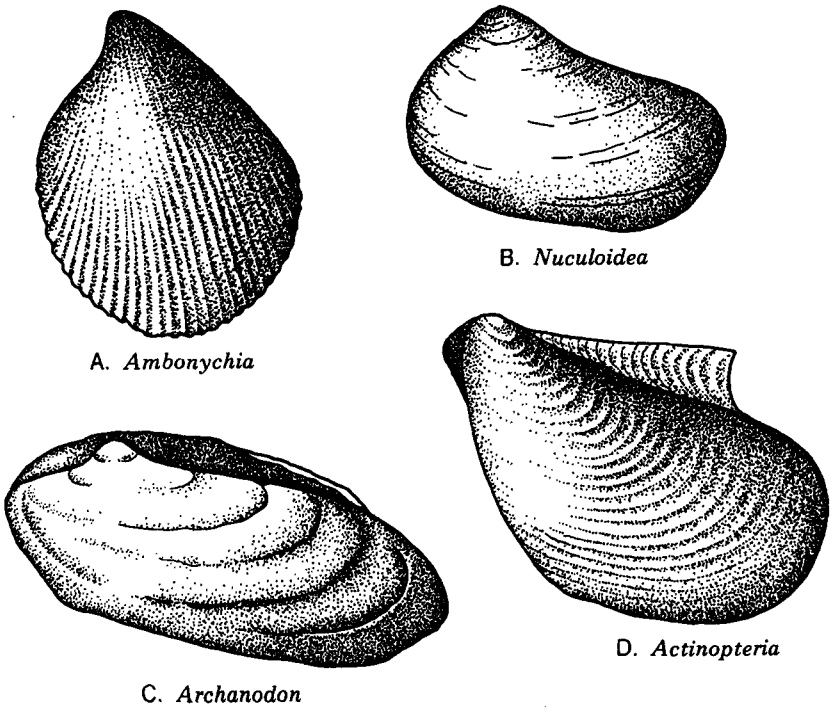


Figure 7-6 Paleozoic bivalves. Approximately natural size. A. *Ambonychia* (Ordovician). B. *Nuculoidea* (Devonian). C. *Archanodon*, nonmarine (Carboniferous). D. *Actinopteria* (Devonian).

the bivalves that swam and cemented themselves to hard substrates. These ecological roles became important in Mesozoic time. Devonian reefal limestones are characterized by large, thick shells of the bivalve *Megalodon*, which was the ancestor of the coral-like rudist bivalves of the Mesozoic described in Chapter 10.

In Middle Devonian time bivalves were able to invade freshwater environments, and their shells appear in post-Devonian coal-bearing successions. Modern freshwater clams disperse their young by attaching the larvae to the gills and fins of fish for a short time. Although there is no evidence, it is presumed that the evolution of this curious piggyback adaptation allowed some marine Paleozoic bivalves to dispatch their young upstream against river currents to lakes on the gills of fish, such as rhipidistians, which, like modern salmon, may have migrated between marine and freshwater environments.

FIRST CEPHALOPOD SUCCESS

Living *Nautilus*:

For fossil groups that do not have living representatives, paleontologists may have great difficulty relating shell and skeleton, which are preserved, to soft tissue, which is not. In the absence of knowledge of the living animal, the relationship of the hard parts to the behavior of the animal remains speculative. Fortunately, remnants of both of the major subdivisions of the cephalopods are alive today but the shell-bearing branch has been reduced to a single genus. Because the pearly nautilus species of the western tropical Pacific are the sole living representatives of a host of fossil cephalopods with external shells, their shells and behavior have been extensively studied, particularly within the last decade (4,5,6).

Most species of *Nautilus* secrete a conical shell that is closely coiled in one plane so that succeeding whorls embrace the previous whorl and only the final one can be seen (Fig. 7–3A). When the shell is cut across the axis of coiling, or X-rayed (Fig. 7–3B,7–7), the septa that divided the coiled cone into gas-filled chambers are revealed. The body occupies the last, or living, chamber and, as it grows, it moves forward periodically in the shell, lets water into the space behind the body, secretes a septum on its back surface, pumps the water out, and separates itself from the abandoned chambers. The addition of chambers stops when the shell has reached mature size in five to ten years. The chamber formed last is filled with water and the recently formed chambers are partly filled, but most of the chambers are filled with a gaseous mixture rich in nitrogen that diffuses into them from the animal. *Nautilus* slowly replaces the fluid in the last-formed chambers and introduces the gas by means of the siphuncle, a string of tissue in a calcareous sheath that extends back from the body through perforations in each septum. The sheath of the siphuncle is formed of two parts: the edges of the septa around the perforations turned backward as necks, and cylinders of poorly calcified tissue called connecting rings that join the free end of the septal neck to the front of the next septum (Fig. 7–7A). *Nautilus* is able to pump fluid out of the chambers using an osmotic mechanism through the permeable connecting rings, and it controls its buoyancy as the body weight grows by the addition of new buoyant chambers and the gradual emptying of the newly

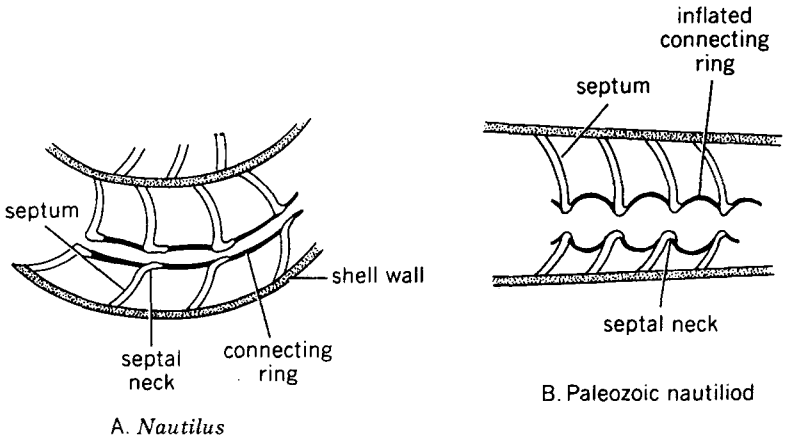


Figure 7-7 Siphuncle structure of modern *Nautilus* and Paleozoic straight nautiloids.

formed chambers. As a result it maintains a slight negative buoyancy.

The shell of *Nautilus* is formed entirely of aragonite. When the outer porcellaneous layer is artifically polished off, the beauty of the mother-of-pearl interior layers is revealed. Application of studies of these shells to the interpretation of the habitats of fossil cephalopods is discussed further in Chapter 13.

Early Paleozoic Cephalopods:

The essential features of the shell of *Nautilus*, the chambered cone and siphuncle of septal necks and connecting rings, are also present in its Paleozoic ancestors. In most, but not all, of these early cephalopods the shell is not coiled but straight or slightly curved. Some of these straight cones were 9 meters long—the largest shells ever secreted by invertebrates. Their internal structure can be understood in terms of the problems of stabilizing such shells.

In coiled cephalopods the gas-filled chambers that exert a buoyant force upward are above the body, which exerts a gravitational force downward, and the animal is suspended in the water in the position shown in Figure 7–3A. The center of gravity is directly below the center of buoyancy, a situation in which the shell is stable and the body chamber is more or less horizontal. A long straight cone can only be propelled parallel to the seafloor through the water if the cone is horizontal. However, the buoyancy of the chambers of a simple straight cone will bring the shell into a vertical position and the heavy body face down (Fig. 7–8A,B). To bring the center of buoyancy and the center of gravity together so that the shell will be horizontal, the center of gravity must be moved back by weighting the apical end, and/or the center of buoyancy must be moved forward by bringing the gas-filled chambers above the heavy body (Fig. 7–8C).

Phylum—Mollusca
- Class—Cephalopoda
  - Subclass—Nautiloidea
  - Subclass—Coleoidea
  - Subclass—Ammonoidea
    - Order—Anarcestida
      - Suborder—Clymeniina
      - Suborder—Bactritina
    - Order—Goniatitida
      - + others (Ch. 10)

Paleozoic cephalopods deposited calcium carbonate around the margins of the chambers in the apical parts of their shells. How the deposition took place is not clear. It has been proposed that the deposit was made from a mantle lining left behind when the body abandoned the chamber, but such a lining could not have been connected to the siphuncle and it has no counterpart in modern *Nautilus*. Possibly the carbonate was deposited on organic membranes supplied by diffusion through the siphuncle when the chambers were full of water. Paleozoic straight cephalopods also formed heavy deposits of six main types in their siphuncles. The most common were annular masses, kidney-shaped in cross section, located on the septal necks (Fig. 7–8C,D,E). In the actinoceratoids these are associated with inflated connecting rings and grew to fill the space of the siphuncle completely, leaving only a few canals. Such siphuncles look like a long row of toy tires (Fig. 7–9). They filled most of the apical part of the shells and are usually the only parts of the shell preserved because they are more massive than the walls or septa. In the endoceratoids, the siphuncle was weighted with a series of nested cones whose apexes were pointed toward the apex of the shell and pierced by the siphuncle (Fig. 7–10A). The siphuncles of other straight cephalopods were weighted with radial plates extending from the periphery to just short of the axis. The effect of the weighted siphuncles was to counterbalance the weight of the body and move the center of gravity toward the back of the shell. They are thickest near the apex where their effect as a counterbalance would be greatest. As the body grew heavier and the shell longer, new deposits were secreted near the living chamber and the old ones were thickened near the apex (Fig. 7–8C). In many straight nautiloids the heavy siphuncle was not central but near the lower margin to resist the tendency of the shell to roll.

A group called the ascocerids added a few large chambers above the body chamber rather than behind it. Their adult shells were short, small, and the apertures of some are partially closed over the body chamber leaving holes for the funnel, tentacles, and eyes (Figs. 7–10B, 7–11). Many early Paleozoic cephalopods balanced their shells, as does *Nautilus*, by coiling the buoyant chambers above the body.

Slightly curved cephalopods (Fig. 7–11) must have had difficulty swimming and are assumed to have floated near the seafloor or crawled on it in a more or less vertical position.

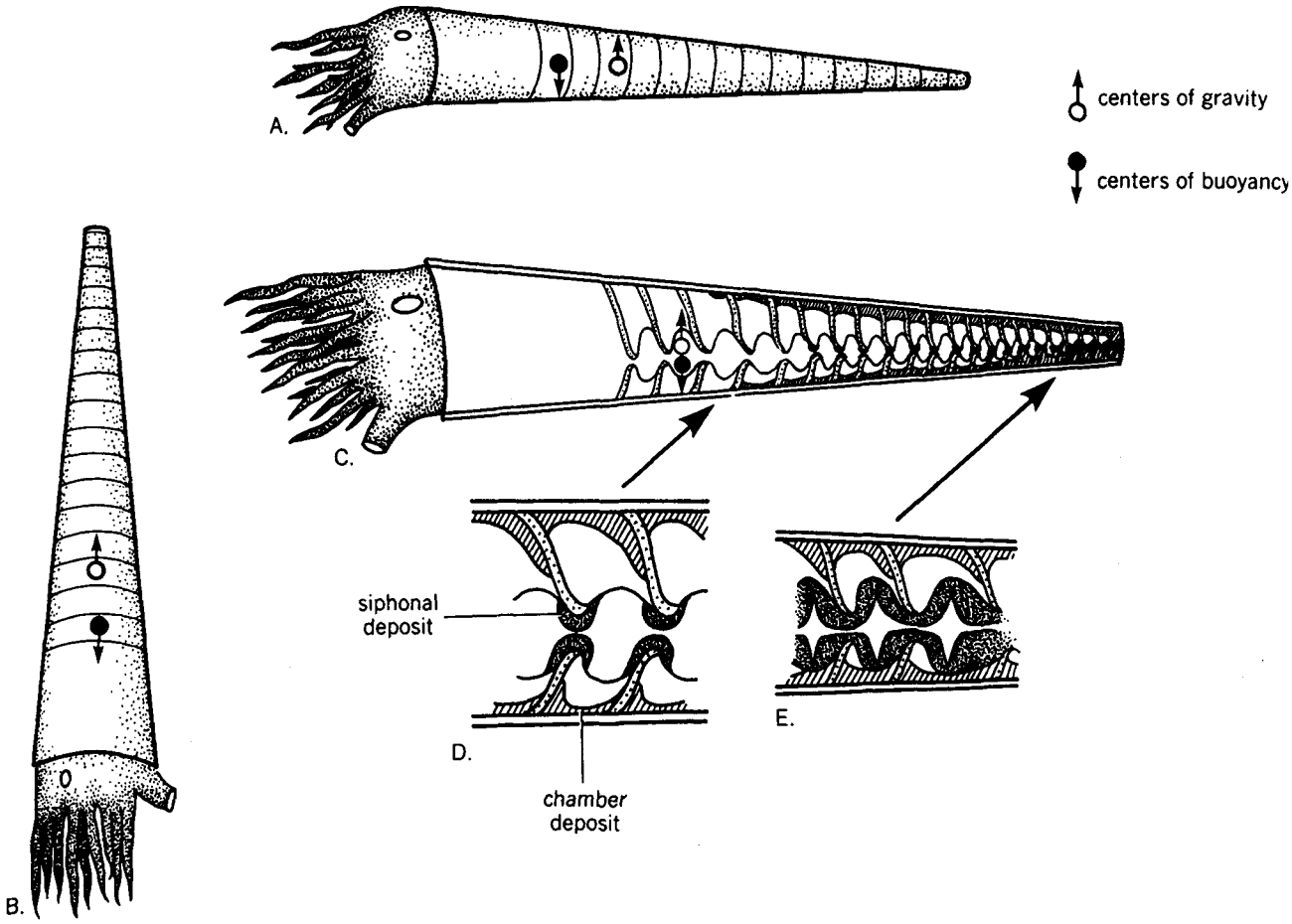


Figure 7-8 Buoyancy control in Paleozoic straight nautiloids. A, B. In a simple unweighted cone the center of buoyancy is at about .75 of the length, the center of gravity is near the front, and the position in the water that results is shown in B. C. Siphuncular and chamber deposits bring the centers of gravity and buoyancy together and the shell floats horizontally. D. Detail of deposits near the living chamber. E. Detail of deposits near the apex showing the development of a heavy siphuncle and the position of the siphuncle near the ventral side of the cone.

Straight cephalopods differ little in exterior form although a few have distinctive ridges and nodes. They may be cut along the siphuncle to reveal the interior structure for identification.

From Paleozoic time to the present, one group of cephalopods replaces another in four periods of rapid expansion, each followed by slow decline or catastrophic disaster. They evolved from monoplacophoran ancestors in Late Cambrian time. Early Ordovician time was the period of greatest expansion for the Nautiloidea. By mid-Ordovician time ten orders were represented in the fossil record and their long, straight cones were abundant fossils in limestones and shales. From that time, the number of orders decreases to nine in mid-Silurian, to six in mid-Devonian, and to four in Early Carboniferous time. By mid-Paleozoic time the endoceratoids and actinoceratoids were extinct. The orthoceratoids reached the Triassic but by middle Mesozoic time only the ancestors of the modern *Nautilus* remained of the early Paleozoic cephalopod fauna.

In Silurian time the nautiloids gave rise to a transitional group, the Bactritina, which in turn began the late Paleozoic expansion phase of the cephalopods, in which the ammonoids were the principal players. The bactritines were small, straight cephalopods, commonly with a bulbous initial chamber and small marginal siphuncle on the lower edge of the cone.

In most animals the lower side is technically called the ventral and the top side is referred to as the dorsal (from Latin words for belly and back). In a coiled shell the lower and upper sides of the coiling tube change places along its length and these terms

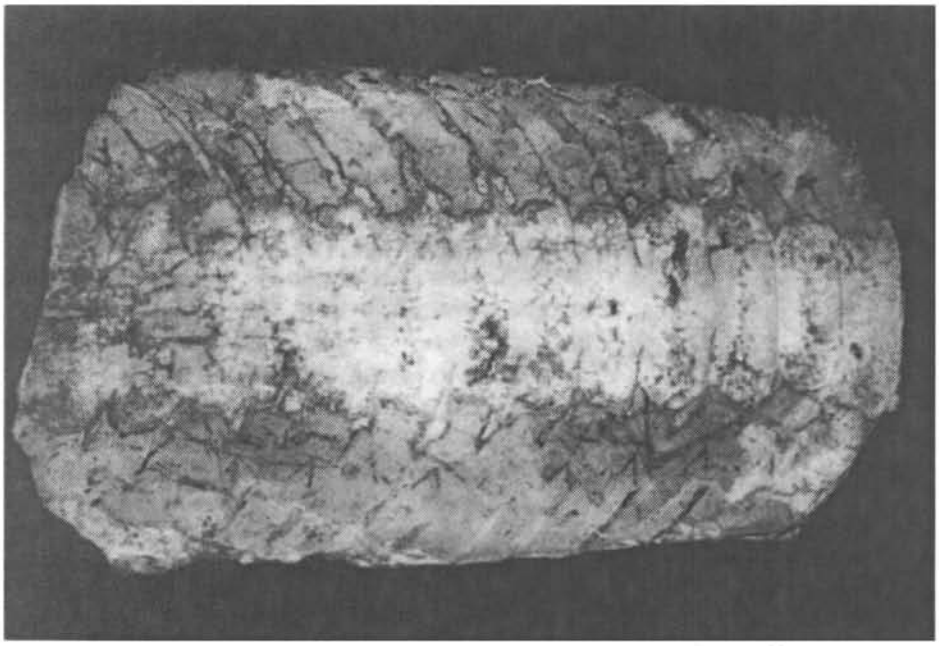


Figure 7-9 *Armenoceras* (Ordovician), a straight nautiloid with a heavy siphuncle (light-colored). The specimen has been cut longitudinally and polished so that the siphuncle is seen in section. The specimen is 16 cm long.

are confusing. The outside edge of a coiled cephalopod shell, which is in the ventral position at the living chamber, is called the venter; the inside edge, the dorsum.

Late Paleozoic Cephalopods:

The second major cephalopod expansion began in Devonian time from bactritine ancestors and involved the subclass Ammonoidea. The following features are typical of this group: (1) shells that are coiled planispirally; (2) cylindrical, unweighted, small marginal siphuncles located on the venter; (3) septa folded radially; (4) small, spherical, embryonic shell in the center of the coil.

Of these features, the folded septa are most distinctive of ammonoid cephalopods. In most early Paleozoic cephalopods, the septa are parts of spherical shells and concave toward the aperture. The line along which the septum meets the shell wall is

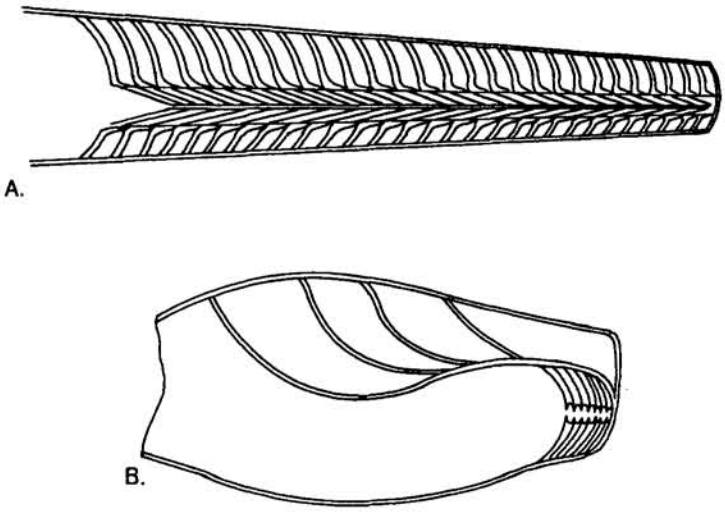
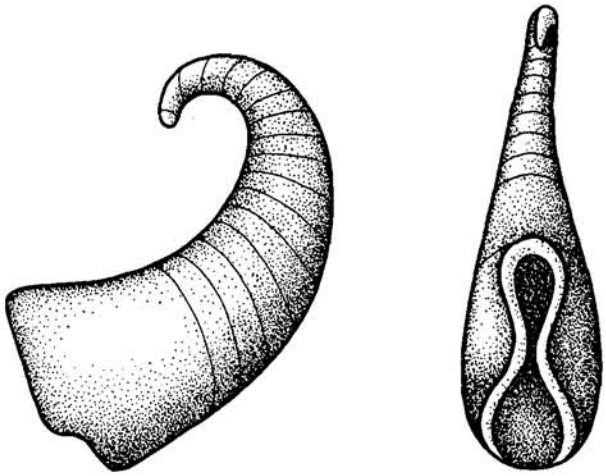


Figure 7-10 Balancing straight nautiloid shells. A. Diagrammatic cross section of *Endoceras*, showing the invaginating cones in the siphuncle. B. Diagrammatic cross section of an ascocerid showing the chambers formed above the living chamber.



Phragmoceras

Figure 7-11 *Phragmoceras* (Silurian), side and front views. Note the curved shell and the restricted aperture.

called the septal suture. It is invisible on the exterior surface of shells in which the wall is preserved, but in fossils the wall is often partially dissolved leaving the edges of the septa exposed where they meet the wall (Fig. 7–12). If the septa are simple concave plates, the suture will be straight or slightly curved, but if the septa are fluted at their margins, the suture line will reflect the complexity of that folding. The lines are commonly illustrated as if removed from the curved surface of the shell and flattened (Fig. 7–13). The folding of the septa increased their strength without increasing their weight, so that they would not break from pressure changes when the animal changed swimming depth (see also Chapter 13).

Ammonoids of the Devonian, Carboniferous, and Permian belong largely to the order Goniatitida. The suture lines of this group are composed of simple open or sharp curves indicative of simple folding of the septa. The goniatites are excellent index fossils for late Paleozoic strata for they, like most of the ammonoids, evolved rapidly and were distributed widely. Not only were they capable of swimming to extend their range, but after death their shells must have remained buoyant and were distributed by currents.

PALEOZOIC GASTROPODS

The first gastropods appear in the Tommotian Stage at the base of the Cambrian System and belong to the genus *Aldanella* (Fig. 7–14). These trochoid shells are accompanied by simple, low, conical shells like

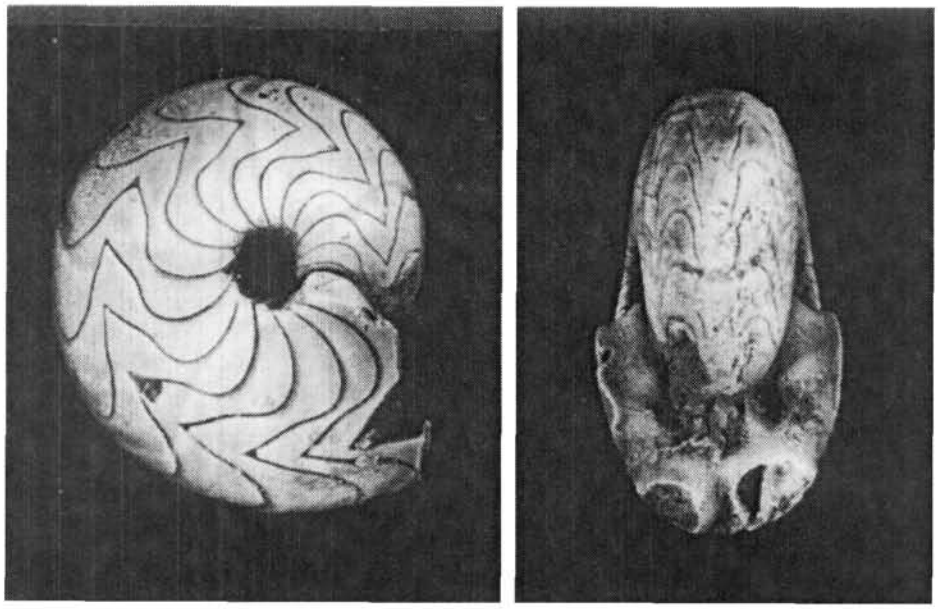


Figure 7-12 Side and apertural views of the goniatite *Bolandiceras* (Carboniferous). The specimen is 2.6 cm across. Coiled cephalopods are conventionally illustrated with the aperture at the top, a completely unnatural position. In this book the aperture is placed at the bottom to approximate a living position. (Courtesy of N. J. Riley and British Geological Survey.)

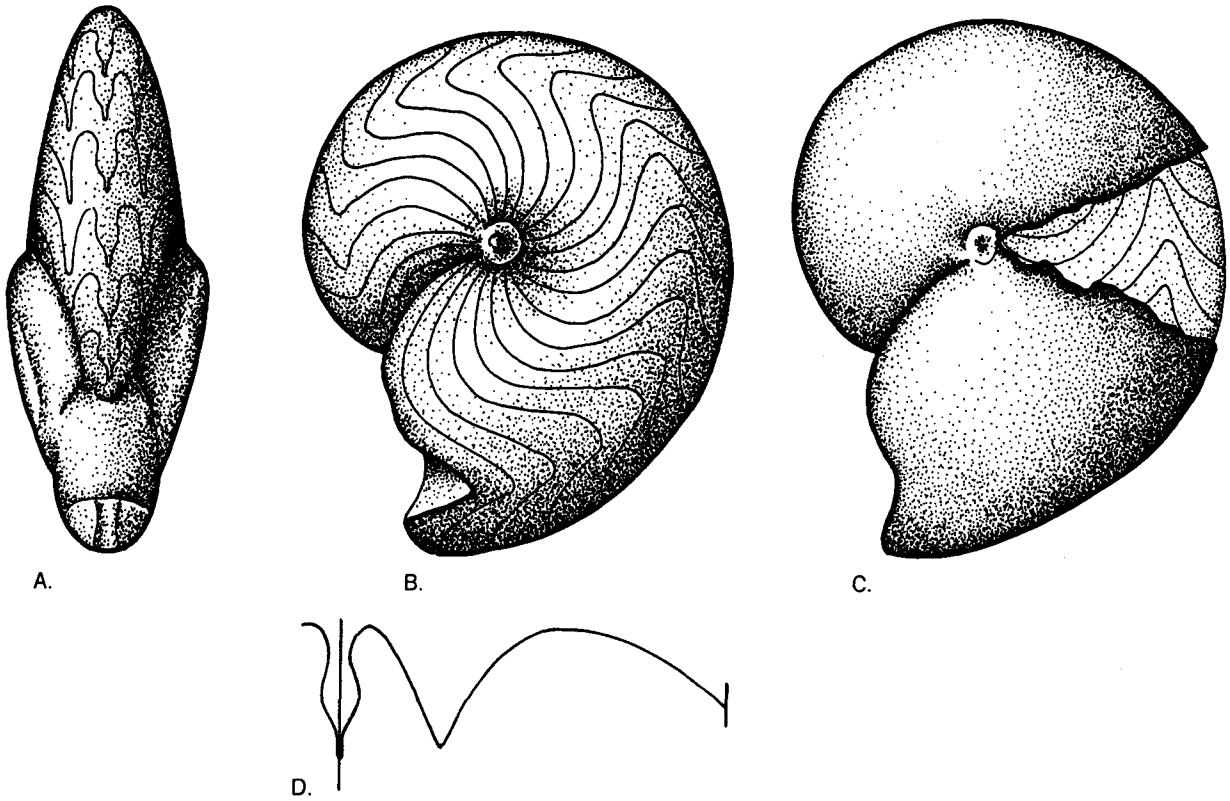


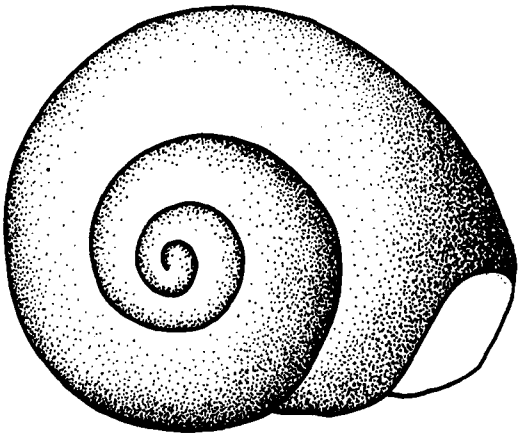
Figure 7-13 The goniatite *Imitoceras* (Carboniferous). A, B. Internal mold of the chambered part of the shell (living chamber missing) from the front and side showing the folded face of the first septum. C. Exterior of the shell broken to show the septal sutures. D. Suture line as commonly illustrated.

those of limpets that cling to rocky, wave-washed shores. These conical shells are members of the Monoplacophora, the group from which the gastropods evolved (Fig. 7–15). The elevation of the cone to accomodate an enlarging visceral mass is believed to have led to the coiling of the shell in a plane (planispiral) so that it was more compact and less likely to be knocked off the rocks by waves. Such planispirally coiled monoplacophorans were probably ancestors of both gastropods and cephalopods (Fig. 7–16). Cephalopods continued to use the planispiral coil extensively but most of the gastropods adopted the asymmetrical trochoid spiral with the shell slung over the shoulder.

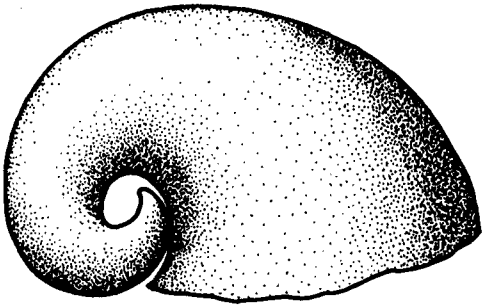
The first gastropods were small and most did not reach a diameter of over a centimeter until the Ordovician Period when they first became abundant. The diversity of gastropods did not wax and wane in cycles like that of the cephalopods, but all orders increased or maintained their diversity through Devonian, Permian, and Cretaceous crises that decimated other invertebrates.

The common types of shell form evolved early in gastropod history: high spired trochoid forms of many whorls, low squat trochoid forms of few whorls, and planispirally coiled forms (Fig. 7–18). Analysis of gastropod shell form by computer is discussed in Chapter 13. One type of coiling evolved in which the spire was depressed below the last whorl instead of being elevated above it as in most gastropods. Such shells have been called both hyperstrophic and ultradextral (*Maclurites, Lecanospira*, Fig. 7–17E,F).

The orders of gastropods are recognized on the basis of their different gill structures and by the modifications of the mantle to supply them with water—features that are not preserved in fossils. However, clues to the plumbing of the mantle cavity are preserved in the margins of the aperture. In advanced gastropods the mantle folds into tubes to control the currents, like the siphons of bivalves. The front siphon brings water to the gill, or gills, above the head, and a rear one empties it behind the animal. Usually the margin of the shell is folded



A. *Aldanella*



B. *Pelagiella*

Figure 7-14 Internal molds of the first gastropods (Cambrian). A. *Aldanella* (0.5 mm). B. *Pelagiella*, possibly a monoplacophoran (1 mm).

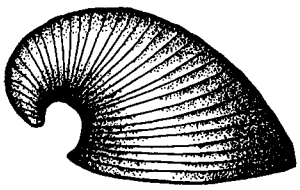
over the siphon to support it, or the siphon occupies a notch in the margin that leaves behind interruptions in the growth lines on the shell (Fig. 7–17A,D). The influence of siphons and water flow on the form of the aperture allows the paleontologist to use a classification that was designed for living gastropods.

Phylum—Mollusca
- Class—Gastropoda
  - Subclass—Opisthobranchia
  - Subclass—Pulmonata
  - Subclass—Prosobranchia
    - Order—Archaeogastropoda
      - Suborder—Bellerophontina
      - Suborder—Pleurotomariina
      - Suborder—Macluritina
      - Suborder—Murchisoniina
      - Suborder—Patellina
      - Suborder—Trochiina
      - Suborder—Neritopsina
    - Order—Mesogastropoda
    - Order—Neogastropoda

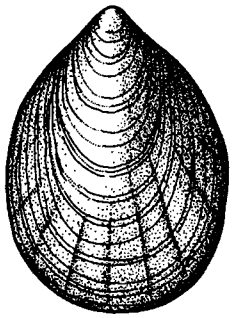
The subclass Prosobranchia is divided into three orders:

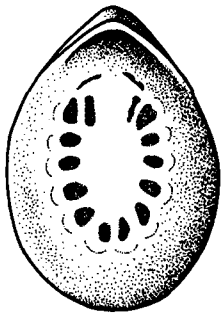
1. Archaeogastropoda—some retain the primitive condition of two gills; others have one. As they are without siphons, the water for the aeration of the gills enters the mantle cavity beneath the edges of the shell.
2. Mesogastropoda—have an improved gill structure and one of the gills is always lost during the torsion process. Advanced members have siphons.
3. Neogastropoda—have a still different gill structure, a single gill, and all have siphons. Many are carnivorous. As this group did not appear until the middle of the Cretaceous Period, their history is described in Chapter 10.

The archaeogastropods are the snails typical of



A. *Cyrtonella*





B. *Pilina*

Figure 7-15 Monoplacophorans. A. *Cyrtonella* (Silurian–Devonian) (25 mm), an advanced curved shell. B, C. Exterior and interior of *Pilina* (Ordovician–Silurian) (35 mm), showing the paired muscle scars.

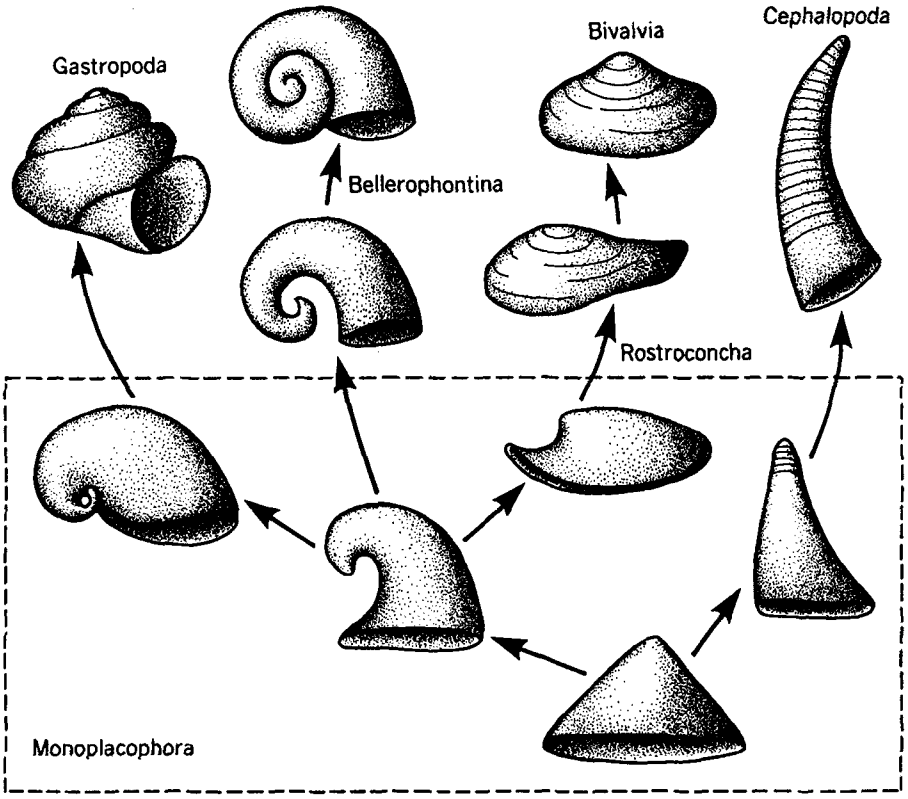


Figure 7-16 Origin of the major molluscan groups from various types of monoplacophorans. (Modified from B. Runnegar, *University of Tennessee, Geology Studies* 13.)

the Paleozoic Era but their descendants are still common in modern oceans. They reached their maximum diversity in the Ordovician Period. Robert Linsley (7) noted that most of them have radial apertures (Fig. 7–18). A radial aperture is one whose plane passes through the axis of coiling of the shell and as a result the shell cannot be carried parallel to the rock, or sediment, on which the snail is crawling. Snails with this type of aperture cannot clamp their shell by means of the muscular foot onto the seafloor when they are attacked but must rely on an operculum plate carried on the back of the foot to close the aperture. To clamp to a surface for protection, the gastropod must have an aperture that is tangential to the circumference of the last whorl.

The bellerophontine archaeogastropods have planispiral shells that increase rapidly in diameter during coiling (Fig. 7–17H,I). In this they resemble the shells of advanced monoplacophorans and some paleontologists believe they should be transferred from the gastropods to this class. Supporting their assignment to the monoplacophorans are paired muscle scars on the inside of the shell that imply that the animal had not undergone torsion; supporting the assignment to the gastropods are notches at the aperture margins of some that imply a circulation of water over a gill above the head which is found only in gastropods. Linsley suggests that the group is not homogeneous and includes both classes of molluscs. The pleurotomarines have low-spired shells with radial apertures and a deep slit in the outer edge of the aperture to channel the outflow of water from the mantle cavity (Fig. 7–17D). The group is common in shallow-water deposits of early Paleozoic age but modern representatives are found only in deep water. The macluritines are large, hyperstrophic shells with depressed spires and flat bottoms that were abundant in Middle and Late Ordovician seas. They are believed to have been sedentary filter feeders (Fig. 7–17E). Many of the high spired forms, like the common Ordovician genus *Hormotoma*, are included in the suborder Murchisoniina. Another group, of which the genus *Platyceras* is representative lived in a parasitic or symbiotic relationship with stalked echinoderms sitting near their anal openings and feeding from their waste (Fig. 7–17G).

Mesogastropods appear in Ordovician time but the order did not begin to diversify rapidly until the end of the Paleozoic and the beginning of the

Chapter 8

Land Plants and Their Ancestors

ALGAE

The photosynthetic eukaryotes can be divided into two groups: those that live on land and require water-gathering and circulating systems, and those that live in water and damp soil and need neither. The water supply system comprises conduits made of vascular tissue and the plants that have it are vascular plants. The Bryophyta, mosses and liverworts, occupy a middle ground between vascular plants and algae; they live on land but only grow actively in damp places where they do not need a vascular system. The largest group of nonvascular plants are the algae.

Soft Algae:

Proterozoic algal cells were only preserved under exceptional circumstances in shales or when impregnated with silica in cherts. In general, algae that did not secrete a covering or support of silica or calcium carbonate did not leave a fossil record. Possibly the seas since Proterozoic time have had a flora of unicellular and more complex soft green and brown algae comparable in diversity and abundance to that of present seas, but impressions of these seaweeds have been left as fossils only in those rare deposits where soft tissue is preserved.

In the Mesozoic Era several groups of unicellular algae became planktonic, abundant, and diverse in the ocean. The dinoflagellates secreted cellulose tests; the coccoliths, calcium carbonate; and the diatoms, silica. The history of these groups is briefly reviewed in Chapter 10.

Kingdom—Plantae
- Subkingdom—Algae
  - Division—Chlorophyta (green)
  - Division—Chrysophyta (diatoms and others)
  - Division—Phaeophyta (brown, soft)
  - Division—Rhodophyta (red)
  - Division—Pyrrhophyta (dinoflagellates)
- Subkingdom—Bryophyta
- Subkingdom—Tracheophyta

Red Algae (Rhodophyta):

The red algae have been important limestone makers since the early Paleozoic. In northern seas they thickly encrust rocks and shells with calcium car-

bonate, and in tropic seas they bind fragments of corals and shells together in reefs. Some form bush-like plants and contribute their jointed stems to the accumulating calcareous sediment when they die.

The carbonate secreted by most algae is on the outside of their tissues but the red algae secrete calcite around the margins of their cells, producing a three-dimensional network structure (Figs. 8–1, 8–2A). The most important superfamily, the Corallinaceae, form the ocean-facing algal ridges in Pacific reefs that take the brunt of the surf. The near-shore zones of many Caribbean reefs are completely covered with these coralline algae. Internally, the skeletal tissue is composed of minute cells, usually in two sizes—an internal coarse layer and an external fine layer containing cavities to house the reproductive spores. The coralline algae first appear in Jurassic rocks, but some late Paleozoic genera have been tentatively assigned to the group.

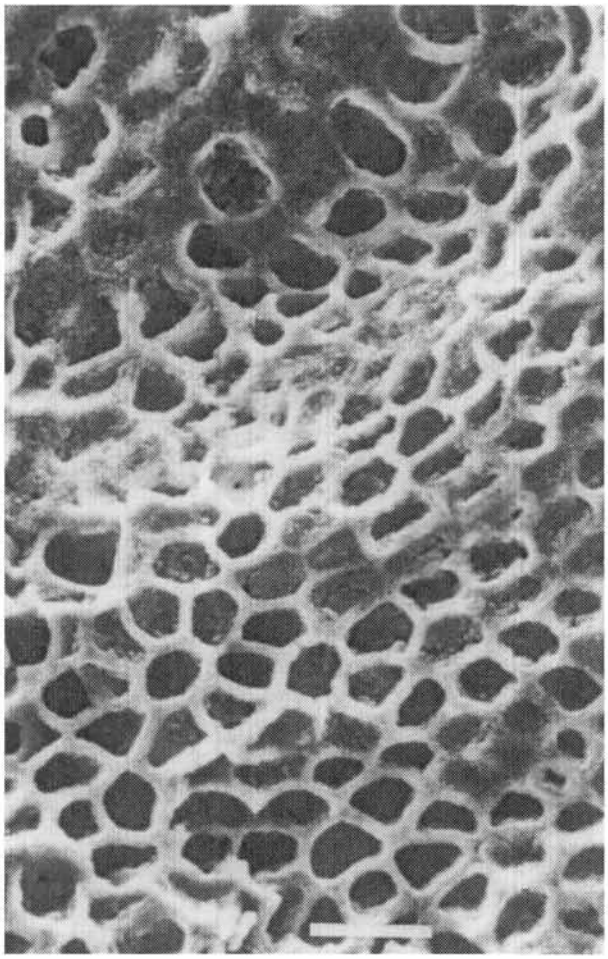
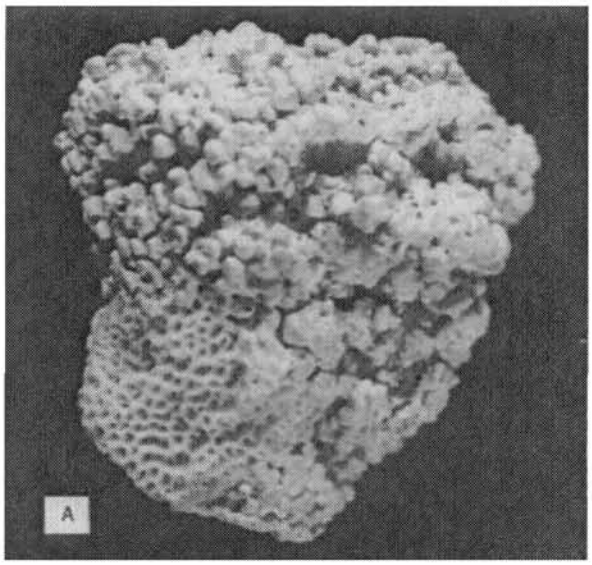


Figure 8-1 Scanning electron micrograph showing the cellular structure of an encrusting coralline red alga from a recent reef in Barbados. The scale bar is 20 micrometers. (C. W. Stearn.)



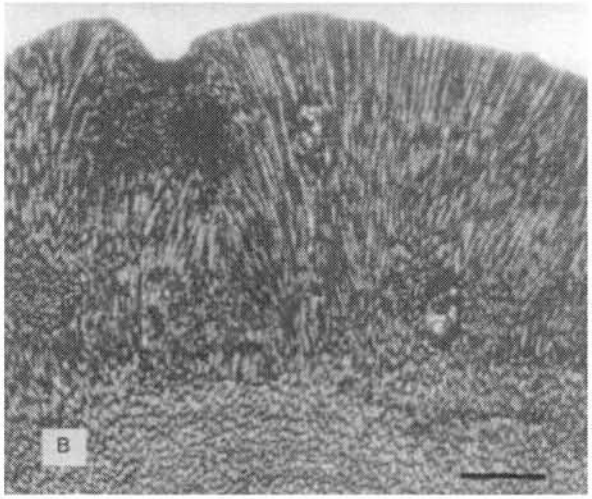


Figure 8-2 Calcareous algae. A. The crustose coralline alga *Lithophyllum* growing in a knobby mass on the scelractinian coral *Agaricia* on a recent fringing reef, Barbados. The specimen is about 9 cm in width. B. *Solenopora* (Ordovician), a fossil commonly assigned to the red algae illustrated in thin section showing the fine tubular structure. The scale bar is 1 mm. (C. W. Stearn.)

The Solenoporaceae (Ordovician to Miocene) are a superfamily, probably ancestral to the coralline algae. Their fossils consist of fibrous rows of cells coarser than those of the true corallines but not differentiated into the two layers (Fig. 8–2B). The

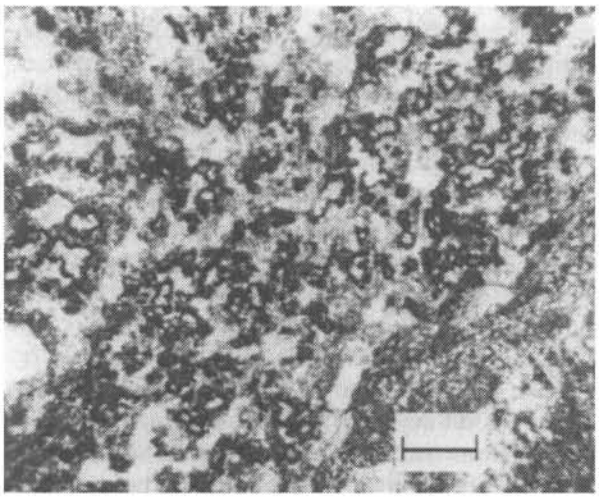


Figure 8-3 *Renalcis*, a thin section of the opaque-walled, irregular chambers of this enigmatic reef-building fossil. Devonian of Alberta. Scale bar is 1 mm. (C. W. Stearn.)

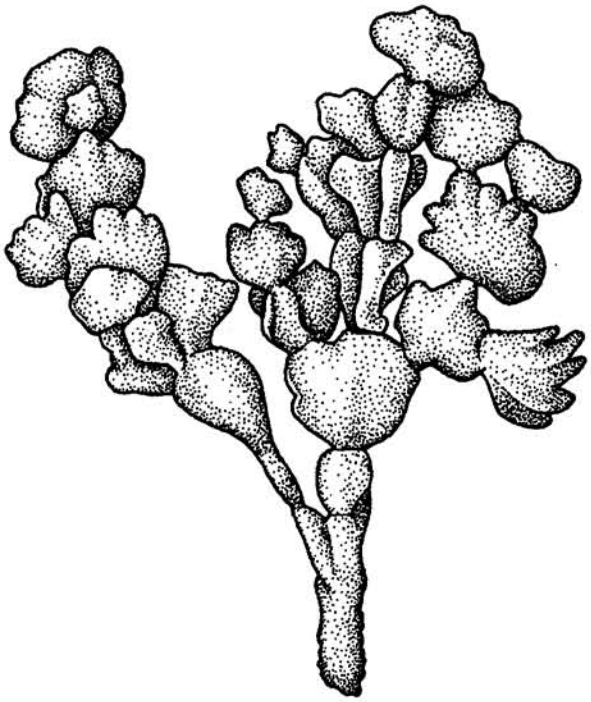
group reaches its greatest abudance in Jurassic reef limestones, but the small nodular fossils are also common in Paleozoic reef limestones.

Two widespread reef-forming organisms of the early Paleozoic may belong in the red algae but paleontologists are uncertain of their classification and some place them in the cyanobacteria. The genera *Renalcis* and *Epiphyton* are aggregates and branching series of rounded to crescentic chambers defined by walls of fine crystalline carbonate that is opaque in thin section (Fig. 8–3). The clumps seem to grow downward from the top of cavities. The two genera are abundant in reefs from Early Cambrian, when they consorted with the archaeocyathids, to Late Devonian time, when they filled spaces between stromatoporoids and corals. In the shallow Carboniferous seas of the central and southwestern United States, leaflike red algae grew abundantly as vertical sheets and formed small banks in the sea. These phylloid algal banks are important petroleum reservoirs in the Four Corners region of Utah and Colorado.

Green Algae (Chlorophyta):

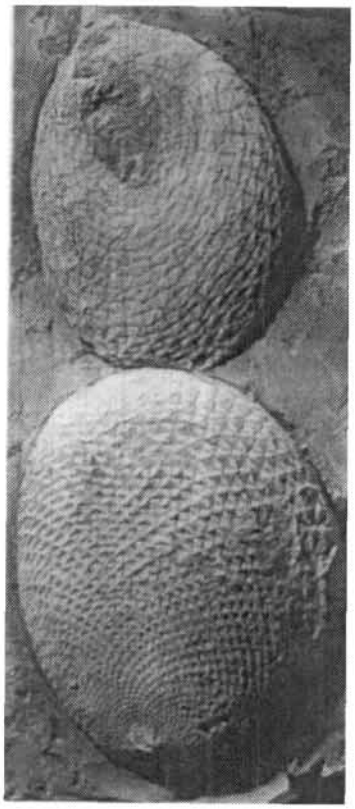
Although most of the marine and freshwater species of this group do not secrete hard tissue, some of them are, and have been, important contributors to carbonate sediments. The codiacean green algae include the genus *Halimeda* (mid-Jurassic to recent), whose heavily calcified plates secreted in branching series (Fig. 8–4) fall apart on death and supply a large part of the carbonate sands around modern reefs. Banks up to 19 meters thick, formed by *Halimeda*, occupy a large part of the platform behind the northern Great Barrier reef near Australia. The plates are 97 percent aragonite. Other codiaceans, such as the living genus *Penicillus*, secrete fine aragonite needles between their filaments and make major contributions to the deposition of lime muds when the soft tissue decays. In the Florida reef area *Penicillus* contributes 25 grams per square meter per year to the accumulating lime muds. Many lime mudstones of the past were probably formed of such fine particles precipitated by algae whose soft parts have completely decayed.

Ischadites (Fig. 8–5A) and *Receptaculites* (Fig. 8–5B) are representatives of an enigmatic group of fossils that are now generally assigned to the green algae. They are pillow or flask-shaped fossils up to tens of centimeters across composed of dumbell-shaped calcareous elements with rhombohedral ends arranged in a spiral pattern. *Receptaculites* is a common fossil in Late Ordovician limestones in western



Halimeda

Figure 8-4 The green alga *Halimeda* (Cenozoic) about natural size.



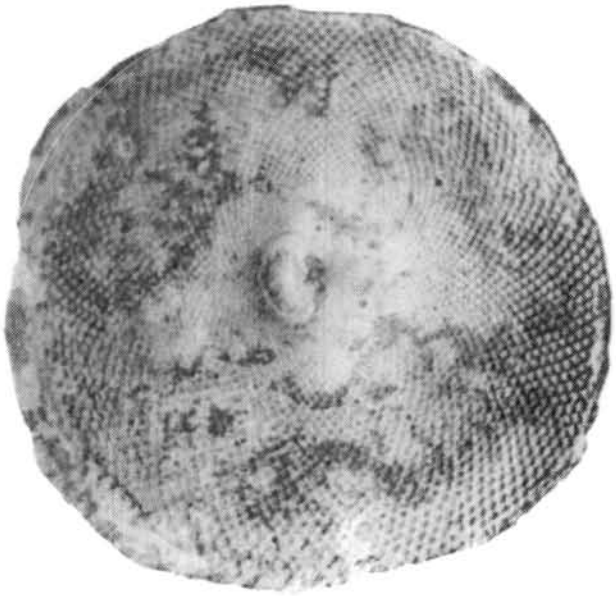


Figure 8-5 Receptaculitids. These sacklike fossils are commonly assigned to the algae. A. *Ischadites* (Silurian). Two specimens about 3 cm across. (Courtesy of Seigfried Reitschel and Forschungsinstitut Senckenberg [*Senckenbergiana lethaea*, v. 50, pl. 3.]) B. *Receptaculites* (Ordovician), the sunflower fossil, about 30 cm in diameter. (Courtesy of R. J. Elias, University of Manitoba.)

North America where it is known as the sunflower fossil because the pattern of plates resembles that of the seeds in a sunflower. The genus ranges from Middle Ordovician to Late Permian but most specimens come from pre-Middle Devonian rocks.

In the organization of their life cycle, their photosynthetic pigments, and biochemistry, some of the green algae appear to be the most likely ancestors of the land plants whose fossils first appear in Silurian rocks. Before this time the land surface was barren of vegetation and the processes of weathering must have been different from those of the present day, for some of the processes are controlled by soil acids derived from decaying plants. Possibly some rocks were covered with lichens, symbioses of fungus and algae, that are still widespread. The fossil record of the lichens is insignificant but a questionable fossil from the Proterozoic of South Africa has been attributed to this group.

BASIC FEATURES OF VASCULAR PLANTS

Because none of the cells of algae is far from water, the plant does not need organs to obtain moisture or to exchange metabolic gases. To live on land, plants had to evolve a system of gathering water and nutrients from the soil and pipe-like cells in the stem to conduct these nutrients to all parts of the body. How this vascular tissue evolved from the tissue of green algae is not clear because we have not yet discovered complete fossils that illustrate intermediate steps by which adaptation to land life was made. Scraps of cyclindrical cells that might have served to conduct water and nutrients have been recovered when sedimentary rocks as old as Early Silurian in age have been dissolved in hydrofluoric acid.

Marine plants withdrawn from water soon dry and die. The first land plants must have had the waxy covering for retaining moisture that characterizes modern land plants. However, the surface, while resisting drying, had to allow the passage of metabolic gases, oxygen, and carbon dioxide and regulate the transpiration of water vapor. For these purposes it was pierced by pores called stomates which are capable of opening and shutting in response to changes in environmental conditions. Algae are supported by water but the first vascular plants also required rigid cells that could support the weight of the plant above the ground.

Alternation of Generations:

All vascular plants have similar life cycles but there are many variations. In the cycle's simplest form as illustrated by ferns, the two phases or generations are separate plants. The sexually produced generation has two sets of chromosomes (diploid condition) and is called the sporophyte. The asexually produced generation has one set (haploid) and is called the gametophyte. The large plant (the fern) produces a single type of haploid spore by meiosis in dotlike cases on the leaves. The spores are dispersed and grow on damp ground into minute plants (gametophytes) that release male (sperm) and female (egg) cells from their lower surfaces. When the female and male elements combine along the base of the gametophyte, the fertilized cells produce a new fern plant (sporophyte). This alternation of generations is similar to that of the foraminiferans—one generation is produced asexually by spores, and the next sexually by fusion of sex cells. In more advanced vascular plants two kinds of spores are released, one that forms the female sex cells, and the other, the male cells. In the most advanced vascular plants, the flowering plants and gymnosperms, the transition from asexually produced spores to sperm cells that are contained in the pollen takes place within the pollen-bearing organs (anthers) of the flower and the transition from spores to eggs or ovules takes place in the ovary of the flower. In a sense the gametophytes have become part of the sporophyte.

The bryophytes (mosses, liverworts, and hornworts) are land plants without stiffened vascular tissue for conducting water and nutrients from the soil. They have a small fossil record that begins in the Devonian System. In bryophytes the plant that produces male and female cells (the gametophyte) is the conspicuous one in the life cycle; in vascular plants this phase, if separate, is minute and the large plant represents the spore-bearing phase (the sporophyte).

The first well-preserved land plant, *Cooksonia*, from Middle Silurian rocks records the success of the adaptation of plants to land.

EARLIEST VASCULAR PLANTS

Paleobotanists are not agreed on the time of appearance of the first vascular plants because they do not agree on the significance of fossil trilete spores. These are spores with three scars on their surfaces. Some have regarded these spores as diagnostic of vascular plants and, since they have been reported from rocks as old as Proterozoic in age, have placed the origin of land plants in that eon. However, others have pointed out that some algae and bryophytes produce spores that are much like trilete spores of higher plants and that the possibility of contamination of the Proterozoic samples by modern spores has not been eliminated. Trilete spores, probably of land plants, are known from the Late Ordovician of Libya, but scraps of vascular tissue are not found in rocks older than those of Early Silurian age. The great diversification of trilete spores in Middle Silurian rocks may reflect the rise then of vascular plants.

Cooksonia and other primitive plants are placed in the division Rhyniophyta. The name is derived from the town of Rhynie, Scotland, where a fossil deposit has provided much of our knowledge of the simplest land plants. Here, in Lower Devonian beds, the detailed structures of the earliest members of several plant groups were preserved impregnated with silica, forming chert. The rhyniophytes were short-stemmed plants branching upward from a horizontally creeping root system. The stems were smooth, without leaves, and carried spore cases at their tips (Fig. 8–6). *Psilophyton*, one of the first Devonian land plants to be described, was more complex than the rhyniophytes. Small branches emerged from the main stem and the spore cases grew on the ends of these side branches (Fig. 8–6). In the Zosterophyllophyta the spore cases are arranged along the main stem and many genera have spiny surfaces. Plants of this last division were the ancestors of the major coal-forming plants of the late Paleozoic, the Lycophyta.

Sub-Kingdom—Tracheophyta (vascular plants)
- Division—Rhyniophyta
- Division—Zosterophyllophyta
- Division—Trimerophytophyta
- Division—Lycophyta
- Division—Sphenophyta
- Division—Pteridophyta (ferns)
- Division—Progymnospermophyta
- Division—Pteridospermophyta (seed ferns)
- Division—Cycadophyta (cycads)
- Division—Cycadeoidophyta
- Division—Gingkophyta
- Division—Coniferophyta (conifers)
- Division—Anthophyta (flowering plants)(angiosperms)

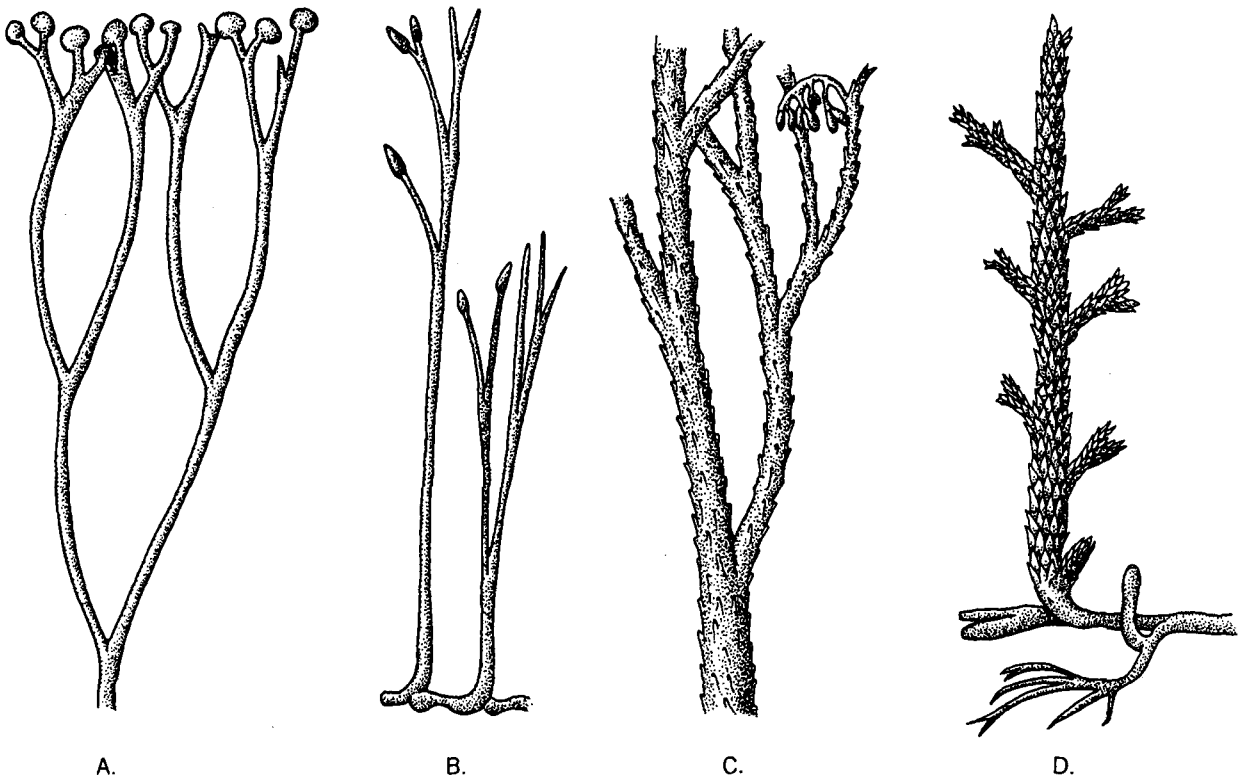


Figure 8-6 Primitive Devonian land plants. These plants were commonly 5 to 20 cm high but *Psilophyton* may have grown as high as 60 cm. A. *Cooksonia*. B. *Rhynia*. C. *Psilophyton*. D. *Asteroxylon*.

LATE PALEOZOIC FLORA

Lycophyta:

In the extensive coal swamp forests of the Carboniferous Period, trees of this division were the largest and most abundant. Coal was formed from partly decayed vegetation slowly transformed by the pressure of overlying sediment into the black rock that is one of our major sources of energy. Most coal today is mined from rocks of Carboniferous and Cretaceous ages and is burned in thermal power stations to make electricity. The details of its plant structure have been obliterated in the decay of plants before burial, during the preservational process, and by compression as the original organic mush was pressed into coal, but where the rock has been infiltrated by calcium carbonate to produce a concretion called a coal ball, the fine structure of the lycophyte trees that formed much of it is well preserved (Fig. 8–7).

The lycophyte trees of the coal swamps grew to heights of 38 meters and to diameters of 2 meters. Their spreading root systems, known by the generic name *Stigmaria*, extended 15 meters from the trunk. Unlike modern trees in drier climates whose roots reach deep to tap the water table, lycophytes had roots that spread out horizontally because the trees grew in swamps.

The trunk of the common lycophytes of the coal swamps had diamond-shaped scars on the surface in a pattern like reptilian scales and for that reason are called *Lepidodendron* (scale tree) (Figs. 8–8, 8–10) and *Lepidophloios* (scale bark). The scars, which are confined to the upper part of the trunk, mark places where leaves have fallen off. The leaves were unlike those of modern deciduous hardwood trees in that they were attached directly to the main trunk and branches. Most of the leaves of lycophytes were short and bladelike but some of *Lepidodendron* were 1 meter long. The tree branched a few times near the top to form a crown, and the spores were carried in cones that hung among the crown branches. In the genus *Sigillaria* the leaf scars appear to be in vertical lines (Figs. 8–8, 8–9, 8–14). Actually, the arrangement of leaf scars in both *Lepidodendron* and *Sigillaria* is helicoidal, that is, like a spring coiling up the trunk. Not all lycophytes were high trees;

Figure 8-7 Cellular structure of the plant matter making up coal, revealed in a coal ball where the plants have been empregnated with calcium carbonate. The lenslike structure at the top is the stem of a leaf of the seed-fern *Medullosa* and is about 4.5 mm thick. (Courtesy of Redpath Museum, C. W. Stearn.)

some were bushes growing in environments away from the coal swamps.

Lycophytes arose from the Zosterophyllophyta in the Early Devonian and some fossils from the Rhynie chert are believed to be the forerunners of these large trees. They persist to the present day as five genera of clubmosses of which the ground pine, *Lycopodium*, a creeping plant of northern forests, is the most familiar. As the Paleozoic Era closed the lycophytes declined, perhaps owing to the cooler and drier climate of that time and after the Paleozoic were insignificant members of the world flora.

Sphenophyta:

Growing with the towering lycophytes of the coal forests were 20 meter trees that looked like giant relatives of the common horsetail or scouring rush that grows now in marshy places. The horsetail (*Equisetum*) is a living fossil in the sense that it is the only surviving genus of a group of plants that were common in late Paleozoic and early Mesozoic landscapes. These plants that belonged to the division Sphenophyta are characterized by stems regularly interrupted by nodes or joints from which other stems or small leaves, like those of the lycophytes grew. The stem between the nodes was vertically ridged (Fig. 8–11).

The most common genus of coal forest sphenophytes is *Calamites* (Figs. 8–10, 8–11, 8–14). Many of the fossils of this tree are fillings of the central hollow in the stem. The circulets of leaves that grew at the joints of *Calamites* stems have been given the generic names *Annularia* or *Asterophyllites* (Fig. 8–12). Different parts of fossil plants are commonly separated before preservation and when found are given different names until they can be associated with a species or genus already named. Intermediate forms between sphenophytes and primitive plants of the Early Devonian have been found in Middle Devonian rocks.

Ferns (Pteridophytes):

The leaves of ferns bear spores, and the two generations are separate plants. Most ferns are small plants but ferns today in the tropics grow to treelike proportions and grew in Carboniferous coal swamps to similar sizes. They have been common plants since the Late Carboniferous but are confined to damp environments because the sperm require a film of water to reach the eggs at the base of the gametophyte. Not all the fernlike leaves preserved in sediments associated with coals belonged to true ferns—several different groups had fernlike leaves in the Carboniferous swamps.

Progymnosperms:

This group is believed to be ancestral to the conifers because the wood of the stems is much like that of conifers, but the leaves are not like the needles of conifers. The wood of the Middle Devonian tree *Archaeopteris* (Fig. 8–13A) was first classified as a conifer and the leaves as a fern before it was realized that they belonged to the same plant that shared these features. In Middle Devonian sandstones of New York, stumps of the progymnosperm *Aneurophyton* that indicate a tree 12 m high have been excavated at the Gilboa reservoir (Fig. 8–13B).

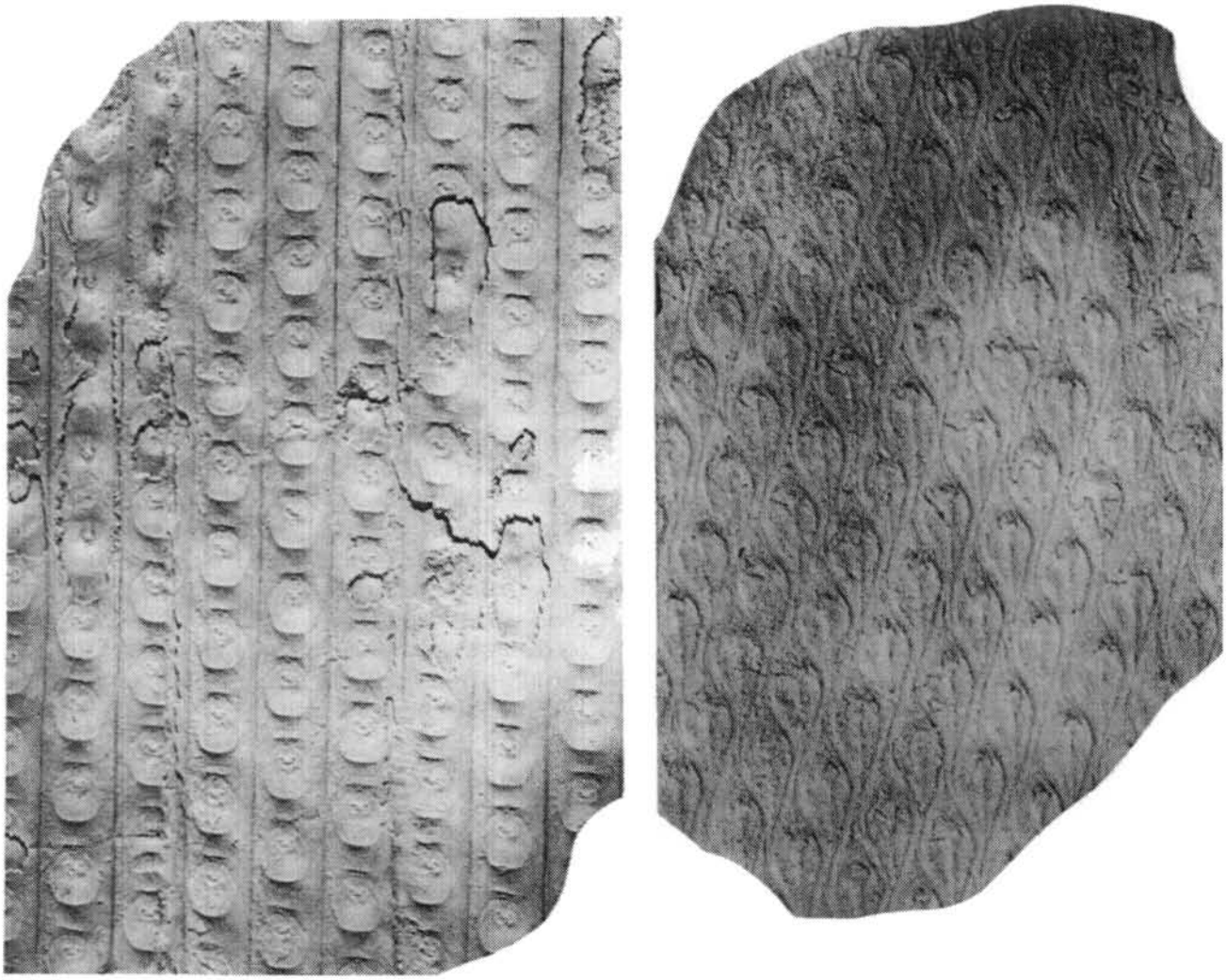
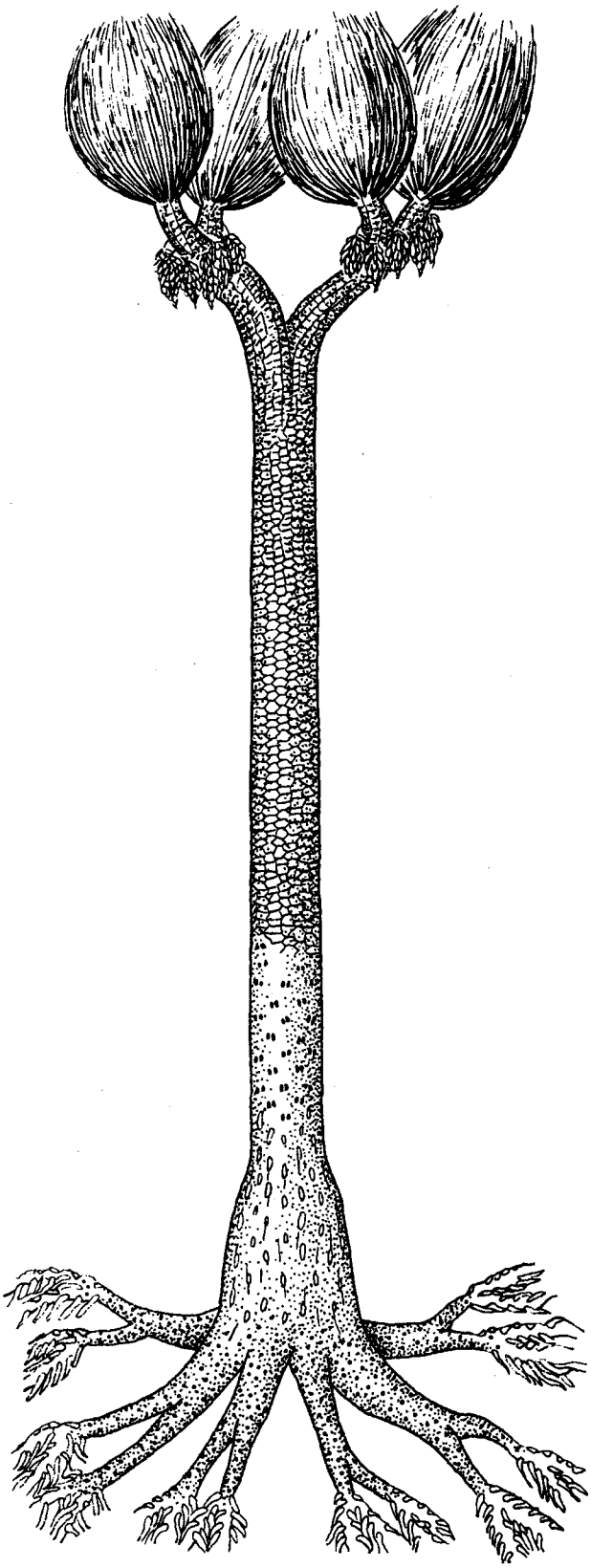


Figure 8-8 Impressions of the bark of lycophytes showing the leaf scars. A. *Sigillaria*. B. *Lepidodendron*. (Courtesy of Redpath Museum.)

Seed Ferns (Pteridospermophytes) and the Origin of Seeds:

All the plants so far discussed distributed small spores that grew into a minute separate plant in which both types of sex cells were formed. Spores that have been separated by acid solution of sediments show that many plants were dispersing two kinds of spores by later Devonian time, large megaspores that gave rise to female gametophytes and small microspores that gave rise to male gametophytes. Seeds evolved when the formation of the eggs and sperm no longer took place outside the tissue of the parental sporophyte. Spores have a single set of chromosomes (haploid) and are formed by meiosis in the sporophyte. In seed plants (the gymnosperms and angiosperm) the microspores develop into haploid pollen grains and the megaspores develop into female sex cells in ovules while still attached to the plants (the sporophyte). In most, both types of sexual organs are attached to the same sporophyte (for example, the male and female cones of conifers), in others the sporophytes themselves may be male or female. When the pollen reaches the ovule and the sperm in the pollen fertilizes the female gametophyte, it develops into a seed. The seed in its capsule then may enter a resting stage lasting many months before it gives rise to an new plant. The oldest fossil seeds come from the Upper Devonian of West Virginia and Belgium.

The seed ferns were fernlike in foliage but seeds hung from the tips of their branches. They are



Sigillaria

Figure 8-9 Reconstruction of the lycophyte *Sigillaria*.

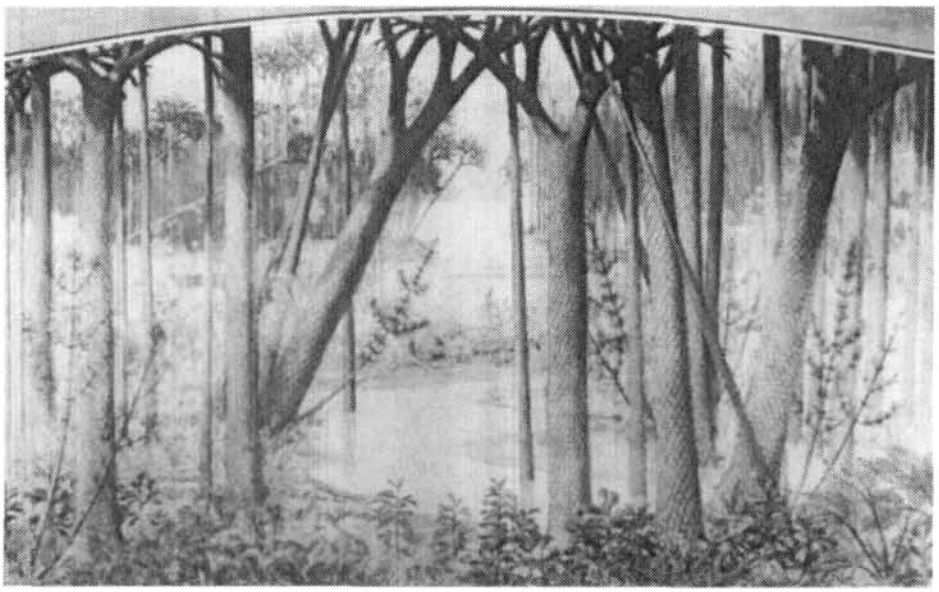


Figure 8-10 Reconstruction of the coal swamps of the Carboniferous Period. Tall branched *Lepidodendron* trees dominate the scene. *Calamites*, with whorls of leaves and many fernlike plants, are prominent in the swamp. (*Source:* Mural by G. A. Reid, courtesy of the Royal Ontario Museum.)

difficult to distinguish from ferns on the basis of foliage alone. They were important contributors to the undergrowth of the coal swamps and were the dominant plants of floodplains and uplands. They survived into mid-Mesozoic time.

Conifers and Cordaites:

Conifers are the familiar cone-bearing evergreens of northern forests, the pines, spruces, and hemlocks. Their leaves are typically needlelike or scalelike. The plants have small cones that release pollen to the wind and larger cones in which the ovules are fertilized by that pollen and grow into seeds that are released when the cone opens. The reproductive cycle is a slow one in some species, taking up to two years to complete. The first conifers appeared in Late Carboniferous time and the group became abundant and diverse in late Paleozoic and early Mesozoic time (Fig. 8–14). The most familiar conifer fossils (*Araucarioxylon*) are the silicified logs of the Petrified Forest in Arizona (Fig. 8–15). These Triassic trees were apparently rafted to the site of their burial, for no traces of leaves or cones have been found in the sediments that enclose them. By mid-Jurassic time all the major families of conifers that are found in the modern fauna had appeared in the fossil record.

The Cordaites are Carboniferous and Permian cone-bearing trees descended from early gymnosperms. The cones were carried on small branches among the leaves which were up to 1 meter long and shaped like straps (Fig. 8–14).

MESOZOIC FLORA

Cycads:

The cycads are squat palmlike trees that grow in Central America and the southern hemisphere. Only ten genera are living but their leaves and trunks are common in Mesozoic sedimentary rocks. Some cycads have short trunks shaped like a pineapple but some have trunks up to 10 meters high. The palmlike compound leaves are attached directly to the trunk and leave prominent scars (Fig. 8–16). The male plants have cones that release pollen which is dispersed by the wind or by beetles to the female plants whose ovules are borne on different cones. The cycads are descendants of seed ferns of the late Paleozoic but did not give rise to higher plants.

Figure 8-11 Jointed stem of *Calamites*. This is a sediment filling the hollow interior of the stem. (Courtesy of the Field Museum of National History (Geo5373), Chicago.)

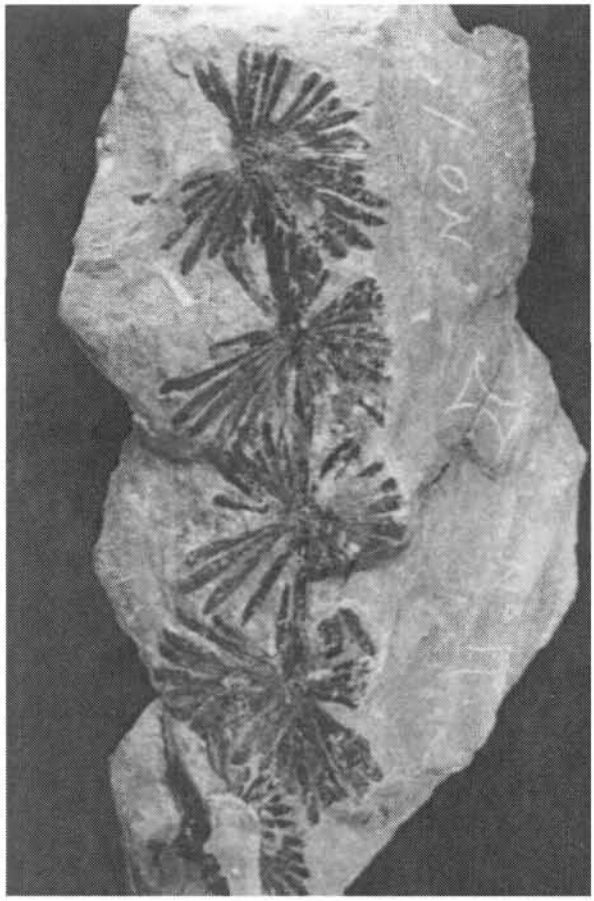


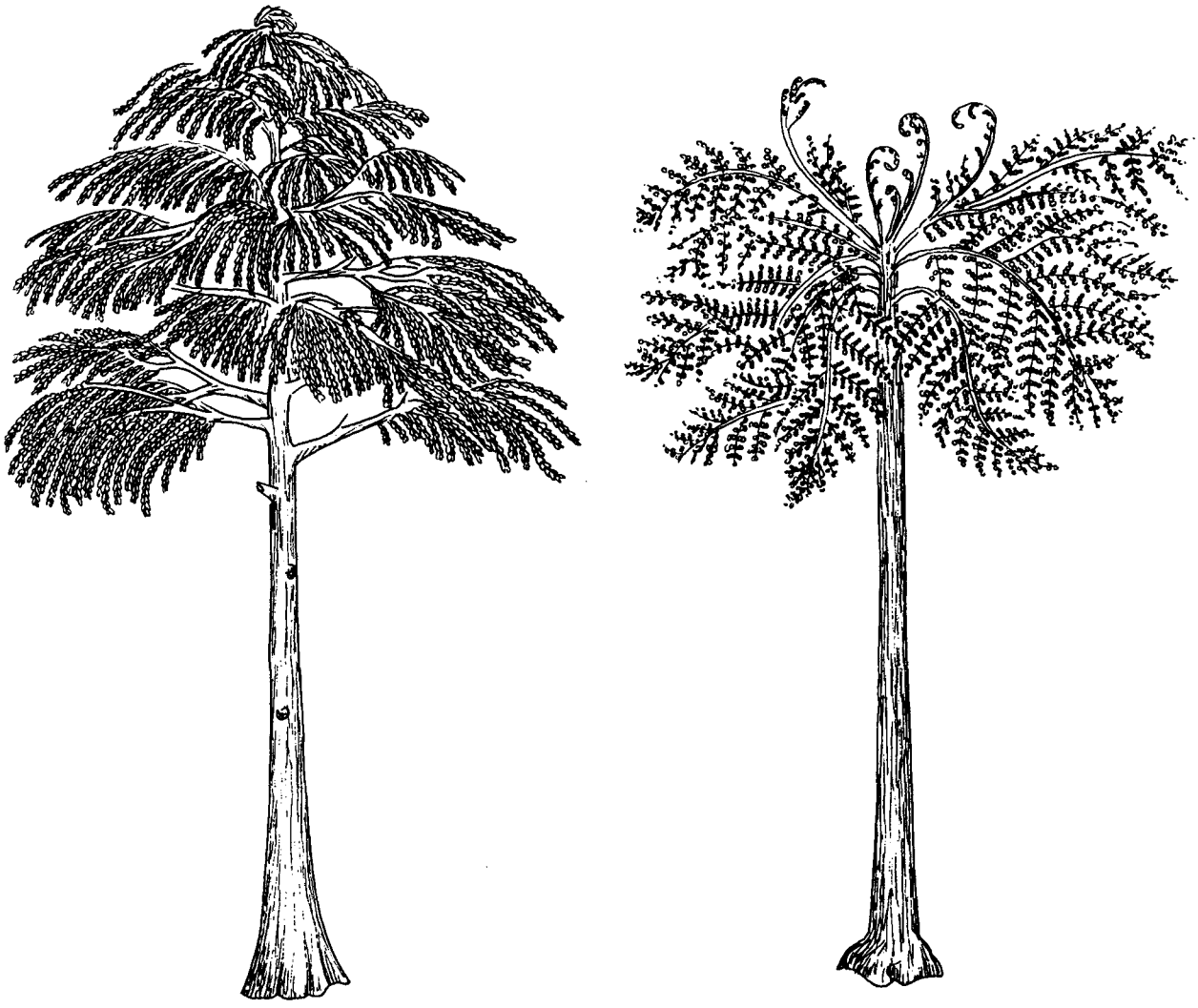
Figure 8-12 *Asterophyllites*, the leaves of an arthrophyte such as *Calamites*. Carboniferous. The specimen is about 15 cm long. (C. W. Stearn, Redpath Museum.)

Cycadeoids:

The cycadeoids are an extinct group with squat trunks covered with leaf scars similar to those of the cycads. These silicified trunks are common in Cretaceous sediments of the Black Hills of South Dakota. The cones are embedded in the trunks and contain both the male and female organs like the flowers of more advanced plants. Some reconstructions show the cycadeoids covered with flowers but there is little evidence that they flowered and some evidence that the cones were closed at the top and the plant practiced self-fertilization. The cycadeoids became extinct at the close of the Cretaceous without giving rise to higher plants.

Flowering Plants (Anthophyta or Angiosperms):

In the seed plants considered so far, the egg is fertilized directly by sperm derived from the pollen and is not encapsulated in an ovary of a flower. Such seed plants are called gymnosperms because the seed is naked (Greek—*gymna* = naked). The



A. *Archaeopteris* B. *Eospermatopteris*

Figure 8-13 Reconstructions of the Late Devonian progymnosperms. A. *Archaeopteris*. B. *Eospermatopteris* and *Aneurophyton*. The trunk of this plant was given the first name and the foliage that is associated with it, the second.

gymnosperms came to dominate plants that dispersed spores for reproduction in late Paleozoic time, but they in turn were dominated in Cretaceous time by the flowering plants. These plants now make up more than 95 percent of the species of vascular plants and include practically all the plants that are useful to humans for food.

Although a strict definition of the flowering plants is difficult, they can be characterized generally as having the following features:

1. The eggs are fertilized by sperm from a pollen tube growing toward them from a collecting organ, the stigma.
2. The ovary is within a flower which evolved as an organ for attracting insects. The success of the flowering plants has depended on insect pollination.
3. Both male and female organs are contained in the flower.
4. Fertilization and the formation of seeds is rapid compared to that in the gymnosperms, usually taking only a few weeks.
5. The pollen tube brings two sperm cells to the

Figure 8-14 Reconstruction of Texas in Permian time. The large tree in the center foreground is *Cordaites*. Three tall *Sigillaria* trees grow nearby. At the extreme right is a *Lepidodendron* and in the distance the early conifers (*Walchia*). The mammal-like reptiles *Dimetrodon* and *Edaphosaurus* lurk in the *Calamites* thickets. (Courtesy of the New York State Museum.)

female gametophyte. One fertilizes an egg cell; the other unites with other nuclei in the gametophyte to produce nutritive tissue with three sets of chromosomes. The seed when released is supplied with a coating of this nourishing tissue that acts as an initial food source as it grows into a new adult plant. This coating is an important component of human diet.

The flowering plants burst upon the world scene in the middle of the Early Cretaceous Epoch. Their

Figure 8-15 Logs of Triassic conifer *Araucarioxylon* in the Chinle Formation, Petrified Forest National Monument, Arizona. (Courtesy of the U.S. Geological Survey.)

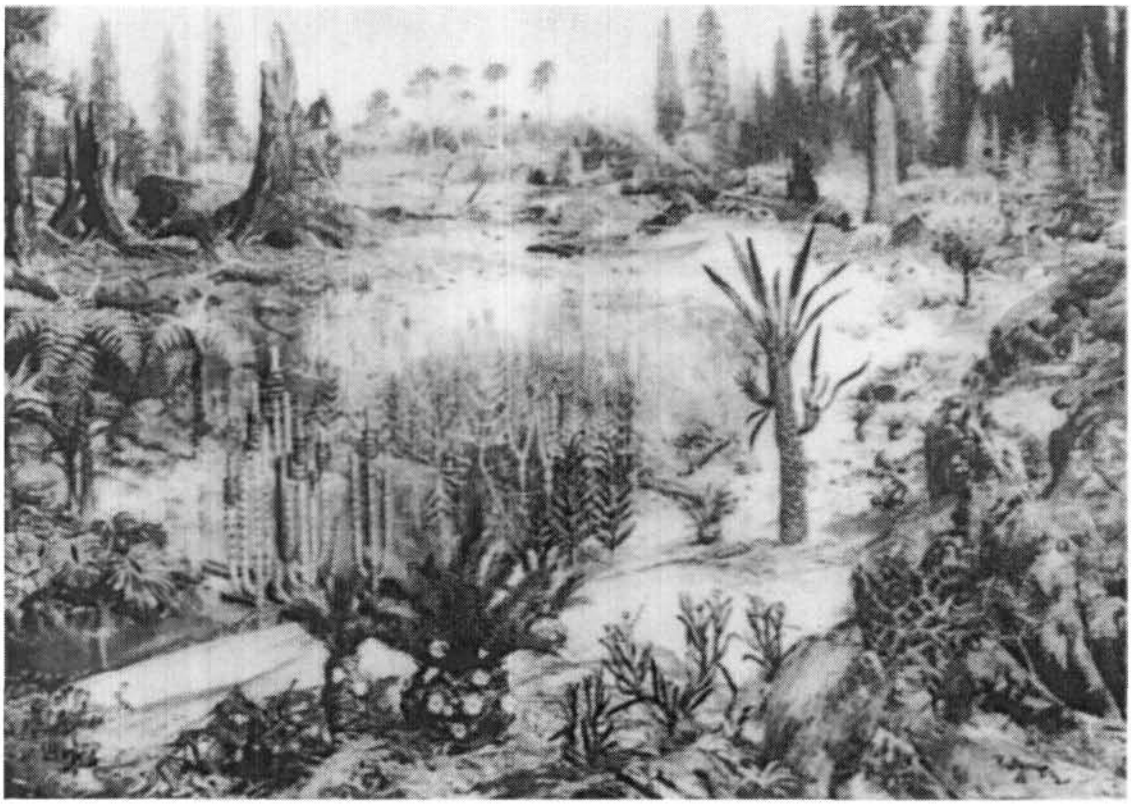


Figure 8-16 Reconstruction of an early Mesozoic landscape. In the marshy foreground are several kinds of *Calamites*. Ferns and cycadeoids on bulbous stems are common. The reconstruction of cycadeoids as flowering plants has been questioned. Conifers dominate the background. (*Source:* Reconstruction by J. Augusta and Z. Burian, from Prehistoric Animals, Spring Books, 1956.)

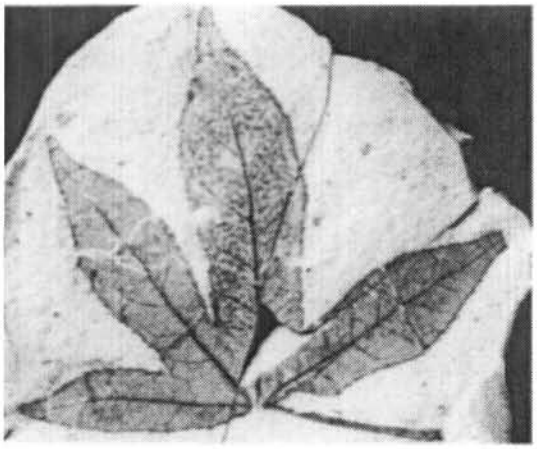


Figure 8-17 Leaf of the angiosperm plant *Liquidambar* from the Cretaceous of the western United States. (Courtesy of the Smithsonian Institution.)

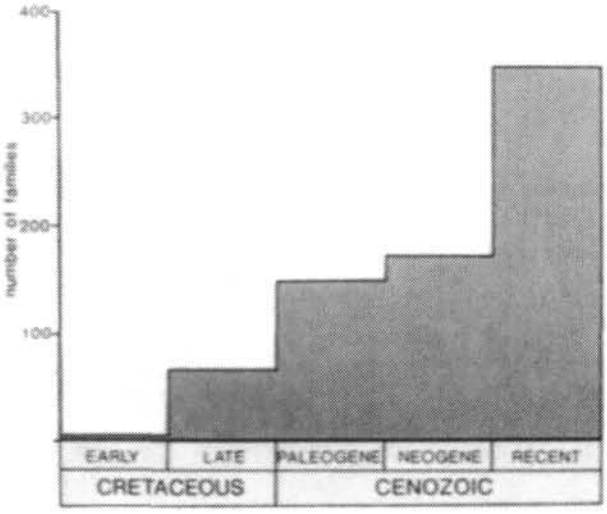


Figure 8-18 Rapid diversification of the anthophytes (angiosperms) in the Late Cretaceous and early Cenozoic. (*Source:* Modified from N. F. Hughes, *Paleobiology of Angiosperm Origins*, 1976.)

appearance without obvious ancestors and their dramatic diversification have posed problems for paleobotanists since the time of Darwin, who called the event "an abominable mystery". The stages of the Lower Cretaceous Series are, from the base upwards, the Neocomian, Barremian, Aptian, and Albian. In Barremian beds a few of the thin flat angiosperm leaves and some pollen believed to be from flowering plants have been found. In Aptian beds several types of angiosperm leaves occur and in the last stage of the Lower Cretaceous, the Albian, these leaves and the characteristic pollen become abundant (Fig. 8–17). During the Late Cretaceous, 67 families of the division Arthrophyta can be recognized in the fossil record (Fig. 8–18).

The identity of the plant group that was ancestral to the flowering plants remains a mystery. Almost certainly the ancestor was a gymnosperm and the seed ferns, the conifers, and the cycadeoids have all been proposed for the role. The flowering plants may not be a monophyletic group, that is, they may have arisen from more than one ancestor. However, no intermediate forms have been discovered to link them with potential ancestors. The sudden success of these advanced plants has been attributed to their more efficient physiology, their more rapid rate of reproduction and greater fertility, their evolution of a partnership with insects in reproduction, their greater adaptability to a range of conditions, and to physical changes in the Early Cretaceous environment. The rise of the angiosperms is likely to have been the result of a combination of these factors.

A relatively late event in angiosperm history had major effects on the evolution of the mammals. In Miocene time the group of flowering plants that we call grasses diversified and rapidly spread across the dry central plains of the continents. In pre-Miocene time most mammals were browsers, that is, they ate soft leaves and flowers and their teeth were not subjected to much abrasion. Grass provided a new source of nourishment to the mammals of the plains but it was nourishment that was hard on the teeth, not only because grass itself is abrasive (it secretes silica), but also because it traps a lot of dust in semiarid climates. The animals that adapted to this new food source are called grazers and they were characterized by high crowned teeth that could resist a lifetime of wear from grass-eating. The story of the grazers, such as the horses and elephants, is continued in Chapter 12.

SUMMARY

The history of plants is marked by four major events. The first was the evolution of the multicelled algae from the unicellular eukaryotes of mid-Proterozoic time. The second was the evolution of vascular tissue that allowed the descendants of algae to live efficiently on land. These first land plants reproduced by means of spores and had two separate generations, one sexual and the other asexual. The third event was the evolution of the seed which was fertilized by pollen. Male and female elements were formed from spores within plants, not in a separate generation. The fourth was the enclosing of the seeds in nutritive tissue and the use of insects attracted by a flower to aid fertilization.

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CHAPTER 9

Paleozoic Vertebrates

THE ORIGIN OF VERTEBRATES

The vertebrates were the last major group of metazoans to appear in the fossil record. Isolated fragments of a bonelike material have been described from the Upper Cambrian (l), but the oldest fossils that can be unquestionably identified as fish are of Middle Ordovician age (2).

The ancestors of vertebrates had probably evolved from other metazoans in the Proterozoic, but they had little likelihood of preservation until they evolved the capacity to form bony exoskeletons.

In the absence of a fossil record of the earliest vertebrates and their immediate ancestors, we must look for distinctive features in later fish to establish their relationship to other animals. Among the distinctive features of primitive living vertebrates are (1), a longitudinal rod, the notochord, which occupies the position of the vertebral column in terrestrial vertebrates such as mammals, (2), a dorsal hollow nerve cord, and (3), numerous gill slits in the area of the pharynx (Fig. 9–1). These structures are present in living protochordates, which are clearly more primitive than vertebrates in lacking a brain or paired sense organs of the head. Because they have a notochord, the protochordates are placed in the phylum Chordata with the vertebrates. Protochordates comprise the subphyla Cephalochordata, Urochordata and Hemichordata.

Phylum—Chordata
Subphylum—Hemichordata
Subphylum—Urochordata
Subphylum—Cephalochordata
Subphylum—Vertebrata

The protochordates and vertebrates are united by unique features of their early development (discussed in Chapter 5), including the pattern of formation of the coelom, mesoderm, and mouth that distinguish them from the major groups of segmented invertebrates—the molluscs, annelids, and arthropods—and suggest that these two major groups evolved separately from primitive metazoans.

The modern cephalochordates, typified by *Branchiostoma* (amphioxus), provide a good model for the type of animal that may have been immediately ancestral to vertebrates. Amphioxus is locally common in coastal marine waters in many parts of the

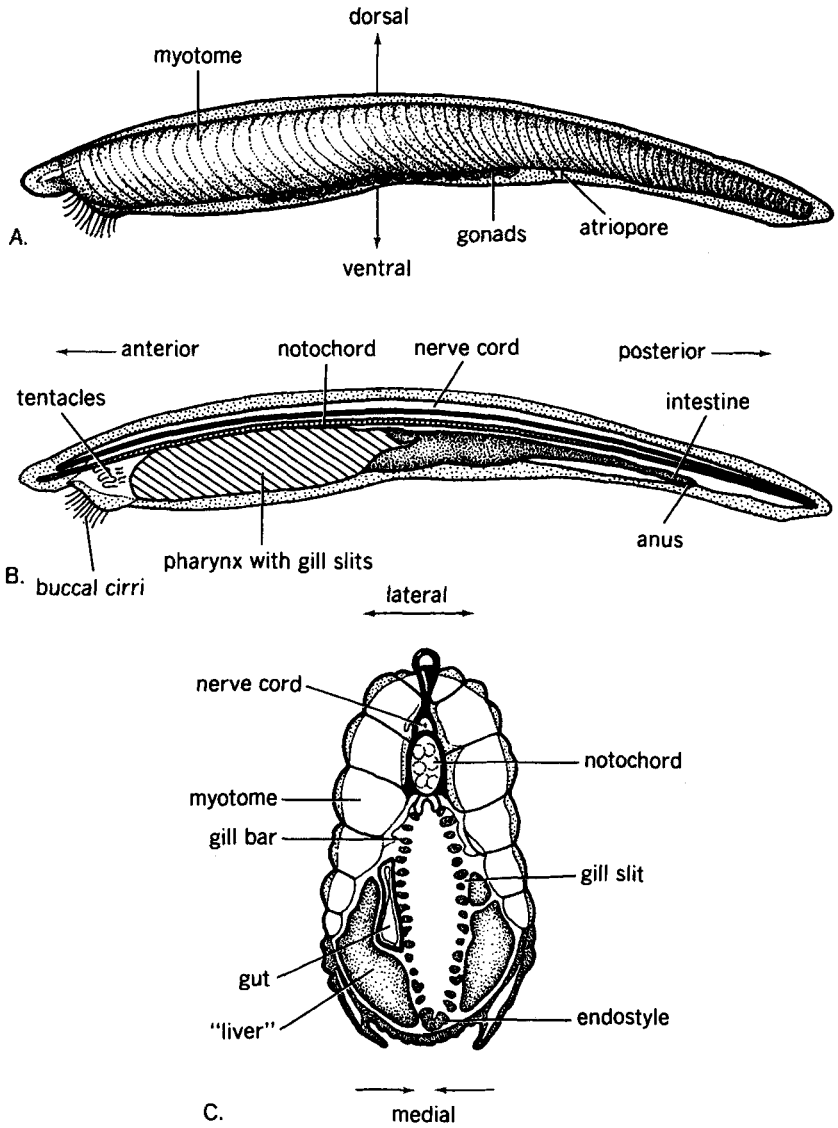


Figure 9-1 Amphioxus, showing the major features of chordates, and the positional terms used in their description. A. External view of amphioxus. B. Longitudinal section. C. Transverse section.

world. It is bilaterally symmetrical and resembles a small, transparent fish. As an adult, it lives partially buried in the sand and feeds by filtering small particles of food out of the water. The feeding structures of all invertebrate chordates and the larval stage of the lamprey, one of the most primitive living fish, indicate that the ancestors of the vertebrates were filter feeders.

Although amphioxus and the larval stage of the lamprey are sedentary, their body shape and pattern of musculature resemble those of actively swimming fish. Much of the body is formed by a series of muscles that are attached to transversely oriented septae anchored to the notochord. Waves of contraction on alternate sides of the body, running from the head to the tail, produce sinuous lateral undulations that move the animal forward in the water. The arrangement of the muscles and accompanying nerves and blood vessels gives a partially segmented appearance to the body of chordates, but it is not comparable to the metamerism of arthropods and annelids which involves the repetition of internal organs and appendages.

Not only do the muscles, notochord, and nerve cord of amphioxus resemble those of vertebrates,

but the pharynx and circulatory system are similar as well. As in fish, the pharynx in amphioxus is pierced by lateral slits. Great amounts of water are drawn in through the mouth by the action of cilia and pass back into the pharynx. Food particles are trapped by mucus secreted from the base of the pharynx. Water is discharged through the slits and enters an external space, the atrium, from which it passes out posteriorly. Food particles pass through the simple gut behind the pharynx, and wastes exit via the anus at the base of the tail.

The geometry of the circulatory system is closely associated with that of the pharynx. The main ventral vessel, the ventral aorta, lies at the base of the pharynx. From the aorta, the branchial arteries extend dorsally between the pharyngeal slits to join the anterior dorsal aortae, through which the blood flows posteriorly. Although the geometry of the vascular system resembles that of primitive vertebrates, it is more primitive in that it lacks a heart and capillaries. The arteries and veins are linked by blood sinuses. Oxygen is carried in solution, without specialized oxygen-carrying pigments, and there are no blood cells. Amphioxus is so small that exchange of respiratory gases can occur through the body surface, and no filimentous gills, such as fish have, are associated with the pharyngeal slits.

Most of the major organ systems in amphioxus are nearly ideal models for the origin of the more complex vertebrate structures. However, neither living animals nor the fossil record give evidence how these basic structures originated. The other groups of protochordates show various chordate traits, but they do not illustrate a simple evolutionary progression.

Cephalochordates are rarely found as fossils, but they have been reported from the Middle Cambrian Burgess shale, and from the Devonian of South Africa (3,4). These fossils superficially resemble amphioxus but provide no additional information as to the origin of chordate characters or vertebrates.

Simple, bilaterally symmetrical animals ancestral to the cephalochordates may have diverged from the early metazoan radiation in the Early Cambrian. These animals evolved an effective method of swimming using segmented muscles anchored to the notochord and a more efficient method of filter feeding by pharyngeal slits. From this lineage diverged the modern cephalochordates and the vertebrates.

In addition to having the anterior end of the nerve cord expanded as a brain associated with complex sense organs for smell (the olfactory or nasal capsules), sight (the eyes), and balance (the inner ear, or otic capsule), vertebrates are advanced over the cephalochordates in the elaboration of the musculature in the area of the mouth and pharynx to supplement the cilia in acquiring food and water. More effective feeding and sensory structures and the complex brain of vertebrates can be associated with the achievement of a metabolic rate higher than that of the protochordates. Invertebrate chordates (protochordates) are not able to increase their metabolic rate to permit short periods of vigorous activity. Vertebrates, in contrast, can increase their metabolic rate at least tenfold when active. This enables them to occupy more demanding ways of life that are not open to the invertebrate chordates (5). Unfortunately, no fossils are known that illustrate the transition between amphioxuslike chordates and vertebrates.

Vertebrates remained uncommon until the Late Silurian. Alfred Romer and others argued that the absence of vertebrates in typical marine deposits in the early Paleozoic was a result of their origin in fresh water. Freshwater deposits are uncommon in the stratigraphic record until Late Silurian time. The fossil record now demonstrates that the earliest members of most groups of primitive fish lived either in shallow nearshore marine deposits, or in brackish water, and only later did they become common in freshwater or normal marine environments. All modern invertebrate chordates are also restricted to nearshore marine habitats. This evidence implies that the origin of vertebrates, involving the elaboration of the brain and cranial sense organs, occurred within the marine environment.

JAWLESS FISH

Vertebrates are divided into two major groups, the Agnatha, or jawless vertebrates including the living hagfish and lamprey (Fig. 9–2), and the jawed vertebrates, or Gnathostomes.

In Upper Silurian and Lower Devonian beds, many distinct groups of early vertebrates are found, but the Ordovician and Lower Silurian fossils are so rare that they do not allow a coherent phylogeny to be formulated. The capacity to form a preservable bony skeleton apparently evolved separately

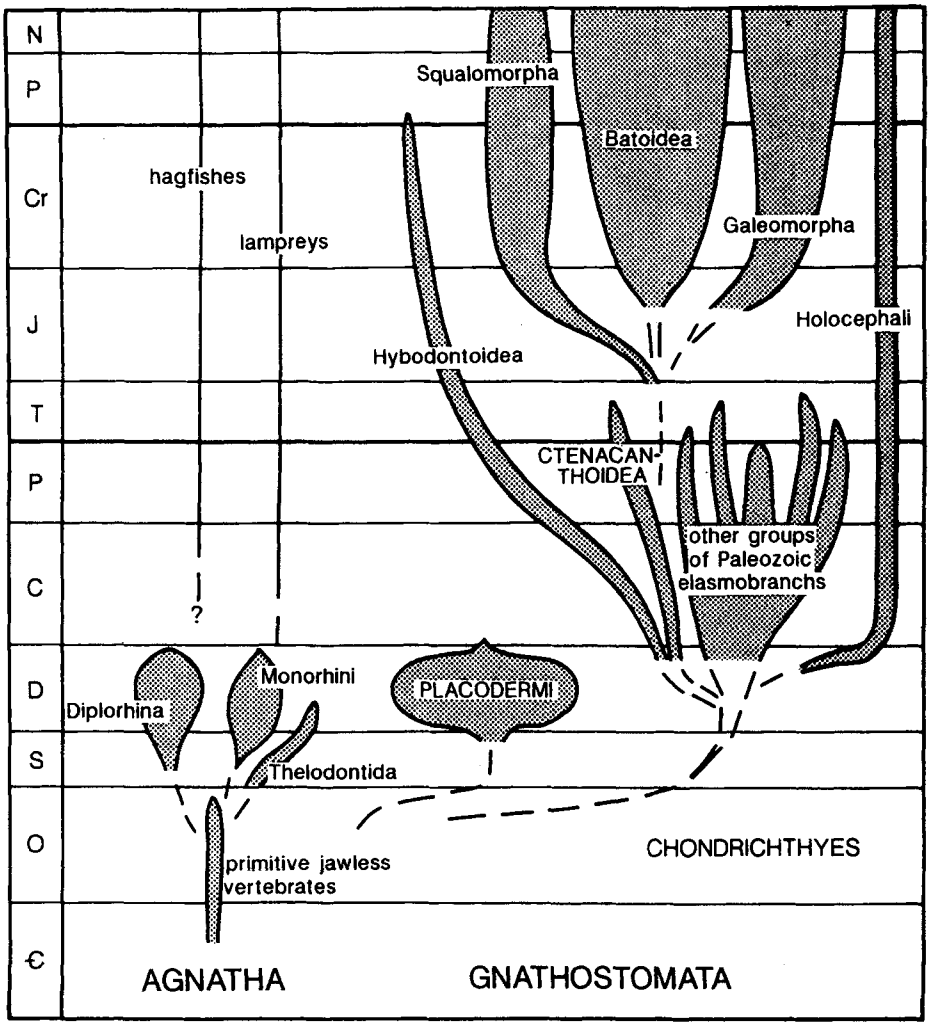


Figure 9-2 Pattern of radiation of fish (excluding Osteichthyes).

in several lineages after the first major radiation of vertebrates. The resulting lineages are all distinct from one another and provide little evidence of their interrelationships.

The first vertebrates were without jaws. Like their ancestors among the invertebrate chordates, they may originally have fed by filtering small prey or particles of food either from the open water or from the substrate. As their size and metabolic requirements increased, they may have become active predators on larger prey, even though they still lacked jaws.

A wide range of jawless vertebrates are known from the Ordovician, Silurian, and Devonian; all are referred to in an informal way as ostracoderms (meaning shell-skinned in Greek) because most are covered with a nearly continuous bony exoskeleton.

Subphylum—Vertebrata
  Class—Agnatha
    Primitive jawless vertebrates,
      Arandaspis and *Astraspis*
    Subclass—Pteraspidomorphi (Diplorhina)
      Order—Heterostraci
        Family—Pterapsidae
        Family—Amphiaspidae
    Subclass—Cephalaspidomorpha
        (Monorhini)
      Order—Osteostraci
      Order—Galeaspida
      Order—Anaspida
      Order—Petromyzontiformes (lamprey)
    *Myxiniformes (hagfish)
    *Thelodontida
* undesignated taxonomic level

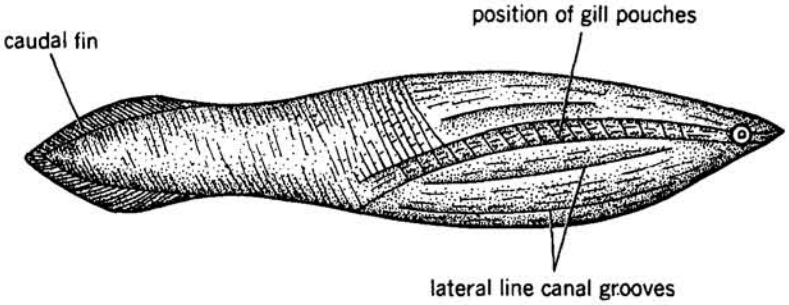


Figure 9-3 The earliest vertebrate, *Arandaspis* from the Middle Ordovician of Australia. (Modified from A. Ritchie & J. Gilbert-Tomlinson, *First Ordovician vertebrates from the Southern Hemisphere*.)

The earliest and most primitive fossils that are clearly those of vertebrates belong to the genus *Arandaspis*, from the Middle Ordovician of Australia. The body reached a length of approximately 14 cm. It was covered anteriorly by a continuous bony carapace and posteriorly by smaller scales (Fig. 9–3). There were no paired, dorsal, or anal fins. A series of gill covers was present along the anterior flank. Remains of a second type of early jawless fish, *Astraspis*, are preserved by the millions in beach deposits along the flanks of what were to become the Rocky Mountains, but were, in mid-Ordovician time, the margin of an inland sea. The carapace of *Astraspis* (Fig. 9–4) was made up of numerous polygonal plates that increased in size during the growth of the fish through the addition of smaller marginal elements. This was one solution to a problem faced by early fish: how to grow and yet retain a solid external covering. Many early genera delayed the secretion of the bony covering until the fish were nearly completely grown. Members of more advanced families evolved the ability to grow at the margins of larger bony plates and could begin ossification at progressively earlier stages in the life of the fish.

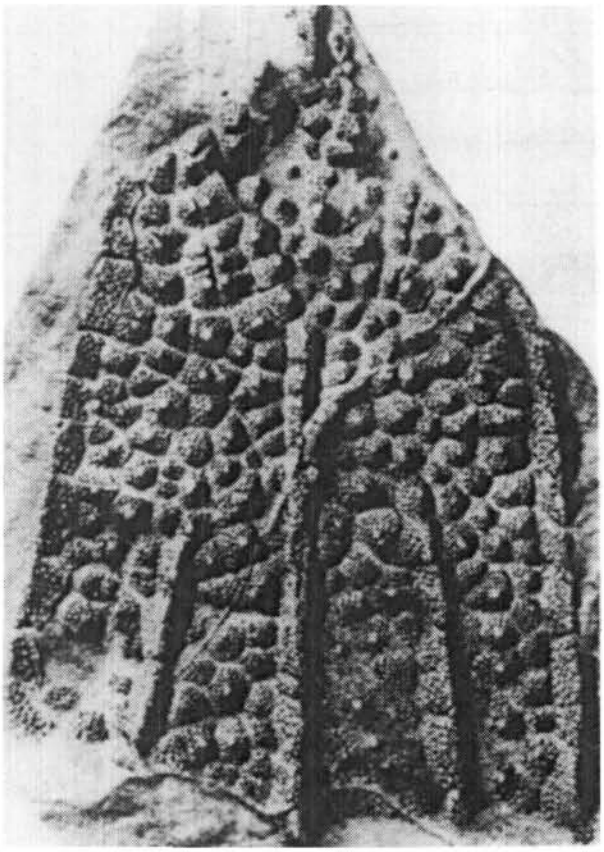


Figure 9-4 Dorsal armor of *Astraspis*, showing the mosaic of small bony plates. The entire fish was several cms long. (Photograph courtesy Dr. Tor Ørvig.)

None of the primitive fish had the capacity to form bone in the deeper layers of this tissue as most modern vertebrates can. Bone clearly served first for protection and only later was used for muscle attachment and internal support of the body and limbs. Bone is composed of calcium phosphate in a form of the mineral hydroxyapatite. Bone is nearly twice as strong as calcium carbonate, which forms the exoskeleton of most invertebrates; it may have been laid down originally as a means of storing phosphates which are vital to many body functions and are in fluctuating supply in nature.

Heterostracans:

Among the most common of the primitive jawless fish were the heterostracans or pteraspidomorphs (Fig. 9–5). Like *Arandaspis*, the anterior portion of the body was covered by a rigid carapace, but the bony plates in most species have growth lines along the margins. Paired openings for the eyes and notches at the front of the head shield show that these animals had sense organs comparable to those of modern vertebrates. The inside surface of the dorsal shield shows impressions of vertical semicircular canals for establishing the direction of move-

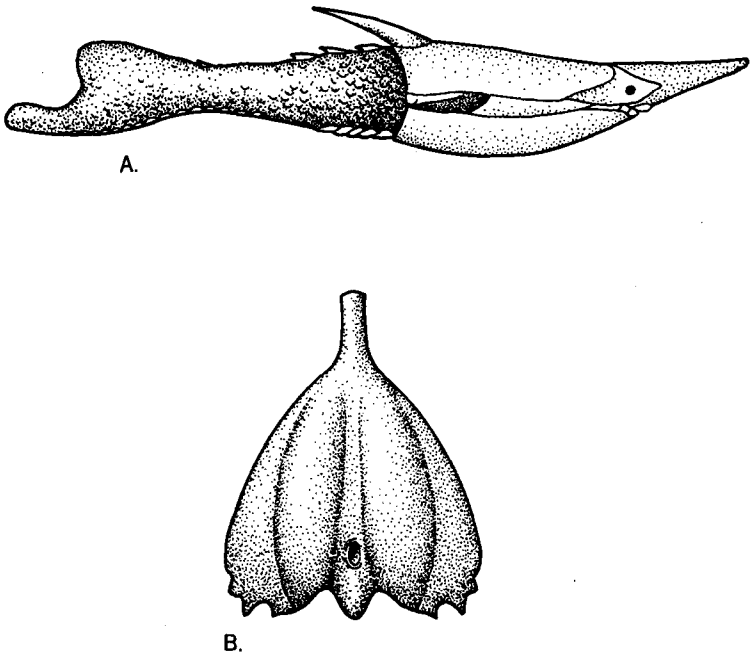


Figure 9-5 Pteraspidomorphs. A. Body of the pteraspid *Pteraspis*. B. Head shield of the amphaspid *Eglonaspis* (note absence of eyes) (J. A. Moy-Thomas & R. S. Miles, *Palaeozoic Fishes*. Courtesy Chapman & Hall, London.).

ments. The semicircular canals, which occupy the inner ear in modern vertebrates, are filled with fluid whose movements displace hairlike structures that send impulses to the brain. Similar structures occur in the lateral line canals of fish which extend along the flanks of the body to the base of the tail and form distinctive patterns along the head and jaws.

Another sensory system that is present in many early fish had the capacity to respond to electrical fields. Flask-shaped structures, revealed by microscopic study of the bones of the head and scales of Paleozoic fish, resemble those of modern species that are used to locate prey and avoid obstacles. These are especially useful in dark or turbid waters. Modern sharks use electrical detectors to locate the electrical impulses emitted during muscle contractions by prey buried in sediments.

The most common heterostracians, the pteraspids, evolved long lateral processes from the carapace that may have helped provide stability in the absence of paired fins. Most of these fish were dorsoventrally flattened, which suggests that they lived on the bottom. Another group, the amphiaspids, are believed to have spent their lives buried in sediments, since the eye openings were covered with bone.

Heterostracan fish have been used by David Dineley (6) to establish correlation between Silurian and Devonian beds in North America and Europe.

The apparently paired nature of the nasal capsules and the absence of internal bone are primitive features of the heterostracians, but they are advanced, relative to other early vertebrates, in having a single external opening for the numerous gill pouches.

Cephalaspidomorphs:

A second major group of primitive armored fish is the Cephalaspidomorpha. This group is also called the Monorhini because the nasal opening is single rather than paired. It opens on top of the head and is connected to the pituitary gland by a common duct. No satisfactory explanation for the evolution of this condition has been proposed, but the presence of a similar pattern in the modern jawless vertebrates, the lamprey and hagfish, suggests that they are closely related to the Cephalaspidomorpha.

Three groups of early armored fish have the monorhine condition: the anaspids, which had a fusiform body for open water swimming, and two groups of flattened bottom dwellers, the osteostracans and the galeaspids (Fig. 9–6). The osteostracans, of which the best known species are referred to as cephalaspids, are the most completely preserved of all the early jawless vertebrates because they had a heavily ossified internal skeleton in the head region. Specimens that have been naturally

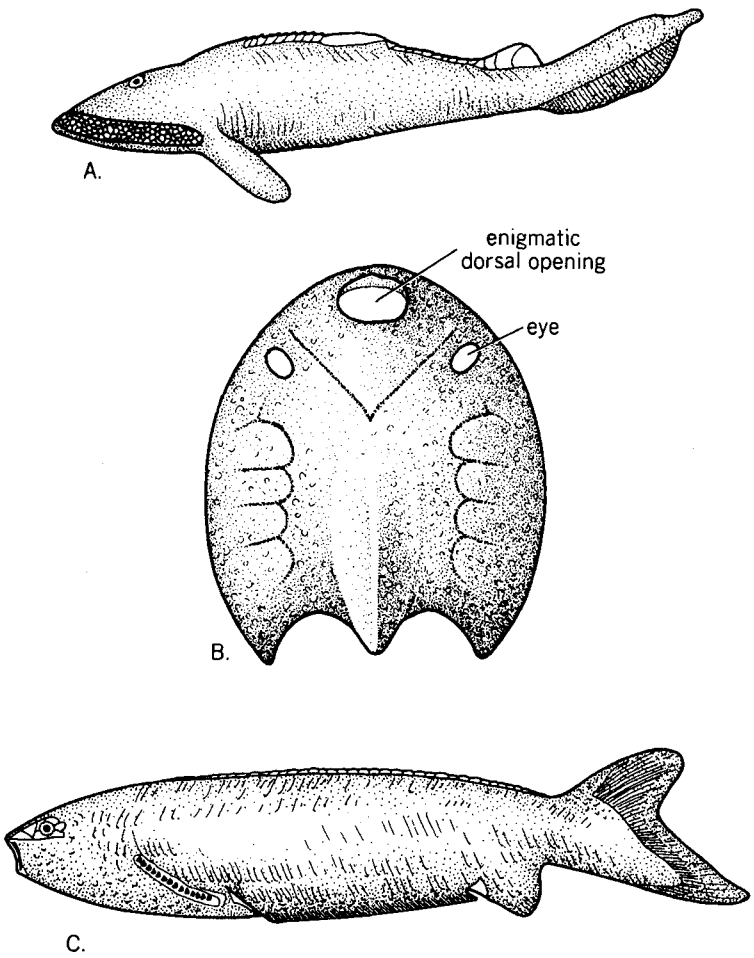


Figure 9-6 Cephalaspidomorphs. A. Osteostracan, B. Head shield of galeaspid, C. Anaspid.

weathered or cut in sections show a multitude of internal structures, including the outline of the brain, the position of the cranial nerves, and two pairs of semicircular canals. Unique to this group are ducts leading from the inner ear to areas on the lateral and dorsal surface of the carapace that may have been sensitive to changes in the pressure of the surrounding water and could therefore warn of the approach of predators (Fig. 9–7).

The surface of the pharynx shows that the many gill pouches opened directly to the exterior rather than via a common duct, as in the Pteraspidomorpha. Some cephalaspids were specialized in the presence of paired anterior (pectoral) limbs just behind the lateral processes of the head shield (Fig. 9–8). No internal skeleton of these appendages has been described and it is uncertain how similar they were to those of more advanced fish. None of the jawless fish had pelvic fins.

The galeaspids resemble the osteostracans in that they have an internal head skeleton and a flattened body, but differ in that they lack cranial sensory fields and have a large opening of unknown function on the upper surface of the skull in front of the eyes. The galeaspids were first recognized as a separate group only a few years ago, but they have since been found to be an extraordinarily diverse assemblage. Galeaspids are restricted to China but range from the Lower Silurian to the Lower Devonian.

The anaspids resemble the galeaspids and osteostracans in the medial position of the nasal opening, but in few other features. Their body was fusiform, suggesting open-water swimming, but the tail, unlike most advanced fish, was bent ventrally. Most anaspids were covered with narrow scales that are presumed to have followed the pattern of underlying muscle segments. Some anaspids, in contrast, have reduced or entirely eliminated the scales. In this they resemble the living jawless fish, the hagfish and lamprey (Fig. 9–9). Primitive members of both of these groups are known from the

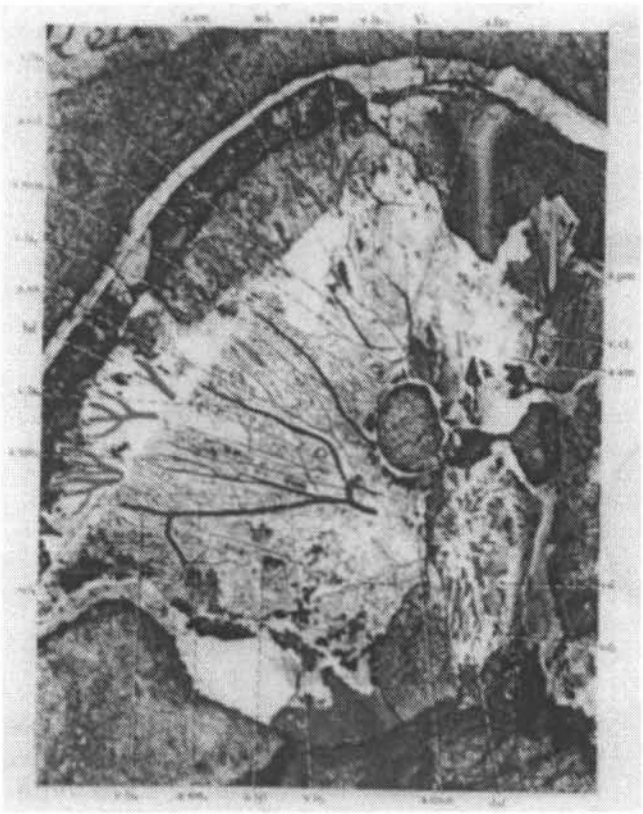


Figure 9-7 Weathered skull of cephalaspid, showing internal anatomical details; lines point to particular nerves and blood vessels. (E. Stensiø, *The Cephalaspids of Great Britain*. By courtesy of the British Museum (Natural History).)

Middle Pennsylvanian of Mazon Creek, Illinois. The living jawless fish differ from their Paleozoic counterparts in that they lack bones and scales; for this reason their fossil record is primarily restricted to this one locality, which also includes a wealth of soft-bodied invertebrates unknown elsewhere (7).

The well-known pteraspidomorphs and cephalaspidomorphs are unlike most modern fish in that they have external armor and peculiar finlike structures. The most enigmatic but possibly most important group of early jawless fish are the coelolepids or thelodonts. Their entire body was covered

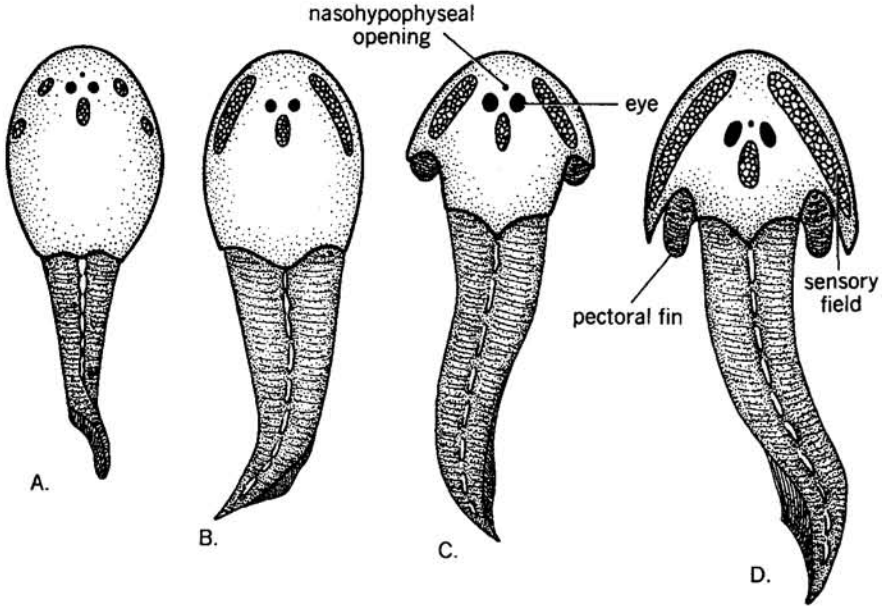


Figure 9-8 Progressive evolution of paired fins in osteostracans.

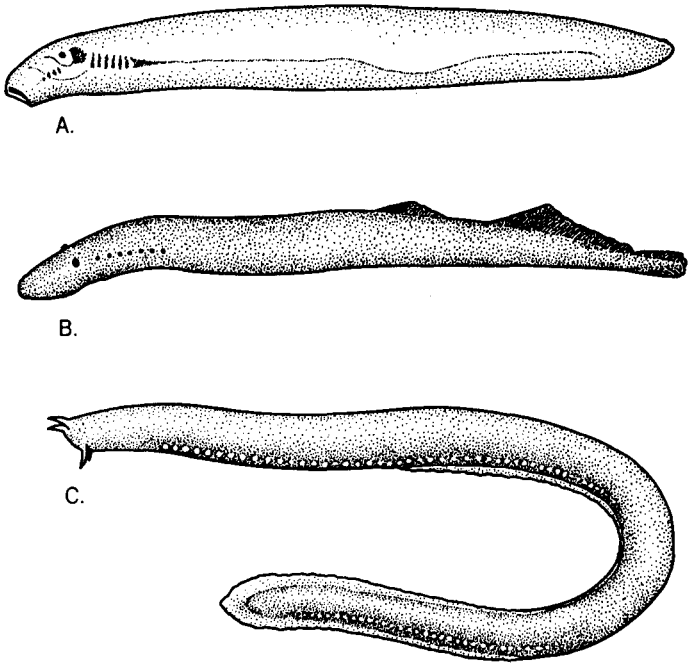


Figure 9-9 Fossil and living agnathans. A. *Mayomazon*, from the Upper Carboniferous, B. Living lamprey *Petromyzon*, C. Living hagfish. (Modified from D. Bardack & R. Zangerl, *First Fossil lamprey: A record from the Pennsylvanian of Illinois.*)

with small scales, but they had no internal skeleton; the fossils are typically so flattened and distorted that few structural details are evident. The body was apparently fusiform, with a slender lateral fold or pectoral fin above a series of gill slits (Fig. 9–10). The thelodonts had a body form that would be appropriate for the ancestry of both jawless and jawed vertebrates. They are known from Lower Silurian to Upper Devonian rocks.

The jawless vertebrates were already diverse when they appeared in the fossil record in the Ordovician. They continued to radiate throughout the Early Devonian, but by the end of that period they had become extinct, except for the lineages that led to the surviving lamprey and hagfish.

JAWED FISH

Although the lamprey and hagfish have a wide distribution today, jawless vertebrates were effectively replaced by jawed vertebrates within the Early Devonian. None of the well-known groups of jawless vertebrates are likely ancestors of the jawed forms. Bobb Schaeffer and Keith Thomson (8) have emphasized that the two groups differ fundamentally in the structure and relation of the gill supports and the filamentous gills. In the modern lamprey and hagfish, the gill supports are lateral to the gill filaments and form a flexible basketlike structure that is compressed by surrounding muscles and expanded by elastic recoil. Jawed vertebrates, in contrast, have the gill supports medial to the gill filaments, and the gill supports are in the form of a series of hingelike elements (Fig. 9–11) whose associated muscles can both contract and expand the pharynx. The different relative position of gill supports and filaments in the two groups suggests that they evolved separately from a common ancestor, like amphioxus, in which the gill slits were not accompanied by filamentous gills.

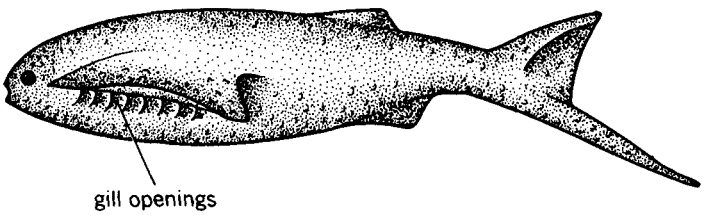


Figure 9-10 Thelodont, a primitive vertebrate with paired fins and multiple gill openings. (Courtesy of L. B. Halstead, S. Turner and Elsevier Science Publishers.)

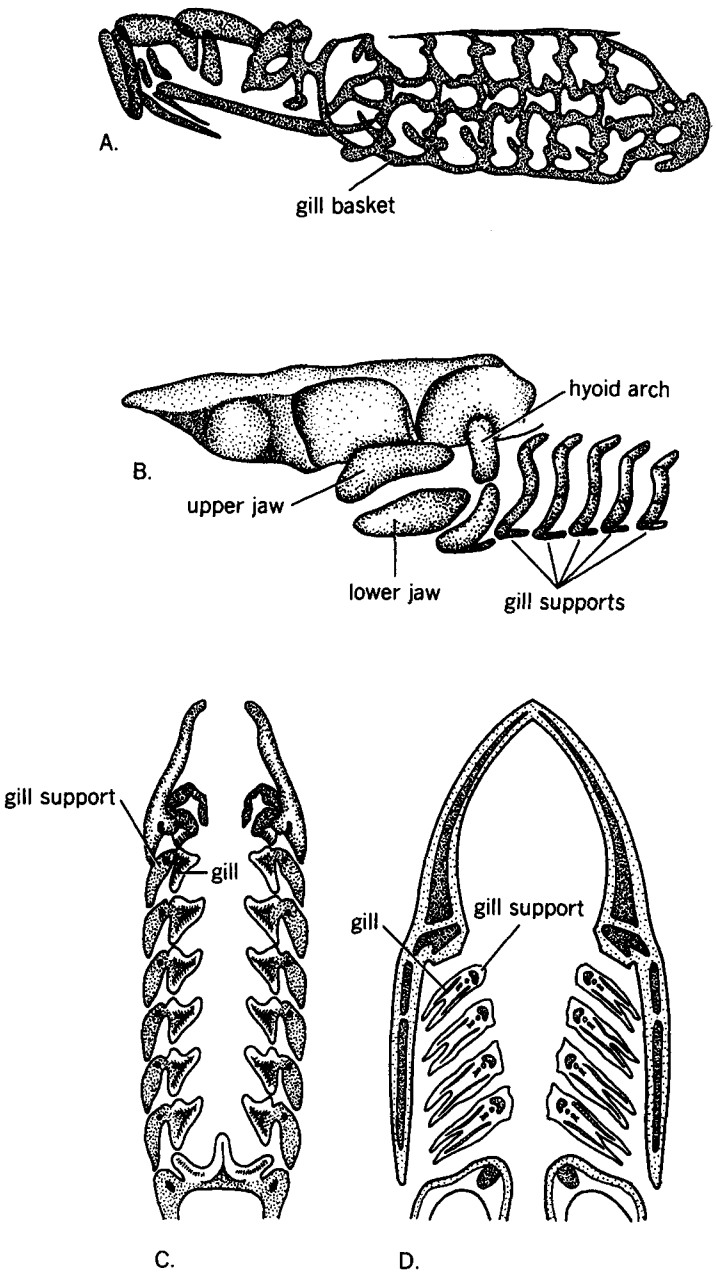


Figure 9-11 Nature of gill supports and relative position of gills in jawless and jawed fish. A. Superficial gill basket in the modern jawless lamprey, B. Medially placed hinged gill supports and jaws of a shark, C. Horizontal section through the head of an agnathan to show position of gills, D. Horizontal section through the head of a gnathosome, showing the position of the gills. (J. A. Moy-Thomas & R. S. Miles, *Palaeozoic Fishes*. Courtesy Chapman & Hall, London [C,D].

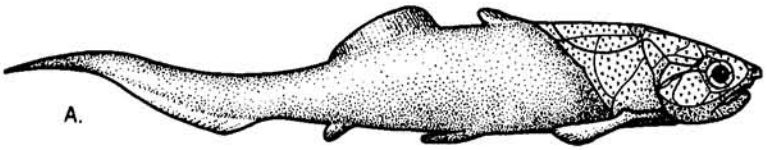
The general form of the gill supports in jawed vertebrates resembles the jaws. This is particularly clear in sharks because the primary gill supports and jaws are not covered by superficial bone as they are in bony fish. Primitive vertebrates were thought to have had a series of similar gill supports in the mouth region, whose anterior elements became specialized as jaws. Study of modern jawless fish and Paleozoic fossils shows that the position of the Vth nerve, which innervates the mouth region, is comparable in all vertebrates. Its position suggests that the mouth had a similar position in both jawless and jawed vertebrates and that there never were gill pouches in the mouth area, as would be implied by the theory that the jaws had evolved from gill supports. Malcolm Jollie (9) suggested that the jaws and gill supports evolved as broadly similar structures since they had comparable functional relationships with the muscles that expanded and contracted both the mouth and the pharynx.

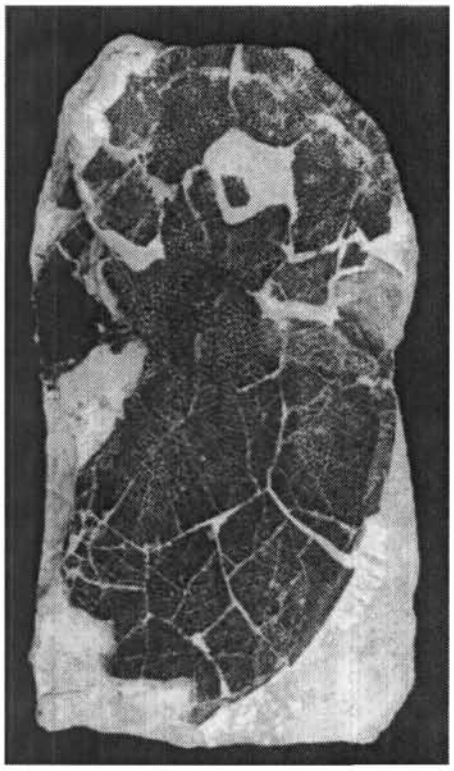
The early jawed fish also possessed both pectoral and pelvic fins and an expanded anterior portion of the brain. This suggests that feeding, locomotion, and enhanced neural control were all important aspects in the origin of jawed vertebrates.

Placoderms:

The oldest remains of jawed vertebrates have been collected from Lower Silurian rocks, and several major groups are known from the Upper Silurian and Lower Devonian. The first group of jawed fish to radiate extensively were the placoderms (Fig. 9–12). Unique to this group was the placement of the jaw closing muscles, which were medial rather than lateral to the primary bone of the upper jaw.

Most placoderms were bottom-dwelling fish like the ostracoderms, and the primitive genera were similarly covered with a nearly continuous carapace of bone, with only the tail free. Placoderms are





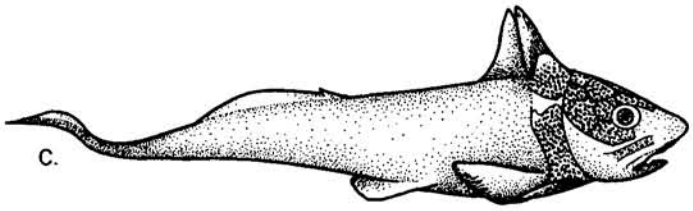


Figure 9-12 Placoderms. A. Reconstruction of *Coccosteus*, a Middle Devonian arthrodire, B. Fossil of the Upper Devonian antiarch *Bothriolepis*, from eastern Canada, dorsal view of head shield and thorax, C. A ptyctodont. (Courtesy of J. Piveteau, *Traité de Paléontologie*, IV, 2 (c) MASSON 1969 [A,C] and Courtesy of Redpath Museum, McGill University [B].)

clearly distinguished from ostracoderms by a joint separating the head from the thorax, which allowed the top of the head to be lifted in opening the mouth. This is presumably an adaptation for bottom-dwelling fish that could not conveniently open the lower jaws.

The largest group of placoderms were the arthrodires. Within this group, numerous lineages show adaption to the role of active, open water predators. The thickness of their armour was reduced, the internal skeleton was replaced with cartilage, and the back of the bony carapace was shortened so that more of the trunk could serve as a flexible swimming organ. Some genera lost the joint between the skull and thorax, and the lower jaw increased in length to provide a wider gape. The largest arthrodires exceeded 3 meters in length and must have been formidable predators.

Other placoderms, such as the antiarchs, accentuated a bottom dwelling way of life. Antiarchs are unique in being very common in fresh water and were the only placoderms to survive into the Carboniferous.

The ptycnodonts (Fig. 9–12C) show the closest resemblance to more advanced jawed fish and have been hypothesized to be closely related to the chimaeroids (Fig. 9–15), which are typically allied with the sharks. Most paleontologists feel that these resemblances are due to convergence, rather than close relationship. Another group of placoderms, the rhenanids, superfically resemble the skates and rays of the Mesozoic and Cenozoic.

The placoderms are almost completely limited to the Devonian Period. The many distinct lineages that are recognized early in that period suggest significant prior evolution. They remained diverse and numerous until near the end of the Devonian before rapidly becoming extinct. The apparent rapidity of their demise may be exaggerated by a change in the pattern of deposition at the end of the Devonian in North America and Europe. Widespread black shales, in which their remains are common in the Late Devonian, are rare in Carboniferous deposits. Only a few antiarchs survive in the Carboniferous. Placoderms are the only extinct class of vertebrates.

The demise of the placoderms may be attributed to the radiation of other, more advanced, jawed fish. All modern jawed fish belong to two large groups, the Chondrichthyes, or cartilagenous fish, including sharks, skates, rays, and chimeroids (or ratfish) and the Osteichthyes, or bony fish, including most of the common modern species such as the trout and salmon, swordfish, flatfish, and sea horses, as well as a host of other living and fossil species. The sharks are important among large predators, but the bony fish are far more diverse.

CARTILAGENOUS FISH (CHONDRICHTHYES)

Fish broadly resembling modern sharks were common and diverse in the Late Devonian and Carboniferous. Scattered remains are known from the Lower Devonian, and isolated scales have been reported from the Upper Silurian. There is no evidence that the ancestors of sharks had a solid bony carapace like the ostracoderms and placoderms. Rather, they were characterized by distinctive scales that resemble teeth in that they have a pulp cavity surrounded by dentine and enamel-like material. The internal skeleton is composed of cartilage, which is much lighter than bone but not nearly as strong. Cartilage itself has little chance of being preserved, but in many genera the surface of the cartilage is calcified by a coating of distinctive prismatic granules.

The fossil record of sharks includes isolated teeth, spines, scales, and elements of the skeleton that are calcified. Rainer Zangerl (10) has described the extensive radiation of sharks in the late Paleozoic. Some ten orders are recognized by distinct patterns of the fin spines, dentition, and body form (Fig. 9–13). The xenacanths lived in fresh water, but most sharks, both Paleozoic and modern, are confined to the sea.

Class—Chondrichthyes
- Subclass—Elasmobranchii
  - Many Paleozoic orders
  - Superorder—Euselachii
    - Order—Ctenacanthiformes (ctenacanths and hybodonts)
    - Order—Xenacanthida
    - Order—Galeomorpha (modern sharks)
    - Order—Squalomorpha (modern sharks)
    - Order—Batoidea (skates and rays)
- Subclass—Holocephali (modern chimaeroids and many Paleozoic groups)
- Subclass—incertae sedis
  - Order—Iniopterygiformes

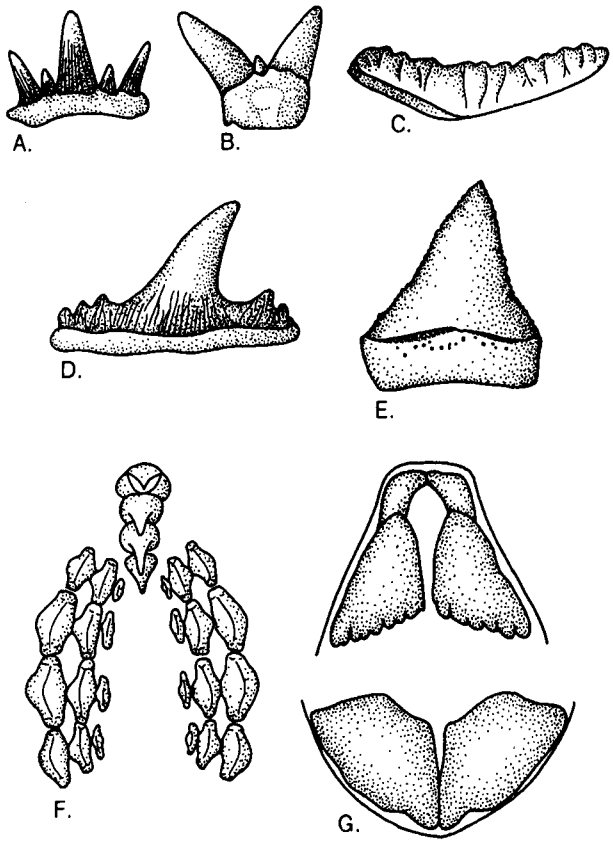


Figure 9-13 Teeth of cartilagenous fish. A. Cladodus tooth, characteristic of *Cladoselache* and other mid-Paleozoic sharks, B. Diplodus tooth, diagnostic of fresh water xenacanth sharks, C. Flat crushing tooth of *Orodus*, D. Hybodont tooth, common to primitive Mesozoic sharks, E. Tooth of modern predaceous galeoid shark *Carcharodon*, F. Tooth plates of Paleozoic petalodont, G. Tooth plates of chimeroid, seen as if looking into an open mouth.

Many groups of Paleozoic chondrichthyians resembled the modern sharks in their general body form, but others were flattened for life on the bottom, like skates and rays. One group, the iniopterygians, had rather short bodies and large skulls. Their dentition is close to the primitive shark pattern, but their limbs were very different (Fig. 9–14).

Most of the shark groups of the Late Devonian and Carboniferous were extinct by the end of the Triassic. One order, the hybodonts, remained dominant into the Mesozoic, and the closely related ctenacanths are close to the ancestry of modern sharks (the neoselachians). The neoselachians are more advanced than early Paleozoic sharks in the development of a tripartiate base of the pectoral fin which gave it greater strength and maneuverability, in the evolution of a solid attachment of the left and right halves of the pectoral and pelvic girdles, and in the calcification of the vertebrae. Most importantly, the upper jaws became less solidly attached to the braincase so that they were much more maneuverable. This is very effective in predaceous sharks, where the jaws can be used like saws to cut pieces from their prey.

The neoselachians radiated rapidly in the Late Triassic and Early Jurassic, giving rise to all the modern shark groups, as well as to skates and rays. Leonard Campagno (11) has shown that most of the modern families had become established by the Early Cretaceous, and many modern genera appeared by the early Cenozoic.

The chimaeroids or holocephalians are rare fish in the modern fauna, with large heads, short bodies, and whiplike tails for which they are called ratfish (Fig. 9–15). Chimaeroids are thought to be closely related to sharks because both groups have similar types of calcified cartilage and practice internal fertilization. Chimaeras differ markedly from sharks in having the upper jaw fused solidly to the braincase, in having only a few pairs of large tooth plates rather than rows of rapidly replaced marginal teeth, and in having an operculum covering the gill openings, rather than a series of gill slits opening separately to the outside. The fossil record of modern chimaerid genera goes back to the Jurassic, and

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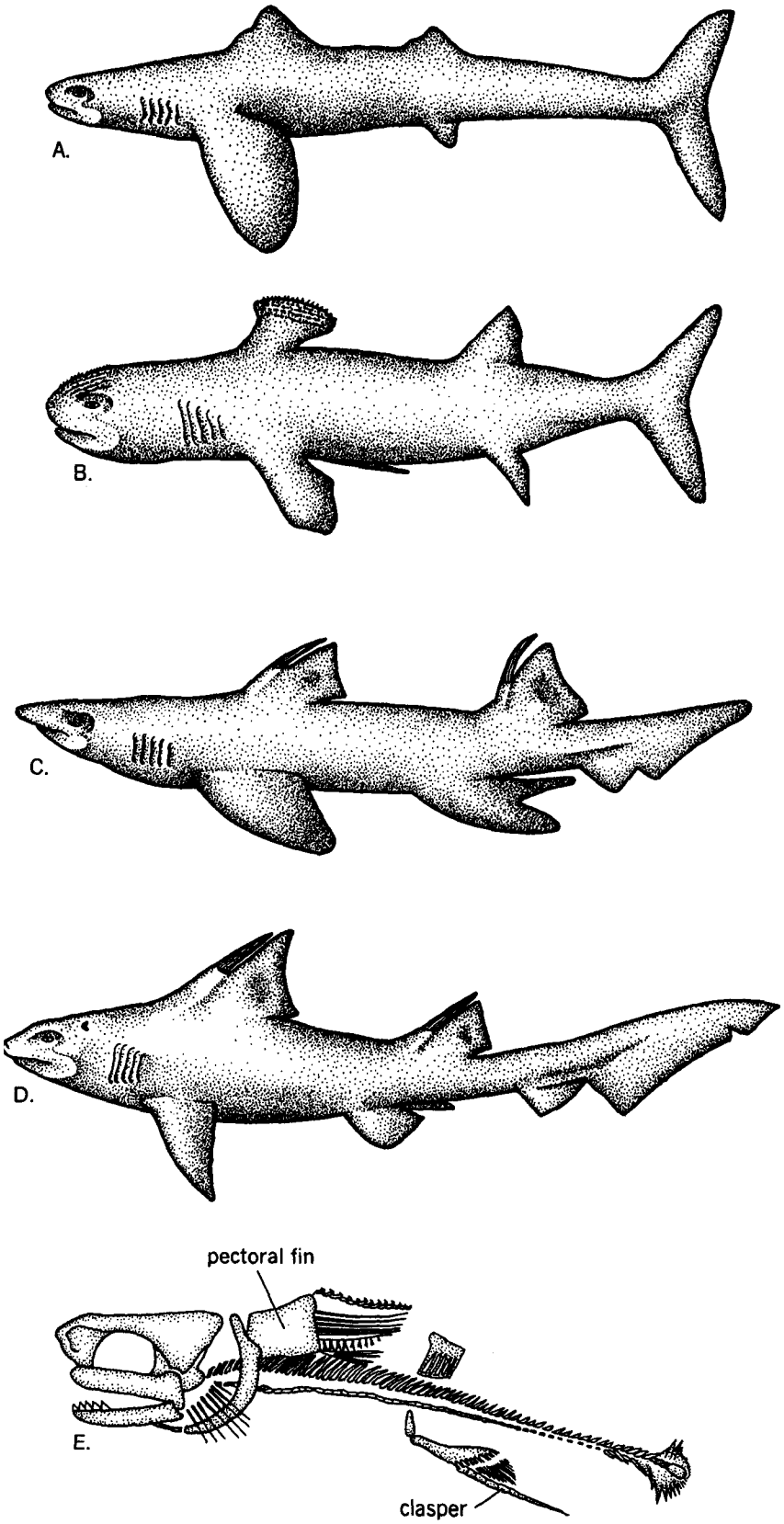


Figure 9-14 Body form in a variety of sharks. A. *Cladoselache*, the only Devonian shark in which the body is well known, B. *Stenacanthus*, from the Carboniferous, in which the anterior dorsal fin is covered with large denticles, C. A Lower Carboniferous hybodont shark, D. The common Mesozoic shark *Hybodus*, E. A Carboniferous inioptery-gian. Note the bizarre pectoral fin. (E, Courtesy of Dr. R. Zangerl & H. P. Schultze (ed) *Handbook of Paleoichthyology*, vol. 3, Gustav Fischer Verlag.)

Chapter 10

The Second Wave:

INVERTEBRATES OF THE MESOZOIC AND CENOZOIC ERAS

INTRODUCTION

At the close of the Paleozoic Era the seas were withdrawn from the continental platforms into the ocean basins, the continents were gathered into a supercontinental mass called Pangaea, the continental shelves where marine invertebrates thrived were highly restricted, and the coastlines of the world were shorter than they had been since late in the Proterozoic, shorter than they would ever be again. Much of the land was arid and where sections of the sea were partially isolated from the oceans many of the world's evaporite deposits were laid down. Marine deposits of Late Permian and Early Triassic age are therefore relatively thin and cover small areas. The effect of these inhospitable conditions on marine life was reviewed at the end of Chapter 7. The marine invertebrate fauna was restricted as never before or since. Similar changes did not occur in land faunas or floras.

Recovery was not immediate. New invertebrate groups began to appear in Middle and Late Triassic time but rapid diversification did not take place until Jurassic time.

FORAMINIFERIDA

The foraminiferans that live on the sediment surface and within it are called benthonic; those that float in the water column are planktonic.

Benthonic Foraminiferida:

The Permian crisis completely wiped out the fusulines and almost eliminated the endothyrids but several families of agglutinated forms (Textulariina) were little affected by its rigors. Recovery from the late Paleozoic crisis was slow, and Triassic foraminiferan faunas are neither diverse nor abundant. The benthonic forams rapidly diversified in Jurassic time both in shallow and deep-water environments; members of the suborders Miliolina and Rotaliina led the way. By mid-Jurassic time the benthonic foraminiferans were again making important contributions to the formation of shallow-water limestones. The Miliolina appear to have arisen from such agglutinated foraminiferans as *Ammodiscus* (Fig. 10–1C) in Carboniferous time, and the Rotaliina, from the endothyrids in the Triassic

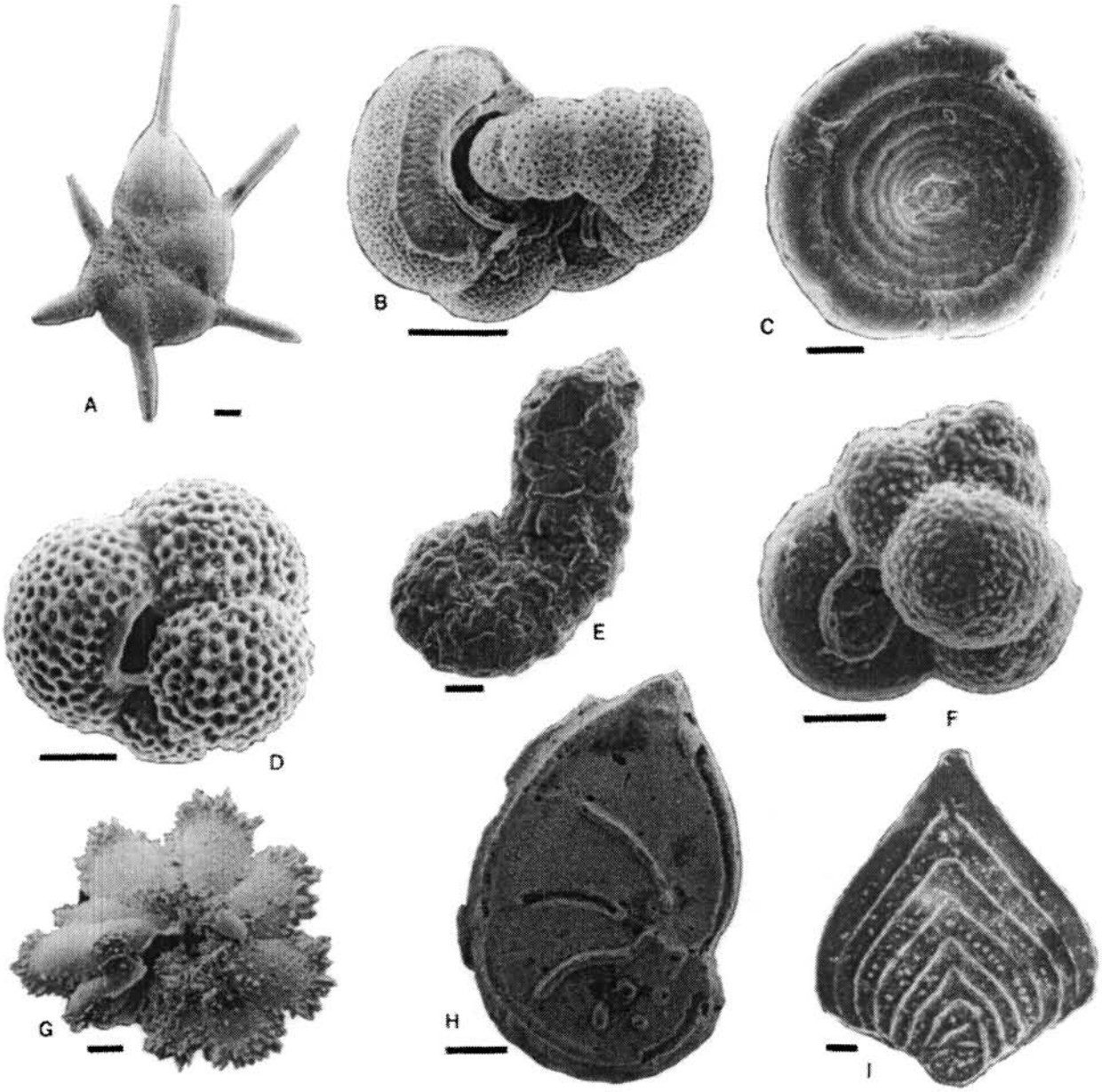
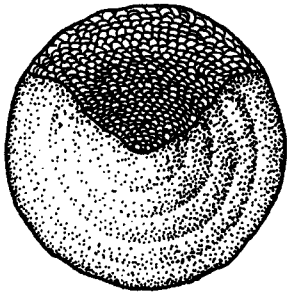


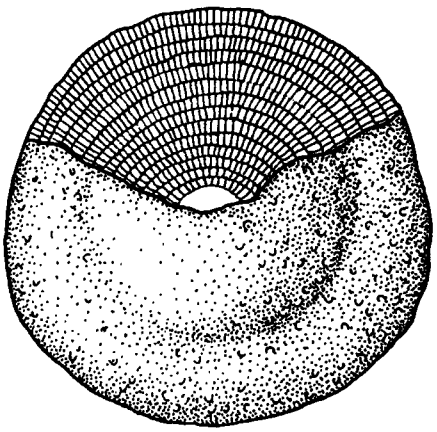
Figure 10-1 Scanning electron micrographs of fossil foraminiferans. The scale bars are 0.1 mm. A. *Hantkenina* (planktonic, Rotaliina), Middle Eocene, Blake Plateau. B. *Ticinella* (planktonic, Rotaliina), Lower Cretaceous, Blake Plateau, C. *Ammodiscus* (agglutinated, Textulariina), Eocene, North Sea. D. *Globigerina* (planktonic, Rotaliina), Miocene, Labrador shelf. E. *Ammobaculites* (coarsely agglutinated, Textulariina), Eocene, Labrador shelf. F. "*Globigerina*" (oldest planktonic foram, Rotaliina), Middle Jurassic, Atlantic shelf. G. *Morosovella* (planktonic, Rotaliina), Middle Eocene, Blake plateau. H. *Lenticulina* (benthonic, Rotaliina), Lower Cretaceous, Blake plateau. I. *Neoflabellina* (benthonic, *Rotaliina*), Upper Cretaceous, Atlantic shelf. (Courtesy of Felix Gradstein and the Geological Survey of Canada.)

Period. The Rotaliina achieved their dominant position in modern foraminiferan faunas by rapid diversification in the middle of Cretaceous time. In some brackish and deep-water environments, the agglutinated Textulariina became dominant (Fig. 10–1).

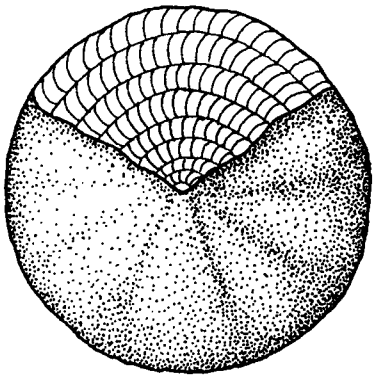
In late Mesozoic time several groups evolved into giants comparable in size to the fusulines. They are



A. *Orbitolites*



B. *Discocyclina*



C. *Nummulites*

Figure 10-2 Larger benthonic foraminiferans cut away in one sector to show the internal structure. All can be as large as several centimeters across. A. *Orbitolites*. B. *Discocyclina* (an orbitoid). C. *Nummulites*.

giants only relative to their miniscule contempories, but many reached the size of a small coin. In Jurassic time giants developed in the agglutinated foraminiferans, and in Cretaceous time in the Miliolina and the Rotaliina. The milioline giants include disk-shaped genera, like the common early Cenozoic genus *Orbitolites* (Fig. 10–2A). One family of the miliolines, the Alveolinidae, which were particularly abundant in Late Cretaceous and Eocene time, evolved forms that are remarkably similar to the late Paleozoic fusulines. The giant rotaliines include the nummulites and orbitoids. The most common genus of the first is *Nummulites* (Fig. 10–2C). These coin-shaped fossils are so common in the Eocene limestones of the Mediterranean region that in Europe this interval has been called the Nummulitic Epoch. Because the limestones were used to build the pyramids of Egypt, these fossils came to the attention of the ancient Greeks and Romans. Heroditus, (about 500 B.C.) described them as the petrified remains of lentiles that the pyramid builders had for lunch. The test of the nummulites is basically a planispiral coil like that of an ammonoid in which the last chambers cover the inner ones. However, the test is complicated by the subdivision of the chambers by internal partitions. The test of orbitoids is thinner and the chambers are added initially in a spiral pattern and in later stages in rings around the periphery of the disk (Fig. 10–2B). Many of the larger foraminiferans, and also the planktonic ones, have developed a symbiotic relationship with unicellular algae that supply them with oxygen through photosynthesis. The relationship is similar to that of molluscs and corals (see following discussion).

Some of the large rotaliines attached themselves to hard surfaces and became encrusting in habit. Two genera are presently common in tropical seas: the red *Homotrema* whose color adds a pink cast to Bermuda beaches, and the brown *Gypsina* which is an important binding agent in Caribbean reefs.

Planktonic Foraminiferans:

In Middle Jurassic time one group of the order Rotalliina adapted to a planktonic existence, floating near the surface of the ocean. These forams have a simple test composed of chambers coiled in a trochoid spiral like that of a gastropod. Many are equipped with spines that may be several times the diameter of the test in length (Fig. 10–3B). The two families, Globigerinidae and Globorotaliidae

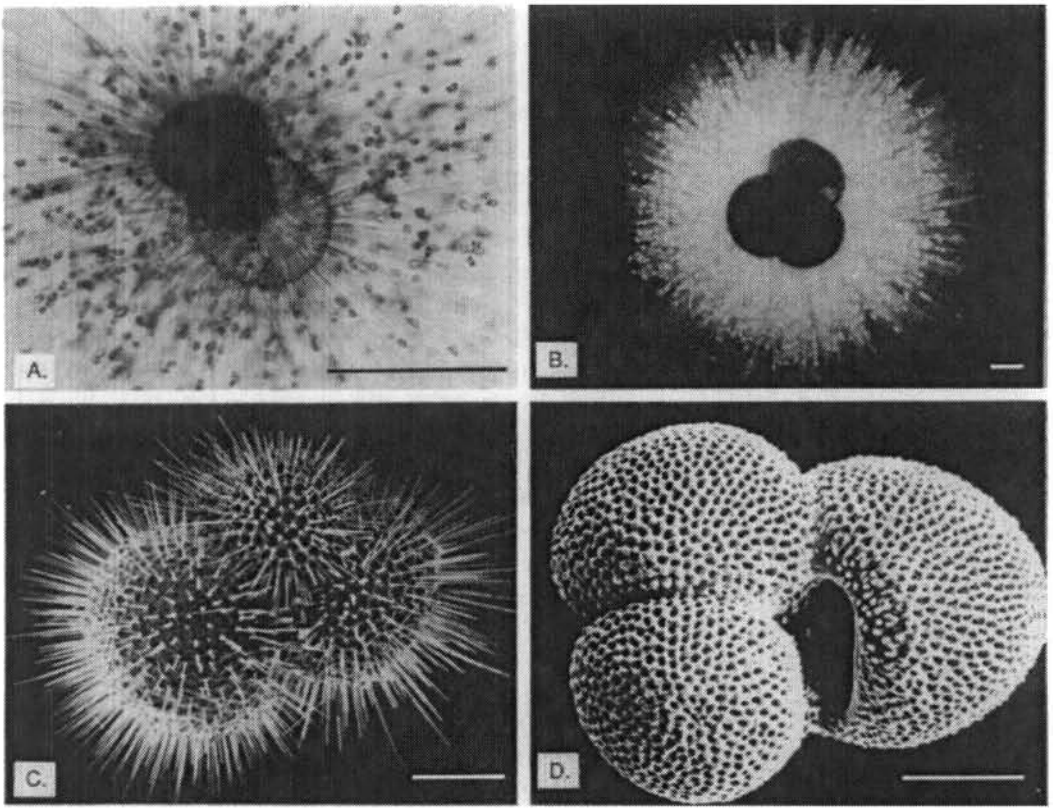


Figure 10-3 Recent planktonic foraminiferans. The scale bars are 0.1 mm. A. Juvenile spinose form showing the symbiotic algae in the pseudopods extended widely from the test. B. *Globigerinoides ruber*, a living specimen. C. Dead test of *Globigerinoides sacculifera* with spines. D. Test of *G. sacculifera* at stage of gametogenesis when the test is thickened. (Courtesy of Roger Anderson, Lamont-Doherty Geological Laboratory and *Micropaleontology*, v. 23(2), pp. 155–179.)

became very abundant in mid-Cretaceous time and were important contributors to the formation of the typical Late Cretaceous carbonate sediment, chalk. Although 87 percent of the genera of planktonic forams became extinct in the Late Cretaceous crisis, the rest made a rapid recovery in Early Cenozoic time and continue to thrive and contribute their tests to the layers of *Globigerina* ooze that now cover 127 million square km of the deep ocean floor. However, both benthonic and planktonic foraminifera were apparently more diverse and abundant at the end of the Mesozoic than they are today. The ranges in time of the species of planktonic foraminifera and their evolution have been studied in great detail because they provide a method of accurately dating the sedimentary layers that are penetrated by drilling in the floor of the oceans.

OTHER PLANKTONIC MICROORGANISMS

Only a few plants and animals that have left a paleontological record lived a planktonic existence in the surface waters of the sea in the Paleozoic Era, but this habitat became much more densely populated in Mesozoic and Cenozoic time. Marine plankton is at the base of the food pyramid. Planktonic plants are the major primary producers of the sea, as they convert inorganic nutrients to food usable by animals. The increasing availability of such microscopic food in Mesozoic time must have influenced the diversity and abundance of marine life. The planktonic foraminiferans and other animals that share this habitat comprise the zooplankton; plants, such as the coccoliths, diatoms, and

dinoflagellates, described in the following discussion, constitute the phytoplankton.

Coccoliths:

If Cretaceous chalk is examined under the high powers of the scanning electron microscope, the grains are revealed to be composed of subangular calcite particles which are locally united into circlets of overlapping platelets (Fig. 10–4A). The circlets, called coccoliths, are secreted by single cells of yellow-green algae (Chrysophyta) which live today for part of their life cycle in great abundance in the surface waters of the sea and are known from rocks as old as Triassic. During life, these coccoliths, a few micrometers across, are arranged around the algal cell to form a coccosphere (Fig. 10–4B). They fall off the sphere when the cell dies, and tend to disintegrate to their constituent platelets which are the grains of chalk. The great chalk cliffs of the English channel are evidence of the abundance of these plants in Cretaceous seas.

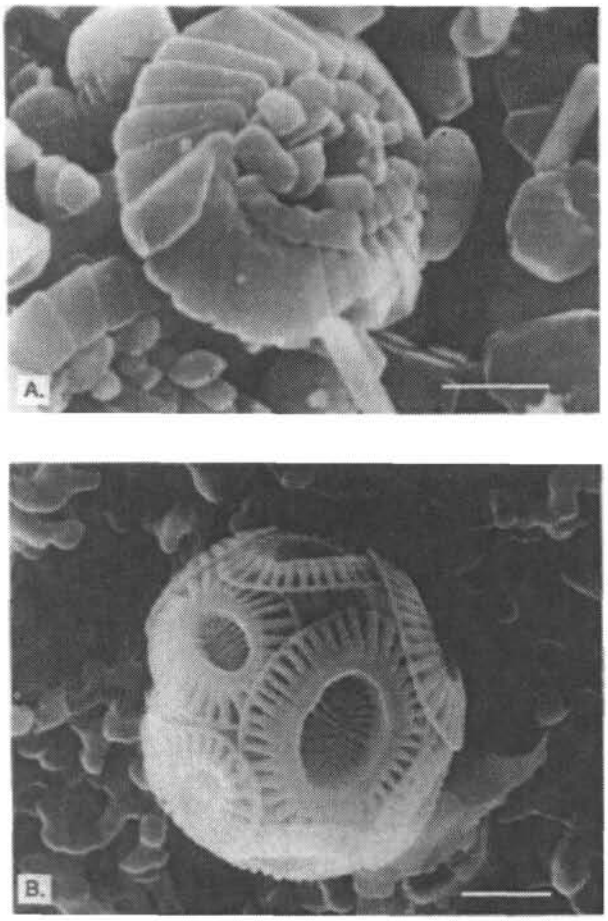


Figure 10-4 Coccoliths and coccosphere. The scale bars are 1 micrometer. A. Coccoliths in Cretaceous chalk. (Courtesy of C. W. Stearn & A. J. Mah.) B. Coccosphere of the living species *Emiliana huxleyi*. (Courtesy of Margaret Goreau.)

Diatoms:

Other members of the chrysophyte algae that appeared in Early Triassic time and became abundant in the plankton of Cretaceous time are the diatoms. These algae secrete a minute skeleton (commonly 10 to 100 micrometers across) whose preservable part is composed of opal—hydrous and noncrystalline silica. The tests are commonly discoidal or oblong in shape, ornamented with knobs and ridges, and consist of two valves that fit into each other like the lid and base of a pill box (Fig. 10–5). Diatoms have, since the Cretaceous, thrived in fresh (Fig. 10–6) and marine water and left their tests behind in the form of a light and minutely porous rock called diatomite. Deposits in the Miocene rocks of California (Monterey Formation) and the Pleistocene of Germany have been exploited for use as fillers, abrasives, filtering media, and originally as the medium which Alfred Nobel used to absorb nitroglycerine to make dynamite.

Dinoflagellates and Acritarchs:

The dinoflagellates are a group of algae some of which secrete cellulose cysts that can be preserved (Fig. 10–7D,E). As the name implies, they are equipped with flagellae. At times some of these plants multiply rapidly in modern oceans and secrete a toxin that causes mass mortality in fish and makes filter feeding clams that are normally edible, poisonous. As the organisms causing this phenomenon, which have reddish pigments, become abundant enough to color the water, these mass mortalities are referred to as red tides. The cysts can be extracted from sedimentary rocks by dissolving the rock in hydrofluoric acid and can be used for dating rocks in the relative time scale. Dinoflagellate cysts first become common in rocks of Late Triassic age but a single genus, regarded by some as the oldest dinoflagellate, is known from Upper Silurian rocks. Carbonized organic capsules commonly ornamented with fine spines have been found

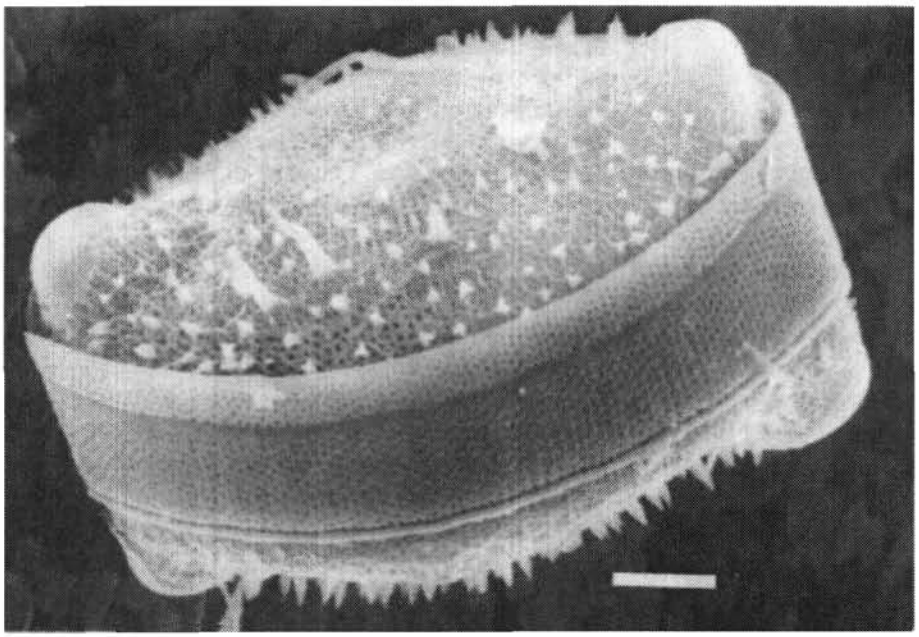


Figure 10-5 The marine diatom *Odontella*. Scanning electron micrograph. The scale bar is 10 micrometers. (C. W. Stearn.)

in insoluble residues of Paleozoic and late Proterozoic rocks (Fig. 10–7F,G). Some paleontologists believe these are related to the dinoflagellates but, since their affinity to a living group is unknown, they are referred to by the nonspecific name, acritarchs. They have also been used in correlation of Paleozoic rocks and have the potential for use as correlators in late Proterozoic rocks.

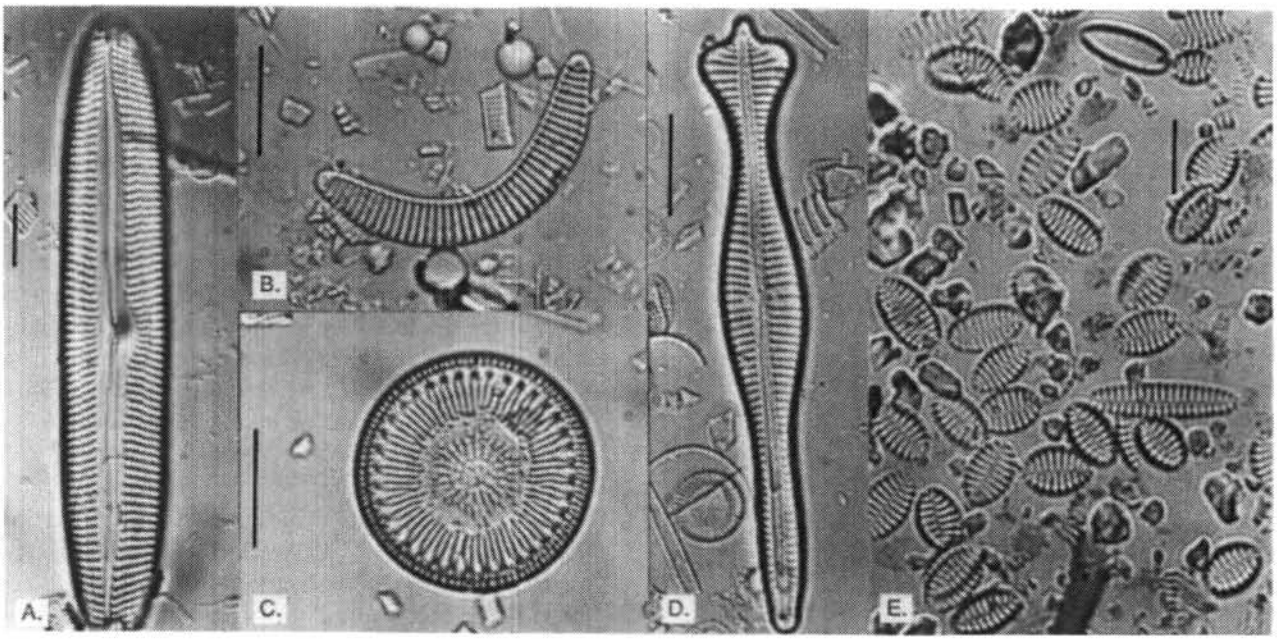


Figure 10-6 Freshwater fossil diatoms from Pleistocene sediments. The scale bars are 10 micrometers. A. *Pinnularia viridis*, B. *Semiorbis hemicyclis*, C. *Cyclotella comta*, D. *Gomphonema acuminatum*, E. *Frigilaria* sp. (Courtesy of John Smol, reproduced with the permission of the Geological Association of Canada, *Geoscience Canada*, v. 14, p. 210.)

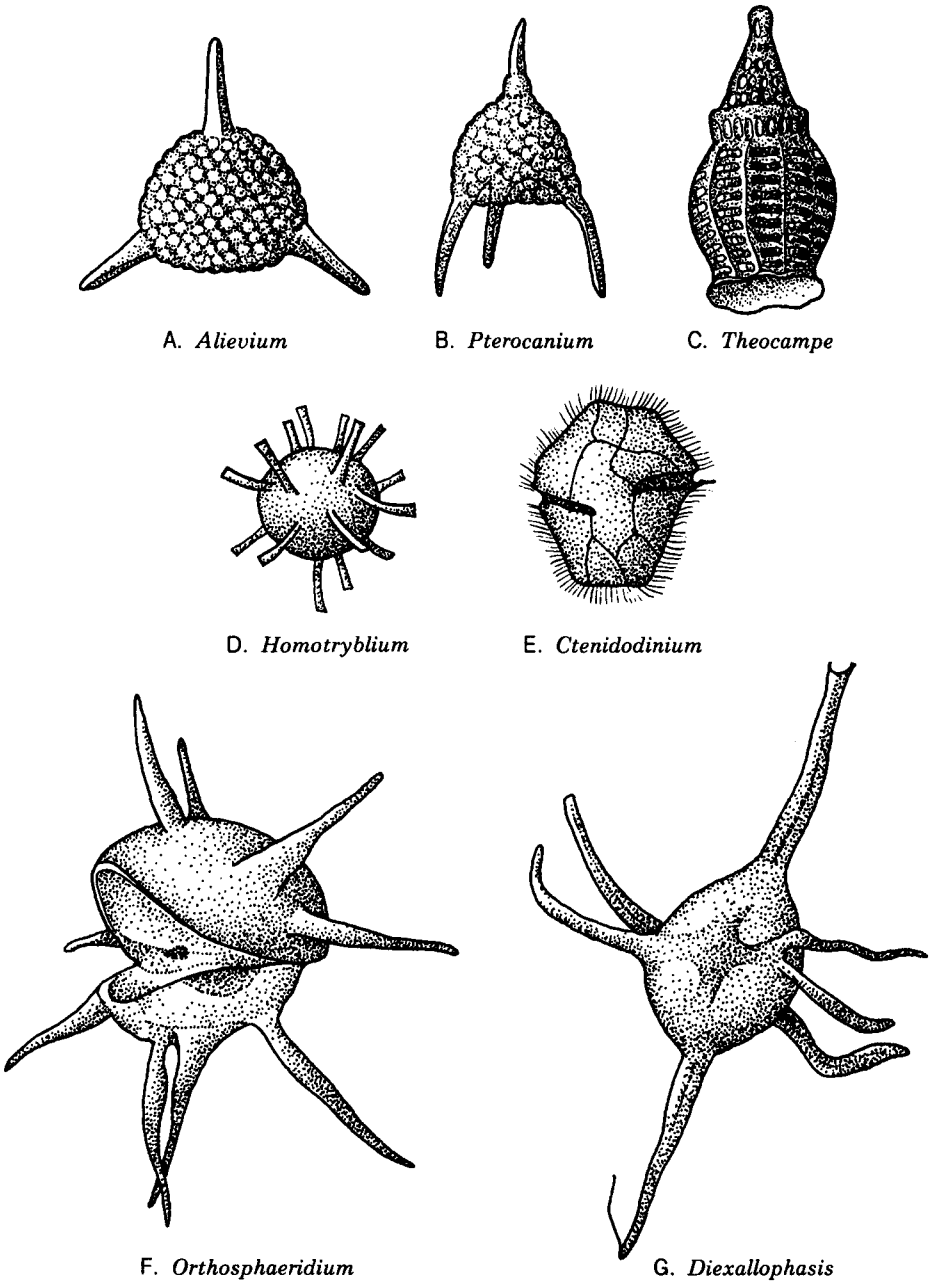


Figure 10-7 Planktonic organisms. A-C. Radiolarians, D, E. Dinoflagellates. F, G. Acritarchs. A. *Alievium* (Cretaceous) (0.2 mm). B. *Pterocanium* (Miocene) (0.2 mm). C. *Theocampe* (Cretaceous) (0.2 mm). D. *Homotryblium* (Cenozoic) (0.05 mm). E. *Ctenidodinium* (Jurassic–Cretaceous) (0.075 mm). F. *Orthosphaeridium* (Ordovician) (0.07 mm). G. *Diexallophasis* (Silurian) (length 0.1 mm).

Radiolaria:

Like the dinoflagellates, the radiolarians secrete a skeleton of opaline silica. Their siliceous tests are spherical with radial spines of great delicacy, or they are helmet-shaped (Fig. 10–7). Although radiolarians are known from Paleozoic rocks (and were locally important contributers to sediments), they did not become abundant until the Mesozoic and are common constituents of modern plankton. Radiolarian oozes are accumulating now on the deep ocean floor in an equatorial belt west of Ecuador.

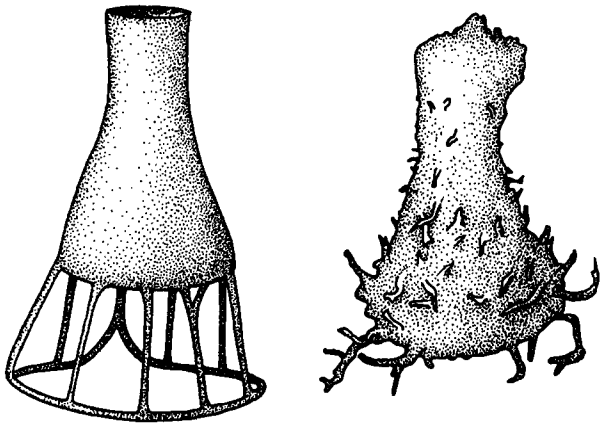
Older deposits to which radiolarians have made significant contributions include the siliceous sediments and cherts of the Arkansas novaculite (Devonian), the cherts of the Cache Creek Group of British Columbia (Permian), the cherts of the Franciscan Formation of California (Jurassic), and the Oceanic Formation of Barbados (middle Cenozoic). Radiolarians are believed to have been contributors to the formation of silceous sediments, such as chert, throughout Phanerozoic time but their skeletons are easily dissolved and reprecipitated after deposition leaving little trace. About one-third of all radiolarians contain algae living in their tissues which supply them with oxygen.

Chitinozoa:

Chitinozoa are minute carbonized flasks found when Paleozoic rocks are dissolved in acid or disaggregated into particles (Fig. 10–8). As they are composed of chitin, they are assigned to the zooplankton, but their affinity is unknown. Some paleontologists have suggested that they are the egg capsules of invertebrates, such as graptolites. They are most abundant in rocks of Ordovician to Devonian age (the time when the graptolites were most abundant) but have been found in rocks as young as Permian in age.

SCLERACTINIAN CORALS

The second wave of corals, the Scleractinia, did not appear in the paleontological record until long after their relatives, the Rugosa, had ceased to be important as reef builders. Although rugose corals lasted until the end of the Permian Period, they were not prominent contributors to the late Paleozoic reefal facies which was formed largely by algae, sponges, and bryozoans. They steadily decreased to extinction at the end of the Paleozoic Era as conditions for invertebrates worsened. No corals of any kind are found in the Lower Triassic Series and the new corals appear at the base of the Middle Triassic.



Clathrochitina *Ancyrochitina*

Figure 10-8 Chitinozoans. A. *Clathrochitina* (Ordovician) (0.2 mm). B. *Ancyrochitina* (Ordovician) (0.14 mm).

In septa, dissepiments, tabulae, corallite shape, and growth form the scleractinians do not differ greatly from the rugose corals but their septa were inserted in a fundamentally different way and they formed their skeleton of aragonite, rather than calcite. In rugose corals after the six original septa have been formed, additional septa are inserted serially in four places as the coral grows. In scleractinians the septa are added six at a time or in multiples of six. In addition, the exterior wall of corallites is not like that of the rugose corals, where it is an independent structure, but is formed by the joining of the ends of the septa. As no intermediates have been found between the two types of corals and their time ranges are separated by the Early Triassic gap, the scleractinians do not appear to have evolved from rugose stock but from uncalcified and unpreserved cnidarians like modern anemones that developed a calcareous skeleton (1).

Modern scleractinians are among the most successful of limestone-forming invertebrates and build atolls, barrier, and fringing reefs in tropical seas (Fig. 10–9). However, not all of them live in tropical reefs; many live at high latitudes in relatively cold and deep water. The reef corals are called hermatypic and the nonreef corals, ahermatypic. The hermatypic corals have developed a symbiotic relationship with unicellular dinoflagellate algae that live within their soft tissue. A symbiotic relationship is one that benefits both organisms—in this particular relationship, the coral obtains oxygen for respiration from the alga, and the alga obtains the carbon dioxide that it needs from the respiration of the waste gas by the coral. The algae make oxygen by photosynthesis and for photosynthesis they need light. Since hermatypic corals have given up other methods of obtaining oxygen, they have become indirectly dependent on light and can only live at depths where sufficient light penetrates to satisfy photosynthetic requirements of their symbiotic algae. The depth below which the corals cannot grow is called the oxygen compensation level. Below this depth they can be said to drown for they

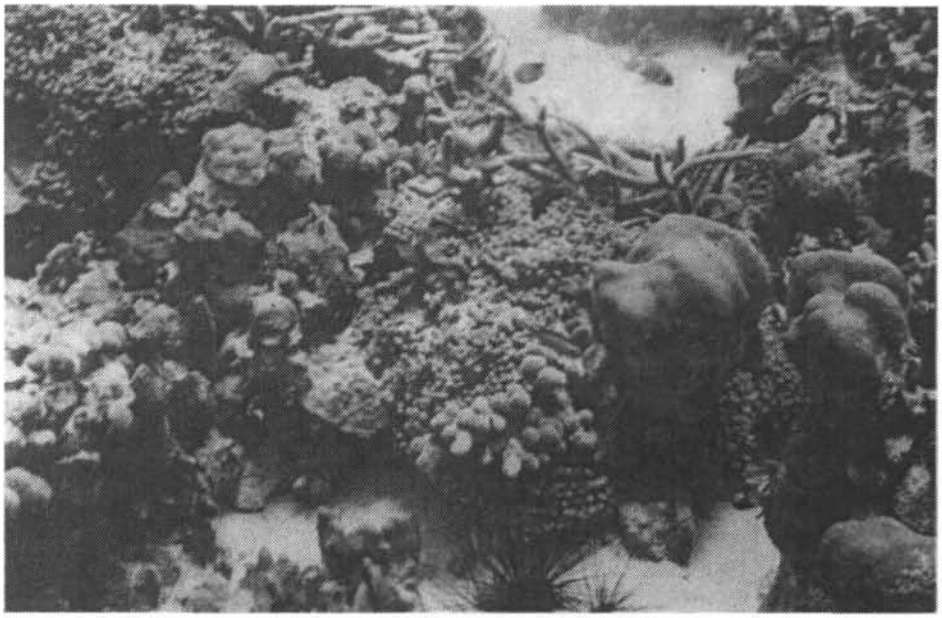


Figure 10-9 Assemblage of scleractinians on a living fringing reef, Discovery Bay, Jamaica. (C. W. Stearn.)

do not get enough oxygen for respiration. The depth varies with all the factors that affect penetration of light into the ocean such as turbidity, turbulence, cloud cover, and latitude, but rarely exceeds about 90 meters. Prolific growth of corals is confined to the upper 20 meters of water. Coral reefs cannot grow to the surface from water that is deeper than 90 meters, and thicker accumulations of corals must have been constructed as the growing corals kept pace with subsidence of the seafloor on which they were established.

The symbiotic algae (a type of dinoflagellate) are called zooxanthellae. They have been suspected of helping the coral to calcify and to eliminate nitrogenous wastes as well as to respire, but the intracellular chemistry by which they operate is still not clear in detail. Corals can live in water that is poor in nutrients and planktonic food because their symbiotic algae supply them with many of the essentials of life. George Stanley (5) believed that the symbiotic relationship was not established until late in the Triassic Period because not until then did the scleractinians become important frame builders. Although the aragonite of modern corals with zooxanthellae may have a different isotopic signature from others, no method has yet been found of determining whether fossil scleractinians or rugose corals had these symbiotes because in their skeletons the isotope ratios have been disturbed.

The growth forms of the Scleractinia duplicate those of Paleozoic colonial invertebrates (Chapter 6). In the brain corals, such as *Diploria* (Fig. 10–10), they evolved a new form. The corallites elongated, become confluent with adjacent ones, and entwined sinuously to produce a colony whose convoluted surface resembles a brain. A few hermatypic and ahermatypic corals are solitary, but most are colonial. The rate of growth and the amount of calcium carbonate extracted from the sea by these animals is remarkable. Hemispherical corals in the Caribbean add 1 cm of skeleton per year, and branching corals may extend by 25 cm per year. The corals on a small, not particularly healthy, Barbados reef extract 2 kg per square meter per year of calcium carbonate from seawater. Modern reefs where corals and algae thrive are the carbonate factories of the sea.

The scleractinians increased in abundance and diversity from Late Triassic to Late Cretaceous time when their ascendancy in the reef community was threatened briefly by the extraordinary success of the rudist bivalves. Since the beginning of the Cenozoic Era the scleractinians have consolidated their dominance of the reef environment.

BIVALVIA

Brachiopods and bivalves are both largely sedentary, small invertebrates enclosed in two calcareous

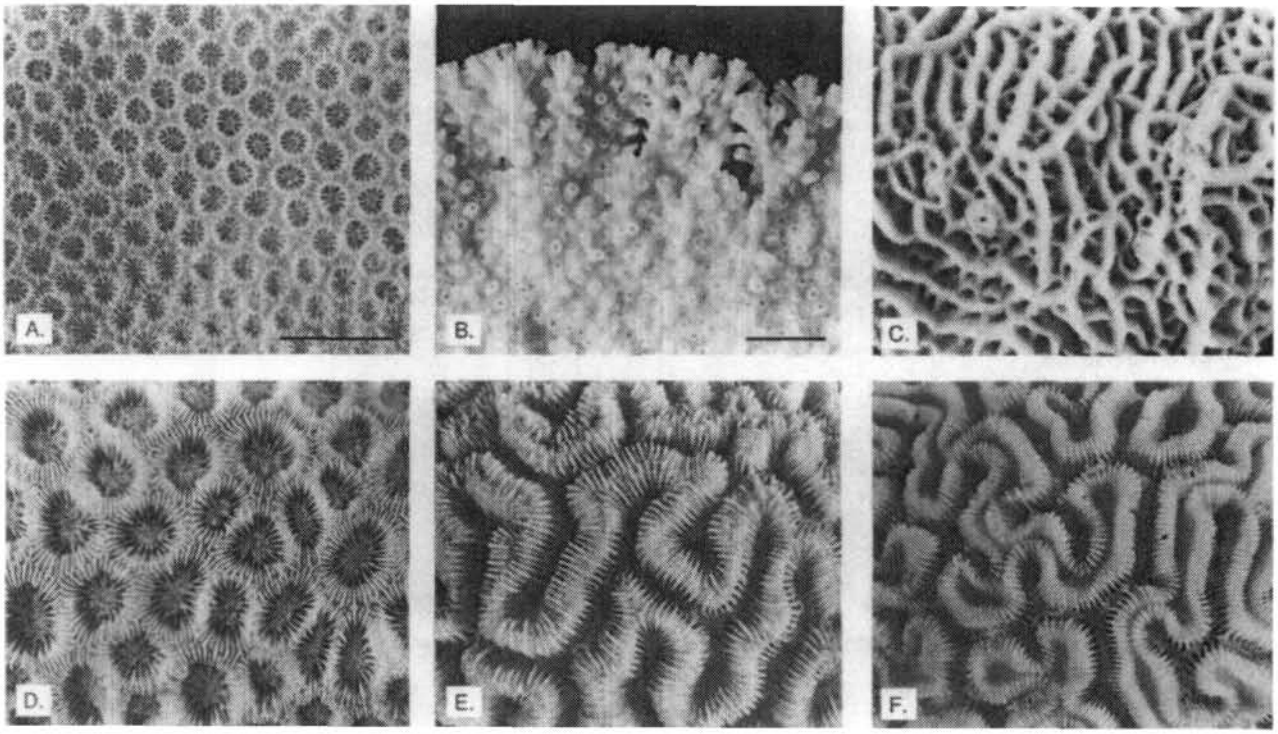


Figure 10-10 Surfaces of modern scleractinian corals from the Caribbean. The scale bars are 1 cm and the bar in B applies to all photographs except A. A. *Montastrea annularis*. B. *Acropora palmata*. C. *Agaricia agaricites*. D. *Montastrea cavernosa*. E. *Diploria strigosa*. F. *Diploria labryrinthiformis*. (C. W. Stearn.)

shells. One dominated shallow marine environments of Paleozoic time and the other has dominated the same environments since the end of that era. We have seen that the brachiopods yielded the inshore and estuarine environments to the bivalves progressively as the Paleozoic passed, but this slow change was interrupted by the Permian invertebrate crisis. David Raup (2) has estimated that 96 percent of brachiopod species became extinct at the end of the Permian Period, yet the major divisions of the bivalves seemed to have been little affected. Some brachiopods survived and continued to live as minor elements of the fauna in Mesozoic and Cenozoic seas but whereas these brachiopods merely survived, the bivalves continued to expand in diversity and number.

In the muscular, digging foot the bivalves had an organ that allowed them literally to penetrate environments that were unavailable to the brachiopods. Most Paleozoic bivalves lived on or near the sediment surface, but a few were burrowers. In the Permian Period many more turned to an existence within the sediment using the foot for burrowing. This movement into the subsurface may have been made possible by the fusion of the two lobes of the mantle to keep sediment grains out of the interior and to form siphons by which the buried animal could stay in contact with the water above. Why did many bivalves move into the sediment at the close of the Paleozoic Era? Geerat Vermeij (3) has suggested that they were escaping recently evolved predators capable of crushing hard shells. Bivalves evolved forms that could live as far as a meter beneath the surface.

Not all post-Paleozoic bivalves were burrowers; they diversified into many other aquatic environments. Some adapted to boring into hard skeletal tissue of other invertebrates or into rock or wood; others retained into adulthood the larval stage of attachment by byssal threads; still others cemented themselves to hard bottoms or other organisms, or reclined on soft sediment. The form of the shells of living bivalves has been accurately correlated with their habitats. With this knowledge paleontologists can deduce the habitat of fossil bivalves.

Classification:

Unfortunately, shell form is not a useful character for establishing relationships because it is highly

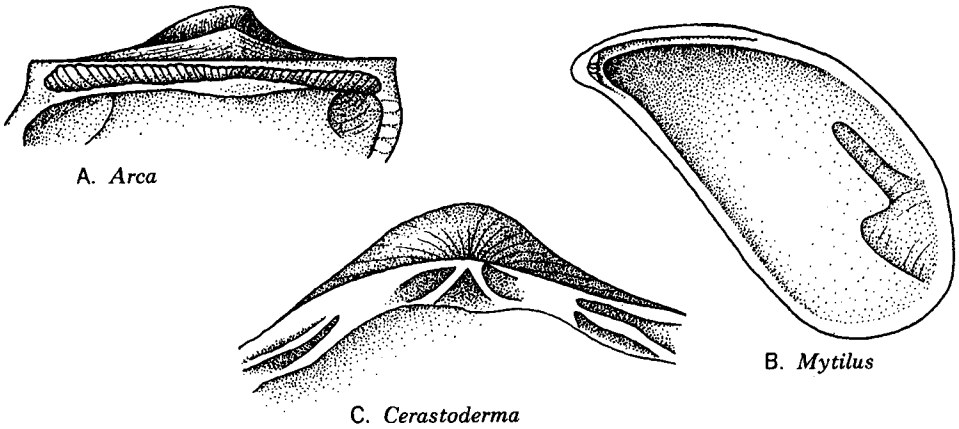


Figure 10-11 Patterns of bivalve dentition. A. Taxodont (*Arca*). B. Dysodont (*Mytilus*). C. Heterodont with central cardinal and lateral teeth (*Cerastoderma*).

correlated with current way of life rather than ancestry. Fossil bivalves, therefore, may be difficult to place in classifications of living bivalves that are based mostly on soft part anatomy. The combination of laminar, cross-laminar, and prismatic layers of calcite and aragonite in mollusc shells produce a bewildering number of microstructures (4) which are considered further in Chapter 19. The teeth are either long lateral ridges placed on either side of the umbo parallel to the hinge line or short cardinal teeth located below the umbo at high angles to the hinge line. The most common pattern, called heterodont, consists of a combination of these two types of teeth (Fig. 10–11C). In taxodont dentition the teeth are all short, like cardinal teeth, but are arranged in a row along the hinge with axes forming a fan pattern. This type of dentition occurs early and persistently in such primitive bivalves as the nuculoids and in modern ark shells (genus *Arca*, Fig. 10–11A). The dysodont type of dentition, found in *Mytilus* and its relatives, consists of single lateral teeth along the edge of the hinge (Fig. 10–11B). Several other patterns of teeth are found in specialized families.

Phylum—Mollusca
- Class—Bivalvia
  - Subclass—Paleotaxodonta
  - Subclass—Isofilibranchia
  - Subclass—Heteroconchia
  - Subclass—Pteriomorphia
  - Subclass—Anomalodesmata

Burrowing Bivalves:

Bivalves that live unattached within sediments tend to be bilaterally symmetrical and to have two subequal adductor muscles. Their shape is adapted to the depth to which they burrow and the nature of the sediment, whether sand, mud, or gravel. Because these bivalves rock their shells forwards and backwards as they move into the substrate, any surface ornament, such as flanges, that interlocks like a rachet with the sediment grains to impede slipping is advantageous. Once in place, most burrowing bivalves move little and only when their position with respect to the surface is altered by scouring of the sediment in storms or by burial by sudden deposition. The lack of a mechanism for any but the most simple burrowing movements within the sediment has limited the environments that this class of molluscs has been able to exploit to a relatively narrow range compared to those exploited by the gastropods. Few Paleozoic bivalves show the pallial sinus that is evidence of the retractable siphons of deep-burrowing clams.

Many familiar and edible clams, such as the quahog (*Mercenaria*) (Fig. 7–1) and the cockle (*Cerastoderma*), today occupy the burrowing habitat. Shallowly burrowing clams generally have thick, highly ribbed shells to resist predator attacks but deeper burrowers have thinner, smoother shells. In such deeply burrowing forms as *Mya* (Fig. 10–12E), the siphons are so large that they cannot be retracted and the valves gape at the back end. Among the most abundant Mesozoic bivalves are a group typified by the genus *Trigonia* (Fig. 10–12D), that de-

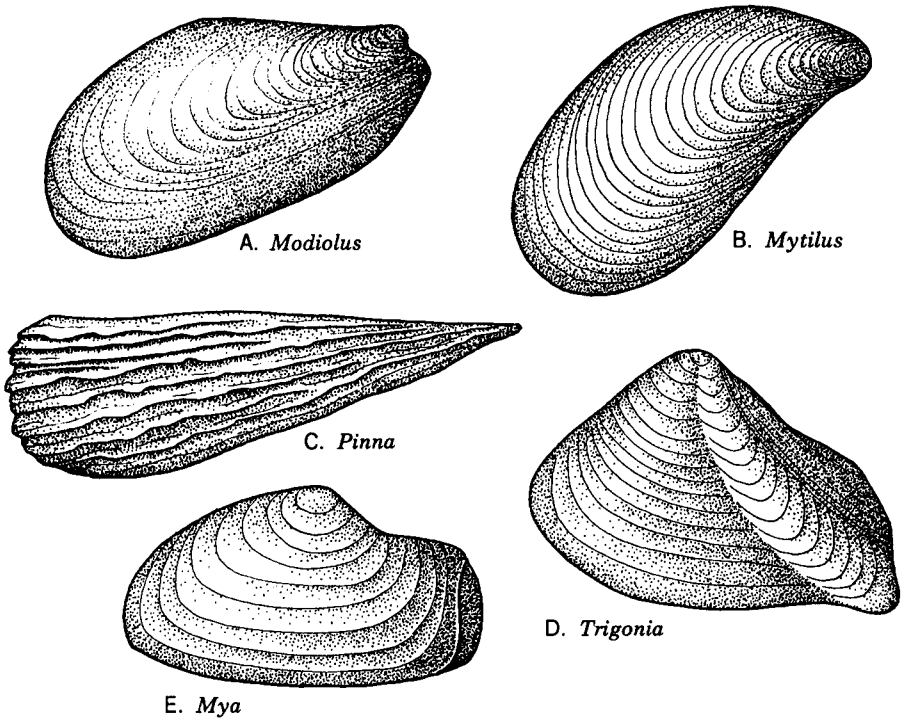


Figure 10-12 Bivalves. *Modiolus* (Carboniferous–recent). B. *Mytilus* (Triassic–recent). C. *Pinna* (Carboniferous–recent). D. *Trigonia* (Triassic–Cretaceous). E. *Mya* (Oligocene–recent).

veloped heavy shells with a distinctive ornament of flanges and knobs that meet along a prominent ridge from the umbo to the lower edge. Freshwater clams first appear in Devonian rocks but are not abundant in the paleontological record at any time. The largest group belongs in the order Unionoida, but some other bivalves also reached this environment. Their shells are characterized by a thick organic coating that protects the carbonate from dissolution. This coating is insubstantial in most marine bivalves because they live in a solution saturated with calcium carbonate.

Byssally Attached Bivalves:

When the swimming larva of most bivalves settles to the bottom, it attaches itself to grains of sediment by fibers that together form the byssus. The byssus is secreted by a gland in the foot. The byssus keeps the minute shell from being swept from its resting place. Most bivalves abandon this attachment as adults to become burrowers, borers, and swimmers, but many retain it. Several lineages remained partly or completely embedded in sediment and anchored by the byssus to sediment grains, but other byssate groups evolved to live on the surface attached to rocks or the shells of other organisms. Those that remained within the sediment have valves that are mirror images, like those of burrowers, but many are highly asymmetric (Fig. 10–12A,B,C). Modern bivalves that live a half-buried life style, typified by the modern genus *Modiolus* (Figs. 10–12A, 10–13B,C), are shaped like some Paleozoic genera that are thought to have lived the same way. The posterior part that stuck out of the sediment surface is elongated and expanded and the anterior part reduced. Another common Jurassic to recent byssally attached bivalve that lives half-submerged in sediment is the fanlike *Pinna* (Fig. 10–12C). Partly buried byssate bivalves develop inequality in the size of the two adductor muscles; the anterior one, submerged in sediment, becomes small, and the posterior one, large (Fig. 10–13). This inequality increased in those bivalves that evolved to live on the sediment surface.

A diverse group of byssate bivalves abandoned life within the sediment to live on the surface. In those that maintained the plane between the valves in a vertical orientation, the valves remained mirror images, but in those that reclined on one side, the valves became not only asymmetrical but also markedly unequal in size. Of the first group *Mytilus* (Triassic to recent), the mussel has a shell flattened at the bottom where it is attached by the byssus, and the muscles are unequal in size (Figs. 10–12B, 10–13D). *Mytilus* grows in great numbers over rocks and its own shells in the tidal zone where it must resist daily drying cycles and freshwater influx. The

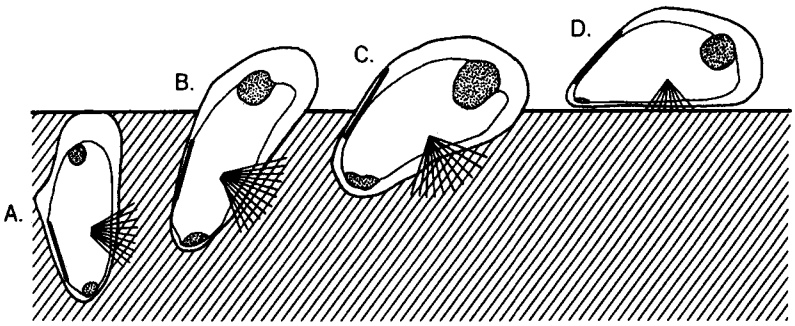


Figure 10-13 Transition in modern mytilid bivalves from completely buried to attached to the sediment surface. Muscles are dotted. A. *Brachidontes*. B, C. *Modiolus*. D. *Mytilus*. (*Source:* Modified from S. Stanley, *Journal of Paleontology*, v. 46, pp. 361–385.)

epifaunal byssate group also includes shells of the *Arca* type (Fig. 10–11A).

The region where the byssus is attached is commonly marked by a re-entrant in the shell known as the byssal notch. The bivalves of the superfamily Pteriacea reclined on one valve attached by a byssus in a notch located below an extension of the hinge line in front of the umbo called an auricle (Fig. 10–14). Similarly shaped valves are common from Ordovician time onward.

A byssate bivalve group in which the valves remain mirror images is represented by the common Cretaceous genus *Inoceramus* (Fig. 10–15F). This thick-shelled bivalve is marked by concentric coarse annulations. The disintegration of its shell after death contributed large quantities of calcite prisms as sediment to the accumulation of chalks of this period.

Swimming Bivalves:

Scallops are characterized by a symmetrical shell that is usually radially ribbed, has the hinge line extended into auricles on either side of the umbo, and has weak teeth (Fig. 10–15E). The typical genus is *Pecten*, which is widely displayed as the symbol of the Shell Oil company. Although *Pecten* and its relatives are byssally attached in the early stages of life (Fig. 10–14), they recline on one valve as adults and are capable of moving through the water by jetting water from the mantle around either side of the auricles. The jets are produced when the valves are snapped together by the contraction of a single drum-shaped adductor muscle that we eat when served a dish of scallops. The snapping motion evolved in most bivalves to expell sediment from between the valves but the scallops have adapted it for propulsion. Fossil bivalves of this shape, and presumably of this life-style, occur in rocks as old as Carboniferous in age. Many members of the superfamily Pectinacea do not swim but retain the byssal connection thoughout life and some can detach the byssus and swim if motivated by predators to flight. The swimming bivalve *Lima* aids the jet propulsion by rowing with tentacles that are extensions of the mantle around the edges of the valves.

Cemented Bivalves:

In late Paleozoic time a group of pteriomorph bivalves, instead of attaching themselves in a reclining position by a byssus, cemented the surface of one of the valves to rocks or other shells. These attached bivalves are commonly called oysters. The lower valve grew larger than the caplike top valve and may conform to the shape of the object to which it was cemented. Only one muscle is present. The oysters were, and are, a highly successful group and encrust hard surfaces in shallow water. Even where the seafloor is soft, once a few shells have made a foothold, oysters will grow on the dead shells of their ancestors to build large carbonate banks. Some oyster banks may reach the dimensions of reefs and are important traps for petroleum in Mesozoic and Cenozoic successions.

Some of the oyster family did not remain cemented throughout their lives but as adults broke free and reclined on the sediment. *Gryphaea* was a common Jurassic oyster with a very thick lower valve coiled like a ram's horn in a vertical plane (Fig. 10–15B). The evolution of *Gryphaea* in the British Jurassic rocks has been studied intensely because its progressive coiling was cited as an example of an evolutionary trend of long duration. *Exogyra*, a common Cretaceous relative, developed an equally thick shell but the umbo coiled in the dorso-ventral plane (Fig. 10–15D).

Rudists:

Descendants of the megalodont bivalves of the Devonian reef facies thrived in Late Jurassic and Cre-

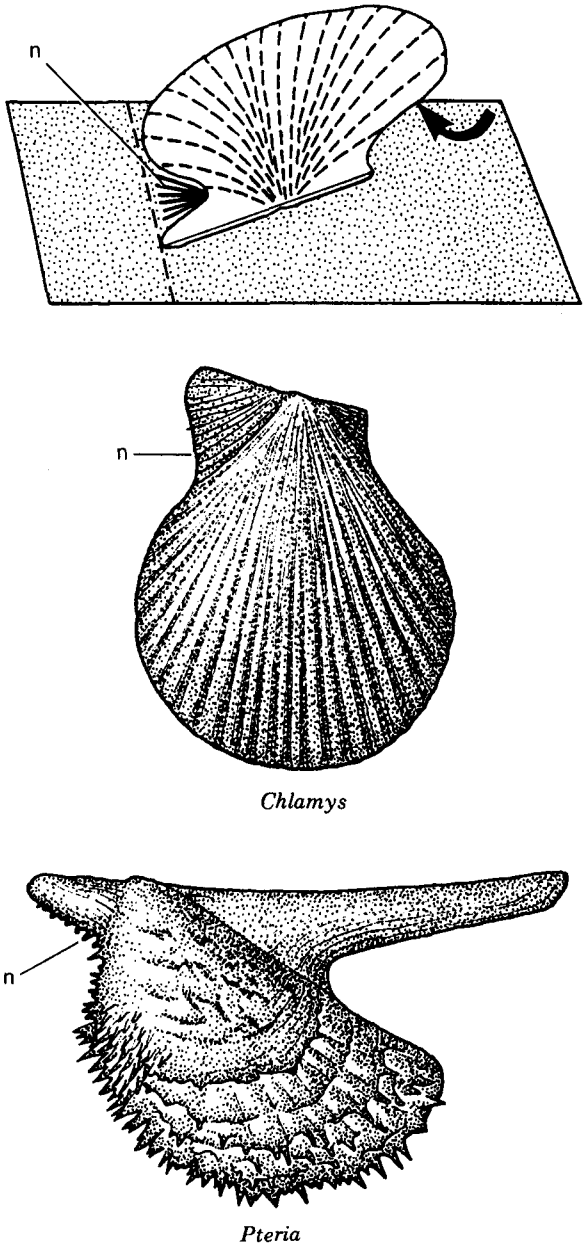


Figure 10-14 Byssate bivalves. A. Attachment at the byssal notch (n) and function of the auricle to prevent overturning by wave action (curved arrow). B. *Chalmys* (Triassic–recent), a pectinacean with a byssal notch. C. *Pteria* (Cretaceous–recent), a pteriomorph with a byssal notch.

taceous time. Nearly all the advanced forms of this group, referred to as rudists, became extinct at the end of the Cretaceous after phenomenal success. A few persisted into the Paleocene of Russia and Cuba, and the thick-shelled reef oyster *Chama* (Fig. 10–15C) of today is a relative. The lower cemented valve of the largest rudists, which may be either the right or left, evolved to conical form and the other valve formed a cap to close the end of the cone (Fig. 10–16). The teeth were highly modified and the upper valve, instead of hinging open, lifted vertically guided by long teeth sliding in slotlike sockets. *Hippurites* and *Radiolites* are typical of this group. In other rudists both valves are thickened into coiled forms (*Diceras*) and reclined on the sediment (Fig. 10–16A). In still others one is coiled and the other is conical (*Caprina*, Fig. 10–16B). During the Cretaceous, caprinids, hippuritids, and radiolitids displaced the corals and sponges as the principal reef builders and built carbonate reefs of regional extent that are important oil exploration targets in the Mediterranean and Caribbean areas. Not only did these bivalves mimic solitary rugose corals in their external form but they also divided the interiors of their valves with horizontal partitions like tabulae and dissepiments, and radial ones like septa. The walls were not solid but were composed of a network of cells. The largest hippuritids are 2 meters in height and grew in thickets so that they supported one another in upright positions. They are widely believed to have achieved such massive skeletons through a symbiotic relationship with photosynthetic algae like the scleractinian corals. The upper valve in some appears to have allowed the mantle to remain exposed when the valves closed to cover the viscera, and in others the valve is so thin that it may have been transparent to allow the algae to photosynthesize when it was closed. The South Pacific genus *Tridacna* is the best-known living bivalve with this relationship to algae. The genus includes the largest known living bivalves but is not related to the rudists. When its valves are open, the edges of the mantle exposed to the light are vividly colored by various strains of symbiotic algae.

The first evolutionary expansion of the rudists in Early Cretaceous time resulted in the deposition of the thick-bedded, cliff-forming limestones around the Mediterranean. Similar rocks of the El Abra Formation are major producers in the Golden Lane and more recently discovered oil fields of southern Mexico. In the second major expansion of Late Cretaceous time the radiolitids spread from the tropics as far north as England and southern Canada. The catastrophic decline of the rudists at the end of the Cretaceous took place at the height of their abundance and diversity.

Next Page

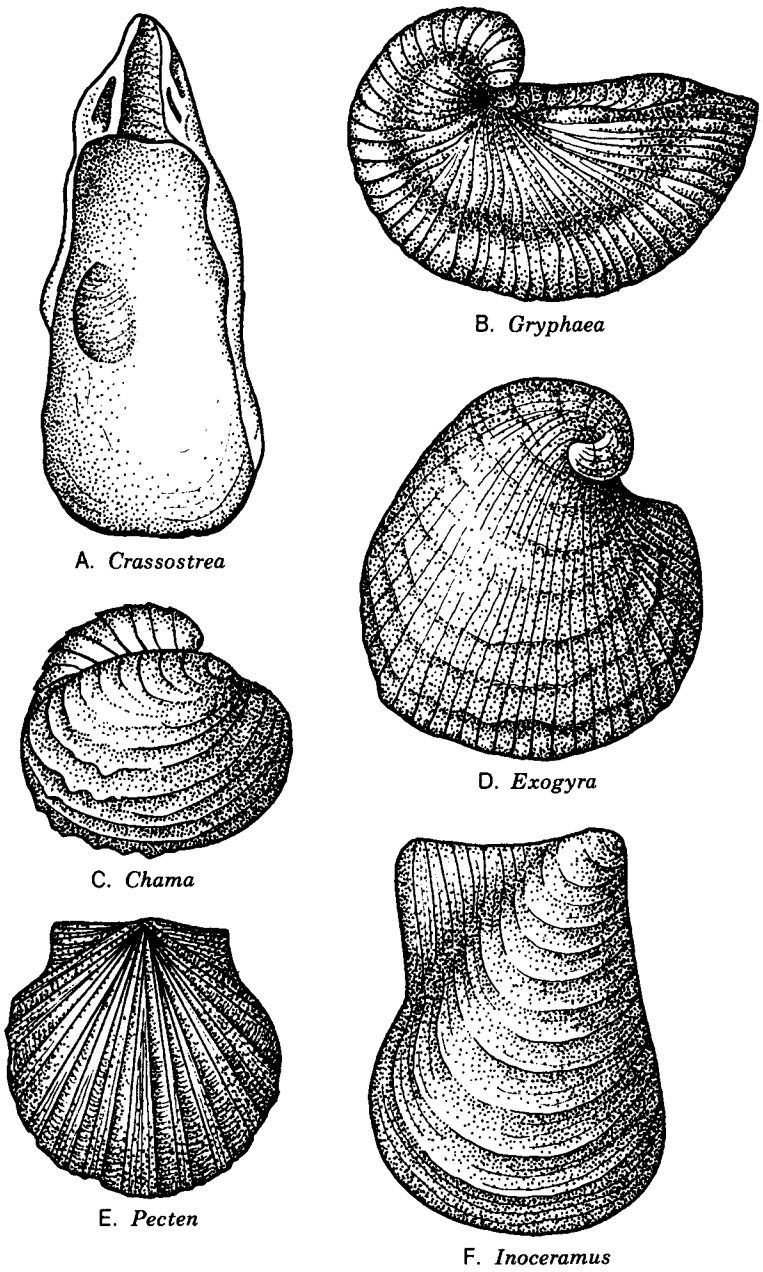


Figure 10-15 Bivalves. A. *Crassostrea* (left, interior) (Cenozoic). B. *Gryphaea* (Triassic–Jurassic). C. *Chama* (Cenozoic). D. *Exogyra* (Cretaceous). E. *Pecten* (Cretaceous–recent). F. *Inoceramus* (Jurassic–Cretaceous).

Borers:

A small number of bivalves of the subclasses Heteroconchia and Pteriomorpha developed the ability to bore into hard substrates, an adaptation that allowed them to escape predators. These borers chip, grind, and file with the rough front edges of the valves against rock, wood, or skeletal tissue of other animals. Some secrete chemicals that dissolve the substrates they attack. Most, such as *Lithophaga* and *Pholas*, are round in cross section and elongate in form (Fig. 10–17). These bivalves are major agents in the destruction of reef limestones in the tropics today and are therefore important in the study of bioerosion. The shipworm, *Teredo*, is typical of bivalves that have developed the ability to penetrate and digest wood. Wooden ships and piers in modern oceans soon fall apart under the attack of these bivalves unless protected by antifouling paints. The shell of many members of the family covers only a

Chapter 11

Evolution of Vertebrates During the Mesozoic

MESOZOIC TERRESTRIAL REPTILES

During the Carboniferous and Early Permian, the terrestrial environment was dominated by archaic amphibians. Reptiles originated in the Late Carboniferous, but it was only in the Late Permian and Mesozoic that they became conspicuous elements of the fauna. During the Mesozoic, the dinosaurs dominated the land while aquatic reptiles abounded in the seas and the pterosaurs and birds took to the air. The Mesozoic also witnessed the emergence of the turtles, lizards, snakes, and crocodiles.

Turtles:

Because they are common members of the modern fauna, turtles do not appear exotic, but their extensive bony armor makes them among the most specialized of all vertebrates. Turtles, already clearly recognizable and providing no evidence of their immediate ancestry, appear in the fossil record in the Upper Triassic (1) (Fig. 11–1). Their lack of lateral or dorsal temporal openings suggests they are not closely related to either diapsids or mammal-like reptiles but evolved from the ancestral or stem reptiles. Turtle skulls are distinguished by openings on the posterior surface through which the jaw muscles extend. Even the earliest fossil turtles had completely lost their marginal teeth and had evolved a horny beak.

No fossils are known that show early stages in the evolution of the turtle shell, although elements of the shell fossilize readily and are easily recognized. The ventral part of the shell, the plastron, incorporates into its anterior margin the ventral portions of the dermal shoulder girdle of primitive reptiles. The remainder of the plastron and the entire dorsal portion of the shell (the carapace) evolved *de novo*. The shell of early turtles not only included all the elements present in modern turtles but also incorporated a fringe of extra marginal elements in the carapace and extra bones in the plastron.

By the Early Jurassic, turtles had split into the two major groups recognized in the modern fauna, the cryptodires and the pleurodires, which are distinguished by the way the head is retracted into the shell (Fig. 11–2). The specialization of the neck vertebrae for vertical or horizontal retraction was not fully evident until the Cenozoic, but early members of both groups can be recognized by the different ways that the palate and braincase are attached and by the modification of different bones

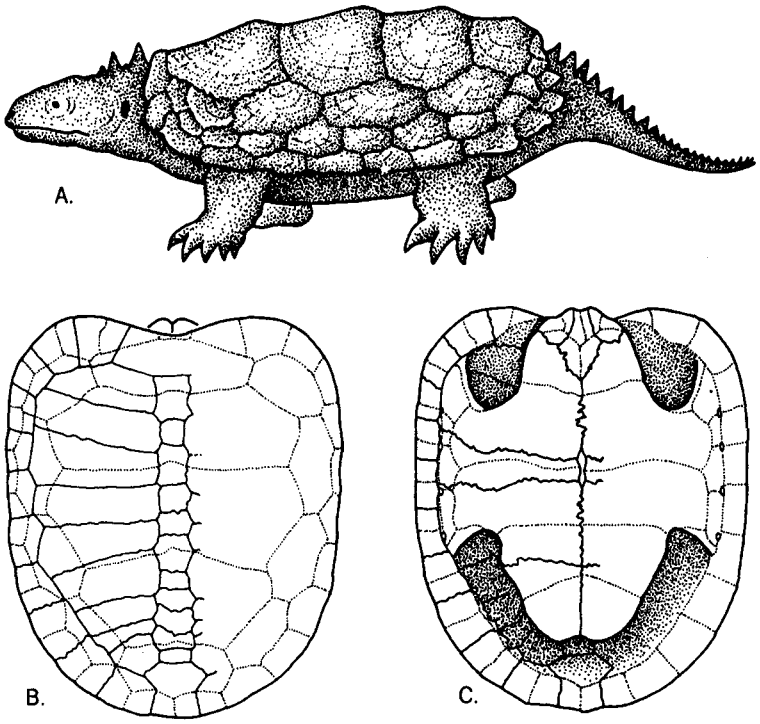


Figure 11-1 Mesozoic turtles. A. Restoration of *Proganochelys*, the oldest known turtle from the Upper Triassic of Germany. B, C. Carapace and plastron of the Lower Jurassic cryptodire turtle, *Kayentachelys*. The solid lines on the left show the division between the bony plates. The dotted lines show the outline of the overlying scutes. *Kayentachelys* has lost the extra marginal plates present in *Proganochelys*. (B & C: Courtesy of E. S. Gaffney and *Science*, v. 237: 289–291, 17 July 1987. Copyright 1987 by the AAAS.)

to form a pulleylike structure for the passage of the major jaw-closing muscles (Fig. 11–3).

Class—Reptilia
Subclass—Testudinata
Order—Chelonia
Suborder—Proganochelydia (Triassic turtles)
Suborder—Pleurodira
Suborder—Cryptodira

Pleurodires appeared in the Late Triassic and were common in the late Mesozoic and early Cenozoic but are now largely limited to the southern continents. The cryptodires apparently achieved a position of dominance at a later time and are now common throughout the world. Of the three modern superfamilies, the sea turtles (Chelonioidea) and the soft-shelled turtles (Trionychoidea) both appeared in the Late Jurassic, while the tortoises and freshwater turtles (Testudinoidea) were first recognized in Lower Cenozoic rocks.

DIAPSID REPTILES

Aside from the stem reptiles of the late Paleozoic, the turtles, and the ancestors of mammals, most reptiles belong to a single extremely diverse assemblage, the Diapsida. In the modern fauna, diapsids are represented by crocodiles, snakes, lizards, and the superficially lizardlike genus, *Sphenodon*, now

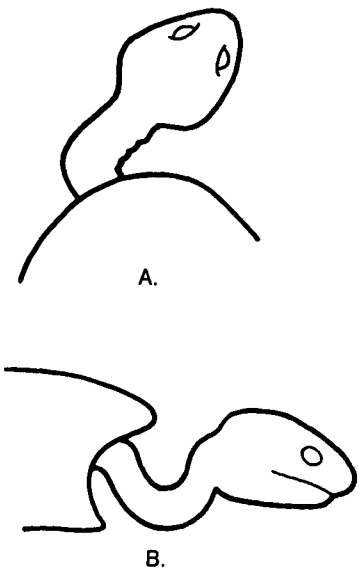


Figure 11-2 Retraction of the head in turtles. A. The horizontal curvature of the neck typical of advanced pleurodires (side necked turtles). B. The vertical curvature of the neck characteristic of advanced cryptodires.

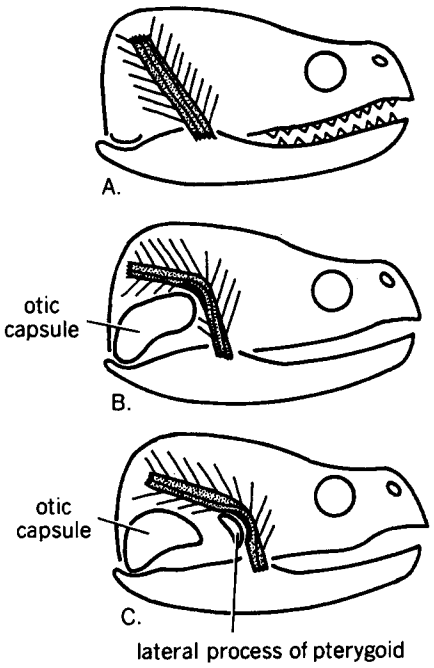


Figure 11-3 Specializations of the jaw closing musculature in turtles. A. Schematic diagram of the major jaw closing muscles in primitive reptiles including *Proganochelys*. The muscles pass in a straight line from the top of the jaw to the back of the skull. B. In cryptodires, the muscles pass over the capsule of the inner ear. C. In pleurodires, the muscles pass over a lateral process of the pterygoid bone. In all turtles the muscle extends posteriorly through openings in the back of the skull. The greater length of the muscle allows the jaw to be opened more widely. (From E. S. Gaffney, *Bulletin of the American Museum of Natural History*, vol. 155.)

limited to a few islands off the coast of New Zealand.

Diapsids were much more diverse in the Mesozoic Era. In addition to early representatives of all the major modern groups, they included two orders of dinosaurs, the flying pterosaurs, and several groups of secondarily aquatic reptiles. Birds were derived from Mesozoic diapsids and should be considered part of this reptilian radiation. Diapsids are the most diverse of all groups classified as reptiles and were the dominant vertebrates on the land, in the sea, and in the air throughout the Mesozoic (Fig. 11–4).

Early Diapsids:

The oldest known diapsid is *Petrolacosaurus* from the Upper Carboniferous of Kansas (Fig. 11–5). It was less than a meter long, including a very long tail. Relative to the trunk, the limbs and neck were both longer than those of such Early Carboniferous reptiles as *Hylonomus*. The most significant differences were in the skull, which had two pairs of clearly defined temporal openings and a new opening in the palate, the suborbital fenestra. These openings may have served to lighten the skull and distribute mechanical forces more effectively.

The fossil record of diapsids is very incomplete during the Permian, but toward the end of that period and at the beginning of the Triassic many lineages appeared, including the ancestors of all the major Mesozoic and Cenozoic groups. A divergent and specialized family, the Coelurosauravidae, appears in the Upper Permian rocks of Madagascar and Europe. The body form of the coelurosauravids was lizardlike, except for the ribs, which were greatly elongated and almost certainly supported a gliding membrane as in the modern lizard *Draco* (Fig. 11–6). Most other diapsids can be grouped into one or the other of two large assemblages, the Lepidosauromorpha and the Archosauromorpha. Lepidosauromorphs include the modern lizards, snakes, and *Sphenodon*, and several broadly similar Mesozoic families. Most lepidosauromorphs are relatively small and, like primitive reptiles, have a sprawling posture and use lateral undulation of the trunk for locomotion. These habits are carried to the extreme by snakes. The archosauromorphs include the living crocodiles and all the large terrestrial reptiles of the Mesozoic. In this group, the limbs are drawn to some degree under the body, and move in a fore and aft direction. The patterns of posture and locomotion are reflected in the bones of the girdles and limbs (Fig. 11–7).

Class—Reptilia
- Subclass—Diapsida
  - Order—Araeoscelida (including *Petrolacosaurus*)
  - Infraclass—Lepidosauromorpha
    - Order—Eosuchia
    - Superorder—Lepidosauria
      - Order—Sphenodontida
      - Order—Squamata
        - Suborder—Lacertilia (lizards)
        - Suborder—Serpentes (snakes)
    - Superorder—Sauropterygia
      - Order—Nothosauria
      - Order—Plesiosauria
        - Superfamily—Plesiosauroidea
        - Superfamily—Pliosauroidea

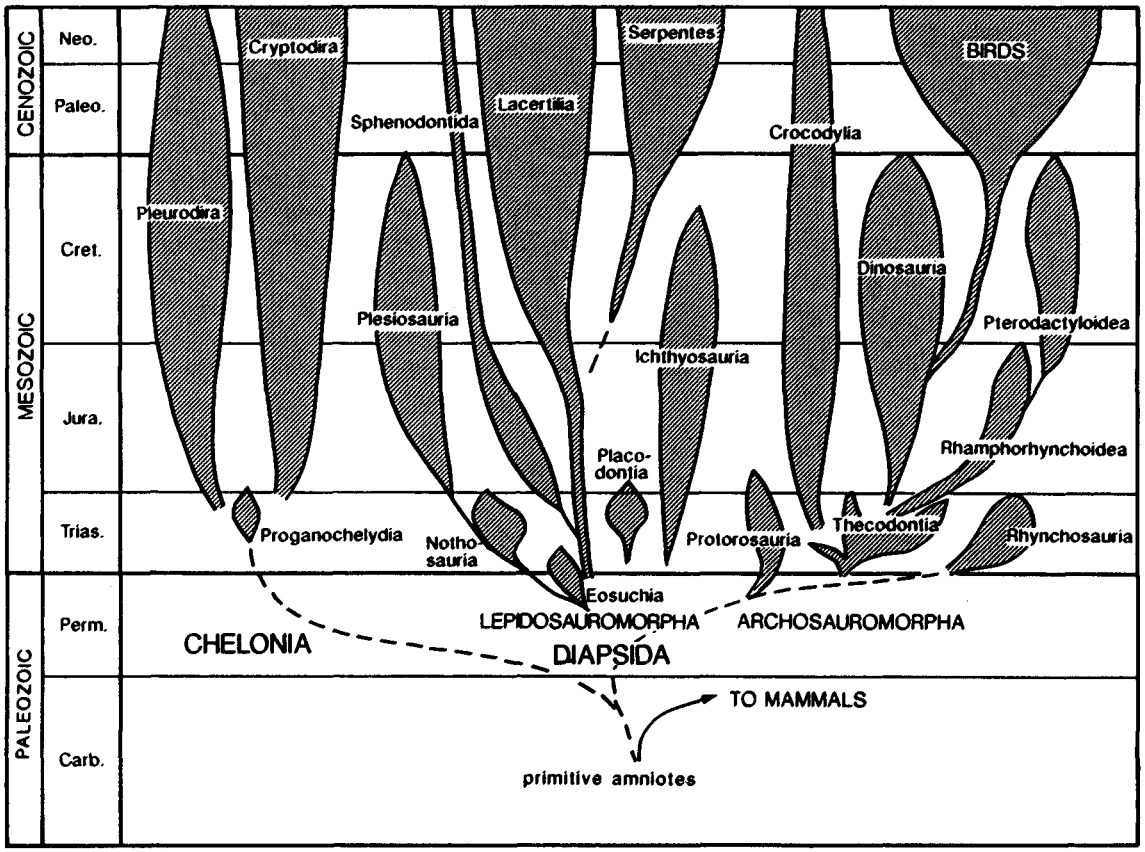


Figure 11-4 The phylogeny of reptiles.

Primitive lepidosauromorphs from Upper Permian and Lower Triassic beds are termed eosuchians. The eosuchians resembled lizards in their body form. They were more advanced than primitive diapsids, having evolved a large sternum (or breast bone) which served as a basis for the rotation of the shoulder girdle to extend the stride of the front limbs. From animals of this general pattern evolved the modern lepidosaur groups, the Squamata, including lizards and snakes, and the Sphenodontida. Both of these groups differ from the eosuchians in that there are separate areas of ossification at the ends of the limb bones, the epiphyses. Epiphyses serve to limit growth to a specific size. Growth occurs in a narrow band of cartilage between the shaft of the limb bone and the epiphyses. At a specific age, the cartilage becomes ossified and growth ceases. The bony epiphyses also form joint surfaces that are better defined that those of other reptiles.

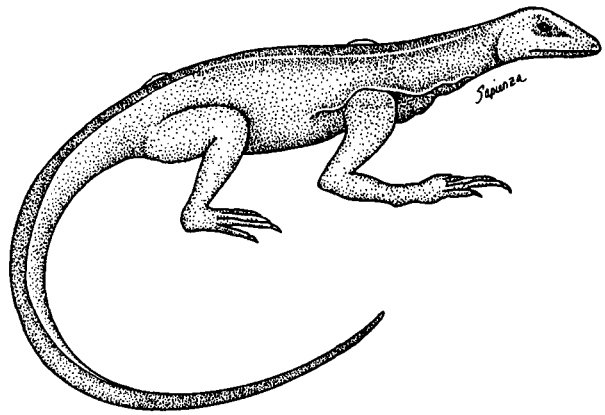


Figure 11-5 Restoration of the oldest known diapsid reptile *Petrolacosaurus*, from the Upper Carboniferous. The skull is illustrated in Figure 9-31.

Like frogs, lepidosaurs evolved an ear structure that was sensitive to airborne sounds. Unlike frogs, a different bone in the cheek, the quadrate, became specialized to support the tympanum (ear drum). In both squamates and sphenodontids, the stapes is a long, narrow rod. The living genus *Sphenodon* lacks a tympanum and a middle ear cavity, as do many burrowing lizards and snakes. Early sphenodontids, from Upper Triassic and Lower Jurassic rocks, more closely resemble typical lizards in the bony structure of the ear region and probably had a large tympanum.

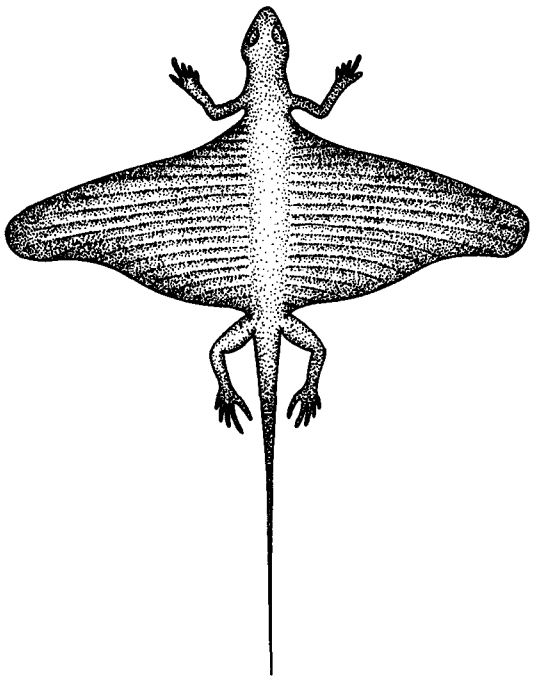


Figure 11-6 Restoration of *Coelurosauravus*, a primitive diapsid reptile from the Upper Permian of Madagascar in which the ribs are greatly elongated to form a gliding surface like that of the modern lizard *Draco*.

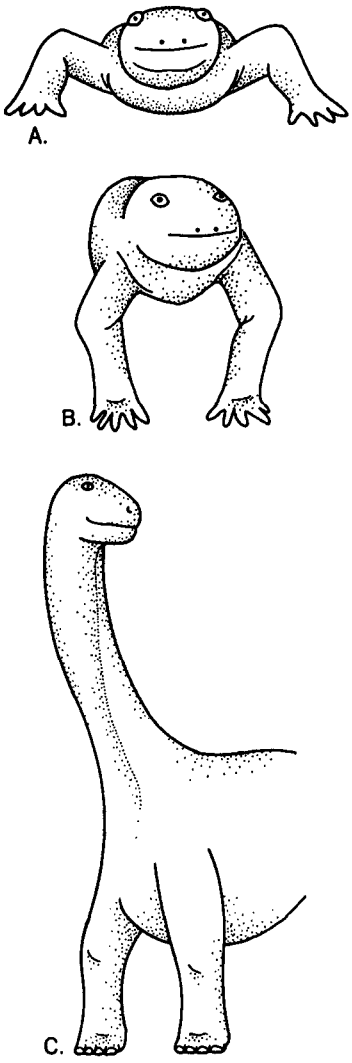


Figure 11-7 A. The sprawling posture of primitive amphibians and reptiles, B. The semi-upright posture of crocodiles and advanced mammal-like reptiles, C. The upright posture of a dinosaur.

Sphenodontida:

Both sphenodontids and lizards appeared in the Triassic Period. Sphenodontids are lizardlike in their general appearance, but most species differ from squamates in having a solid bar below the lower temporal opening, as in primitive eosuchians. Sphenodontids also differ from most other reptiles in having their teeth fused to the margin of the jaw. In most lizards, the teeth are loosely attached to the side of the jaw. Unlike most other reptiles, the teeth of sphenodontids are not replaced, but are subject to wear throughout their life. In some sphenodontids, the edges of the teeth in the upper and lower jaws shear past one another vertically. In the living genus *Sphenodon*, the lower jaw moves anteriorly and posteriorly so that the teeth move across their prey like the teeth of a saw.

Sphenodontids were common and diverse from the Late Triassic through the Jurassic but their fossils are rare in Cretaceous deposits. Sphenodontids have no Cenozoic fossil record. Presumably they reached New Zealand during the early Mesozoic, before it became isolated from Australia. The survival of *Sphenodon* on these isolated islands may be explained by the rarity of competing lizards. *Sphenodon* is typically cited as an example of a living fossil (12) since it closely resembles its Triassic ancestors. On the other hand, a group of marine reptiles, the pleurosaurs, diverged from the same ancestral stock and evolved rapidly during the Jurassic and Early Cretaceous to become highly adapted for aquatic locomotion.

Squamata:

A skull from the Upper Permian or Lower Triassic rocks of southern Africa is the oldest fossil that may belong to a lizard (Fig. 11–8). The quadrate, unlike

that of eosuchians and sphenodontids, is not firmly attached to the palate and the lower temporal bar is lost. The upper surface of the quadrate is articulated with the skull so that the lower end of this bone could move forward and backward. Mobility of the quadrate, termed streptostyly, is characteristic of most squamates (Fig. 11–9).

Primitive members of most of the modern lizard infraorders appeared by the Late Jurassic, and the modern families by the Late Cretaceous (3). Nearly 4000 species are present in the modern fauna. Lizards have a sparse record in the late Mesozoic and Cenozoic, but many modern genera are known from the Miocene.

Most fossil lizards broadly resemble the modern forms, with one striking exception. During the Late Cretaceous, one family related to the modern Komoto dragon *Varanus* became highly adapted to an aquatic existence. This family, the Mosasauridae, were among the largest marine reptiles in the latest Cretaceous seas and achieved a worldwide distribution in shallow, nearshore marine environments.

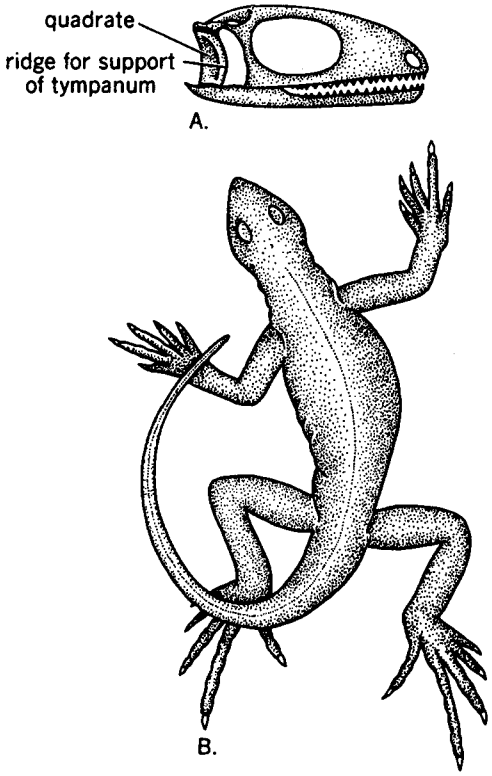


Figure 11-8 A. The skull of the oldest known lizard, *Paliguana* from the Upper Permian or Lower Triassic of southern Africa. The quadrate is embayed posteriorly for support of a tympanum, and the lower temporal bar is lost. B. Restoration of a paliguanid lizard, slightly less than life size.

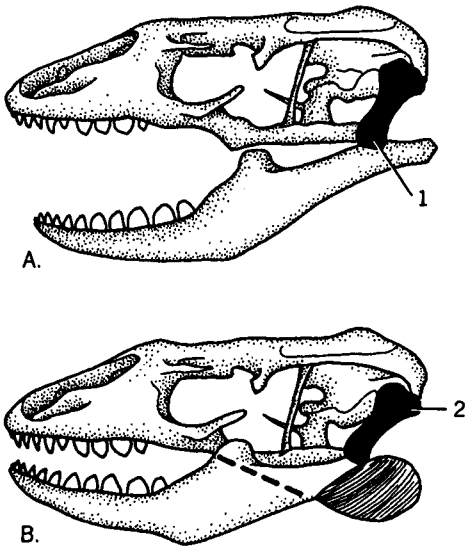


Figure 11-9 Skull of a modern lizard showing the function of quadrate mobility (streptostyly). A. Skull with jaw open and jaw articulation (1) in posterior position, B. Skull with jaw nearly closed. Jaw articulation has moved forward as the joint between the quadrate (black) and the skull roof (2) becomes functional. Dashed line shows the course of the pterygoideus muscle. Muscles can extert their greatest force when they act at right angles to the bone being moved. The pterygoideus is nearly horizontal so it can exert a greater force in moving the nearly vertical quadrate than it can on the lower jaw when it is nearly closed. (Courtesy of K. K. Smith. Reprinted by permission from *Nature* Vol. 283, pp. 778–779. Copyright (©) 1980 Macmillan Magazines Ltd.)

Mosasaurs reached a length of up to 10 meters and had a fusiform body, like moderately fast-swimming fish (Fig. 11–10). The fore and hind limbs were in the shape of paddles and the tail evolved a caudal fin. Tooth marks of mosasaurs are found in many large ammonites. The aigialosaurs from the mid-Cretaceous are nearly ideal intermediates between terrestrial varanoid lizards and mosasaurs.

Varanoid lizards may also include the ancestors of snakes. Snakes are represented by isolated vertebrae in deposits as old as Early Cretaceous (4). There are approximately 3000 species of snakes in the modern fauna, but their fossil record is difficult to interpret because most specimens are nothing but vertebrae. The skulls of most snakes have a very flexible, latticelike construction which allows them to swallow very large prey. Elongation of the body with reduction of the limbs has evolved among many lizard groups. The closest intermediates between lizards and snakes appear to be the genera *Pachyrhachis* and *Ophiomorphus* from the Lower Cretaceous of Israel (5).

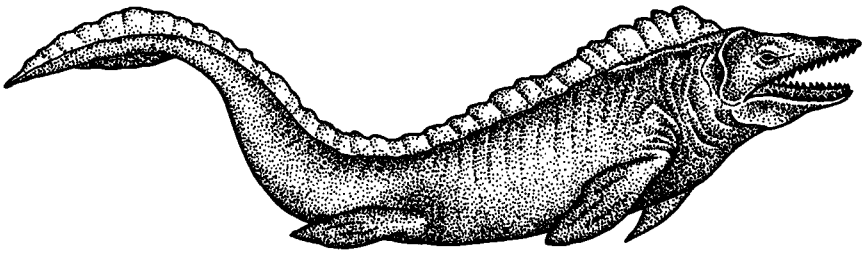


Figure 11-10 A mosasaur, a giant marine lizard from the Upper Cretaceous. Some species were as long as 10 meters.

Unlike other reptilian groups, the snakes are still a rapidly evolving assemblage. Most modern genera belong to families whose major radiation has occurred in the late Cenozoic.

ARCHOSAUROMORPHA

Primitive Archosauromorphs:

The archosauromorphs are first known in Upper Permian rocks. By the Early Triassic, several major orders had evolved, including the ancestors of the dinosaurs, pterosaurs, and crocodiles. Divergent groups included the protorosaurs and the rhynchosaurs. All archosauromorphs are characterized by advances in the structure of the rear limbs to facilitate a more upright posture. In primitive archosauromorphs, the ankle joint allowed rotation so that the foot faced more or less forward throughout the stride, although the knee still swept through a lateral arc during retraction. Much of the rest of the skeleton remained primitive. A sternum of the type seen in lepidosauromorphs never evolved in this group, and the bones of the wrist and hand are reduced.

Class—Reptilia
- Infraclass—Archosauromorpha
  - Order—Protorosauria
  - Order—Rhynchosauria
  - Superorder—Archosauria
    - Order—Thecodontia
      - Suborder—Proterosuchia
      - Suborder—Ornithosuchia
      - Suborder—Aetosauria
      - Suborder—Phytosauria
    - Order—Crocodylia
    - Order—Pterosauria
      - Suborder—Rhamphorhynchoidea
      - Suborder—Pterodactyloidea
    - Order—Saurischia
    - Order—Ornithischia

The protorosaurs appeared in the Late Permian and continued into the Early Jurassic. They are specialized in the great elongation of the neck and the reduction of the lower temporal bar (Fig. 11–11). Rhynchosaurs were large-headed herbivores common for most of the Triassic.

The most important of the early archosauromorphs are the thecodonts, a group of primarily carnivorous families that include the ancestors of all the large terrestrial reptiles of the later Mesozoic as well as the crocodiles and birds. Thecodonts can be distinguished from other primitive archosauromorphs by the presence of an opening in front of the eye, the antorbital fenestra, of unknown function (Fig. 11–12).

Thecodonts appeared at the end of the Permian and diversified throughout the Triassic Period. The most primitive of the several groups are the protosuchians such as *Chasmatosaurus*, which were sprawling animals resembling crocodiles. Other groups, including the heavily armored, herbivorous aetosaurs and the long-snouted aquatic phytosaurs, were limited to Late Triassic time.

Several thecodont groups were more advanced than these in their limb structure and may have been at least facultatively bipedal. Included in these advanced groups are *Gracilosuchus*, which may be close to the ancestry of crocodiles, and the ornithosuchids, which may be close to the ancestry of dinosaurs (Fig. 11–13).

The most dinosaurlike of all the thecodonts are the lagosuchids (Fig. 11–14A), in which the head of the femur is inflected so that the leg can be held nearly vertical. The knee and ankle joints were modified so that the rear limb could be moved directly fore and aft.

Crocodiles:

Crocodiles appeared in the Late Triassic and continue to be important elements in the world fauna. The skulls of even the earliest crocodiles resemble their modern counterparts in having a very low profile and a solidly attached jaw suspension to re-

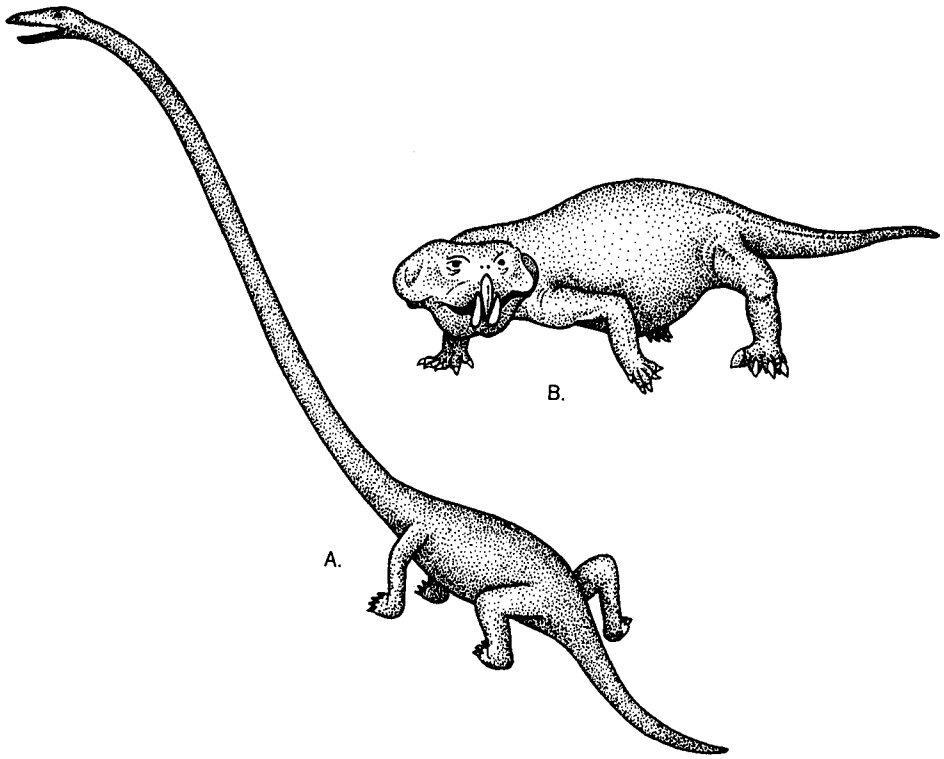


Figure 11-11 Primitive archosauromorph reptiles. A. The extremely long-necked genus *Tanystropheus* from the Middle Triassic of Europe, B. A Triassic rhynchosaur. Rhynchosaurs were herbivores characterized by the presence of many rows of teeth set in deep sockets. (A: Modified from R. Wild, *Schweiz. Palaeontol. Abh.*, v. 95. B: From S. Chatterjee. Courtesy of *Mém. Soc. géol. France, N. S.* 139, p. 64, fig. 4.)

sist the massive jaw musculature. The long limbs of early crocodiles suggest that they were fast-running, terrestrial animals, without skeletal evidence of the semi-aquatic or amphibious habits of most modern crocodiles and many of the Jurassic and Cretaceous genera (Fig. 11–14B). Four suborders of crocodiles can be recognized. The sphenosuchids, restricted to the Late Triassic, are the most primitive and show a close link with the thecodonts. The proterosuchians (Upper Triassic and Lower Jurassic) retained the primitive terrestrial life-style, but the skull is more similar to that of modern crocodiles. Most of the Jurassic and Cretaceous crocodiles are included in the Mesosuchia, which consists primarily of semi-aquatic and marine forms. Several families were highly adapted to an aquatic way of life, with a greatly elongated snout and a variable degree of modification of the limbs into paddles.

All modern crocodiles and most of the Late Cretaceous and early Cenozoic genera are included in the suborder Eusuchia, characterized by the great posterior extent of the secondary palate and the specialized articulating surfaces between the vertebrae. The range and diversity of crocodiles has been steadily reduced throughout the Cenozoic because of the cooling of the climate and the gradual geographical restriction of the tropics.

DINOSAURS

Although many dinosaurs have been described, knowledge of their fossil record is still very incomplete, particularly in the Middle to Late Triassic when the group began its major radiation. The earliest dinosaur, *Staurikosaurus*, is known from upper Middle Triassic beds of South America (6). Its remains are incomplete, but suggest that it may have reached a length of approximately 2 m. The large skull and piercing teeth indicate a carnivorous habit, and the great length of the rear limbs suggests that it was a fast-running animal. Features other than the skull and teeth, which are like later theropods, are primitive for dinosaurs, and this genus may be close to the ancestry of the entire group. In the Upper Triassic, representatives of a least six major

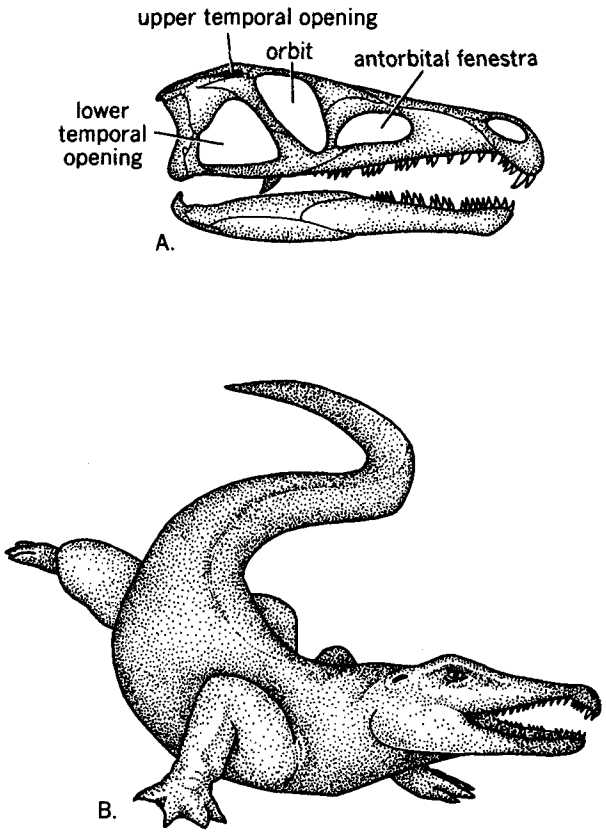


Figure 11-12 The protosuchian thecodont *Chasmatosaurus*. A. Skull showing antorbital fenestra, B. Reconstruction. This genus was approximately 1.5 meters long. (Courtesy of A. J. Charig and H.-D. Sues. From Kuhn/Wellnhofer, *Handbuch der Paläoherpetologie*, Part 13 (Charig/Krebs/Sues, Thecodontia). Gustav Fischer Verlag Stuttgart, 1976.)

lineages are known, but their specific interrelationships have not been established.

Dinosaurs have long been separated into two distinct orders, the Saurischia and Ornithischia, based on different patterns of the pelvis (Fig. 11–15). It is now recognized that all dinosaurs show similar advanced features of the pelvis and rear limbs associated with a more upright posture that indicate an immediate common ancestry. The triradiate pattern of the ilium, ischium, and pubis in saurischians is primitive for all dinosaurs and so does not demonstrate that the saurischians had a separate ancestry from that of ornithischians. The ornithischian pelvis, in which the pubis is directed posteriorly, does demonstrate the common origin of this group, since it is a unique specialization.

Two major groups have been classified among the saurischians, the carnivorous theropods and the herbivorous sauropodomorphs (Fig. 11–16).

Order—Saurischia
- Suborder—Staurikosauria
- Suborder—Theropoda
- Suborder—Sauropodomorpha
  - Infraorder—Prosauropoda (Plateosauria)
  - Infraorder—Sauropoda

Order—Ornithischia
- Suborder—Ornithopoda
- Suborder—Pachycephalosauria
- Suborder—Stegosauria
- Suborder—Ankylosauria
- Suborder—Ceratopsia

Carnivorous Dinosaurs:

The theropod dinosaurs were the largest terrestrial carnivores that ever existed, weighing as much as 7000 kg with lengths of 15 m. All were obligatorily bipedal. The skull of the Late Cretaceous genus *Tyrannosaurus* was more than a meter in length, with individual teeth 15 cm long. The largest and latest genera, in the family Tyrannosauridae, have only two fingers in the hand and such a short front limb that it is difficult to understand how it was used (Fig. 11–17).

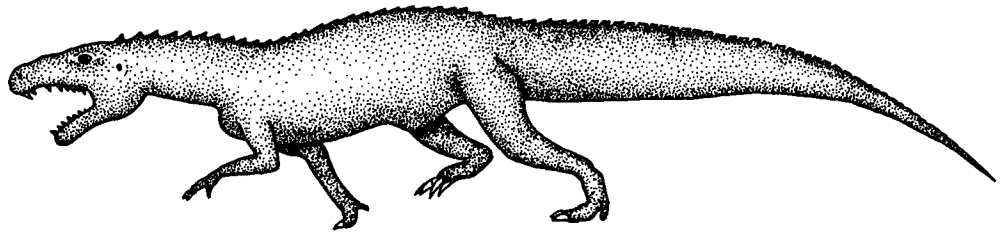


Figure 11-13 The ornithosuchian thecodont *Riojasuchus* from the Upper Triassic of South Africa. The limbs were held nearly vertically but the gait remained quadrupedal.

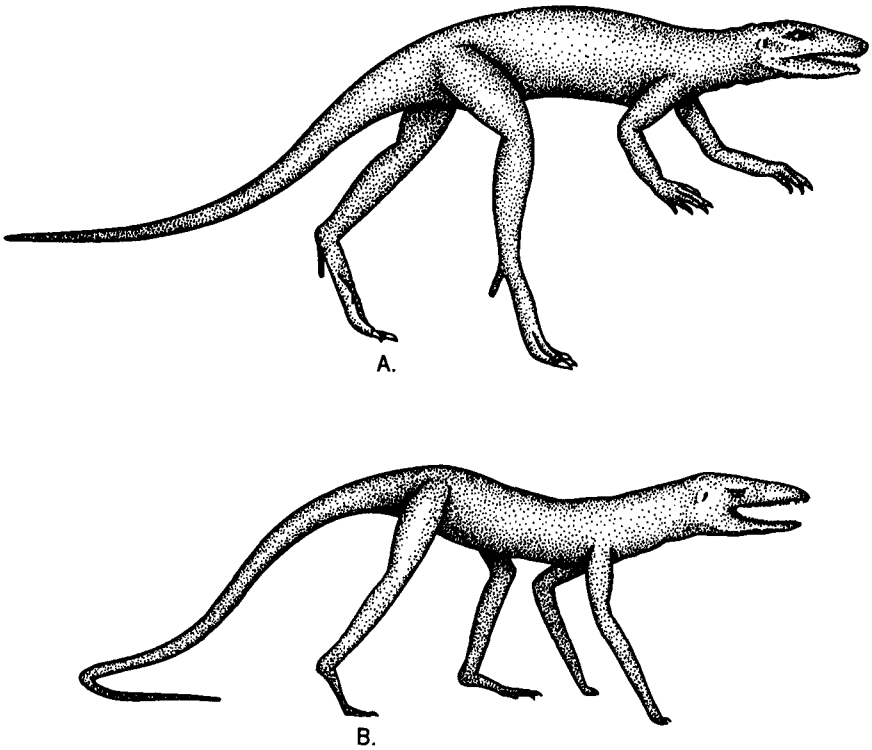


Figure 11-14 A. The faculatitively bipedal Middle Triassic thecodont *Lagosuchus* that may be close to the ancestry of dinosaurs and pterosaurs. This genus walked on its toes, as did primitive dinosaurs, rather than flat on its feet, as did more primitive reptiles. B. The primitive crocodile *Terrestrisuchus* from the Upper Triassic of Europe. The limbs were very long, in contrast to those of most later crocodiles. (A: Modified from J. F. Bonaparte, *Opera Lilloana*, 26. B: Modified from P. J. Crush, *Palaeontology*, v. 27.)

For a long time, theropods were divided into two subgroups, the carnosaurs, generally with heavy bodies, short forelimbs, and large skulls, and the smaller, more lightly built coelurosaurs, most of which had larger forelimbs, but smaller skulls. Discoveries during the past ten years of several large genera with long arms and large skulls, which cannot be categorized as either carnosaurs or coelurosaurs, makes this distinction difficult to maintain. Approximately 17 families of theropods have been recognized.

The early theropods included such small and agile genera as *Coelophysis* of the Late Triassic, which reached a length of approximately 3 meters. From

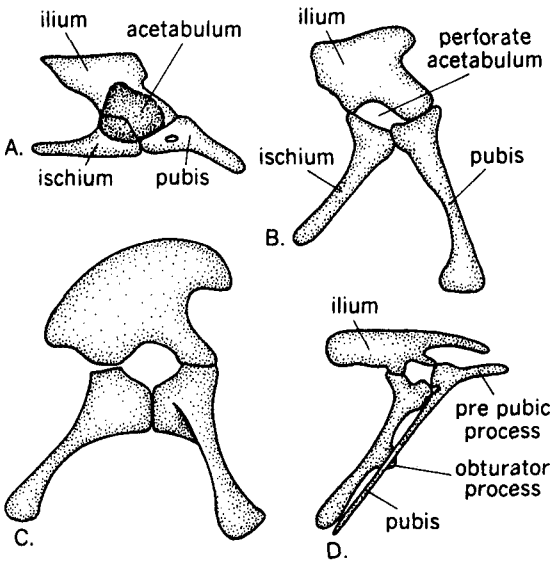


Figure 11-15 The pelves of archosaurs. A. The Lower Triassic thecodont *Chasmatosaurus*. The pubis and ischium form a flat plate for the origin of the large muscles to lift the body on the rear limbs. B. The primitive dinosaur *Staurikosaurus* from the late Middle Triassic of South America. The pubis and ischium are elongated. They now serve for the origin of muscles that swing the rear limbs anteriorly and posteriorly. The area of the acetabulum is not ossified because the main force of the rear limbs is directed dorsally towards the ilium, rather than medially, as in primitive reptiles with a more sprawling posture. C. A sauropod dinosaur. The ilium is expanded anteriorly and posteriorly from the attachment of up to six pairs of sacral ribs. D. The ornithischian dinosaur *Hypsilophodon*. Typical of this group, the pubis is oriented posteriorly and lies alongside the ischium. A new structure, the prepubic process, extends anteriorly. The obturator process is a characteristic of ornithopod dinosaurs that is not present in other ornithischians.

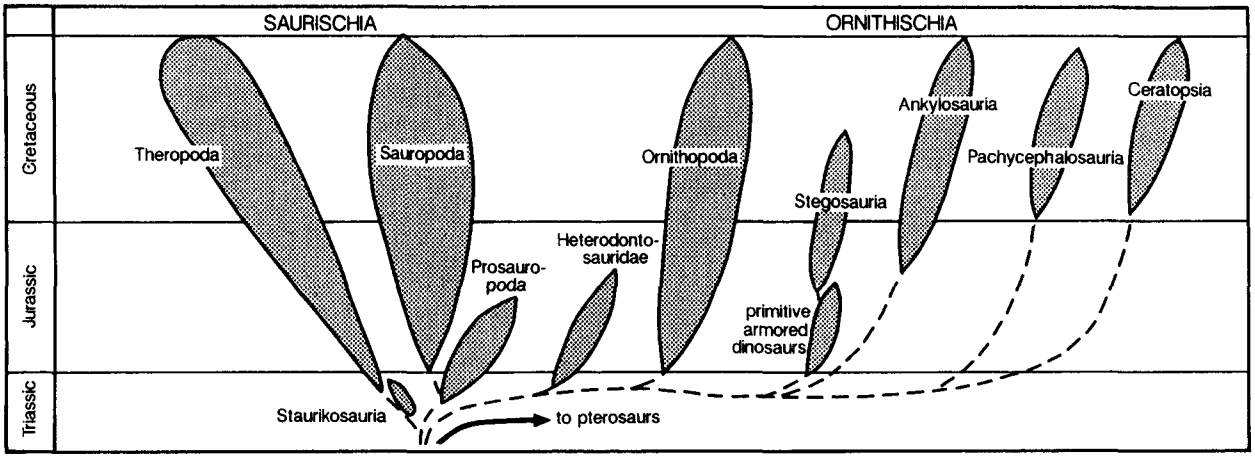


Figure 11-16 The phylogeny of dinosaurs.

such animals, several lines of small to moderate size genera evolved. *Deinonychus*, described in detail by John Ostrom (7), appears to have been a particularly effective predator with an extremely large claw on the second digit of the rear foot that was probably used to disembowel prey. *Deinonychus* and members of the related family Saurornithoididae had very large braincases, suggesting a brain of comparable size to that of advanced mammals. A divergent lineage, the ornithomimids or ostrich dinosaurs, lost their teeth and had birdlike skulls.

Larger and more massively built theropods, assigned to the family Megalosauridae, are known from the Late Triassic into the Late Cretaceous. It is not known whether the well-known genera *Allosaurus* and *Tyrannosaurus* shared a close common ancestry with them or evolved separately from smaller theropods.

Herbivorous Dinosaurs:

All other dinosaur groups were herbivores. The largest of the herbivores were the sauropods, which were common throughout much of the world in the Jurassic and Cretaceous. Edwin Colbert estimated that some reached sizes in excess of 80,000 kg (8). Incomplete remains are known of individuals that may have been considerably larger. The well-known genus *Diplodocus*, with its small head, long neck, stocky body supported on elephantine legs, and long tail, is characteristic of sauropods.

Six families of sauropods are recognized on the basis of consistent differences in the number of trunk and neck vertebrae, limb proportions, and details of skull anatomy. To reduce their weight, the vertebrae of all sauropods have large openings that give them the appearance of lattice work. The limb bones were solid and held in a nearly vertical position. The joint surfaces of the ankles and wrists were much less well ossifed than in smaller dinosaurs. The presence of large amounts of cartilage distributed the weight more uniformly, since cartilage is more capable of deformation without breakage than is bone. The great size of sauropods has led to speculations regarding the ability of the bones to support the body. It was once thought that they spent their lives in the water, since the buoyancy of water would assist in their support. Foot prints demonstrate that sauropods were capable of supporting themselves on land, and recent reconstructions imply considerable agility (Fig. 11–18). The skulls of sauropods are relatively much smaller than those of theropods, and the relative brain size was probably smaller than that of modern crocodiles.

Fossils from the Upper Triassic and Lower Jurassic are transitional between typical, obligatorily quadrupedal sauropods and a group of smaller facultatively bipedal herbivores from the Upper Triassic, the prosauropods. Prosauropods were a common and diverse assemblage on most continents. Their skeleton resembled that of the most primitive dinosaurs, but the laterally compressed and crenulated teeth are like those of some modern lizards, indicating a herbivorous diet. The hind limbs of primitive prosauropods were considerably larger than the front limbs, indicating at least facultative bipedality and close affinities with the lagosuchids and staurikosaurids.

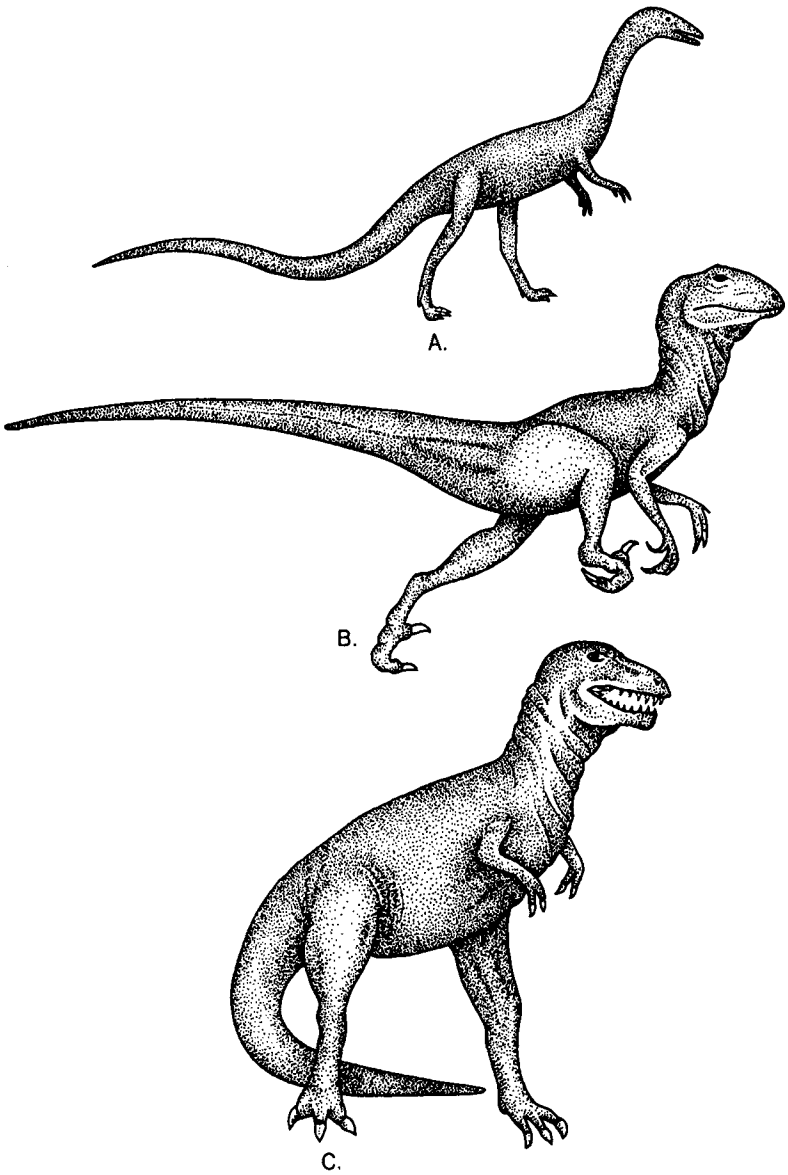


Figure 11-17 Theropod dinosaurs. A. The Upper Triassic genus *Coelophysis*, B. The Lower Cretaceous genus *Deinonychus*, C. *Tyrannosaurus*, from the Upper Cretaceous. This genus is known from both North America and Asia.

The ornithischians constitute a second, much more diverse assemblage of herbivorous dinosaurs, common from the end of the Triassic until the close of the Mesozoic. In addition to the structure of their pelvis, they are distinguished from saurischians by the presence of a medial bone at the front of the lower jaws, the predentary.

The Early Jurassic genus *Fabrosaurus* was a small, bipedal dinosaur that may be close to the ancestry of all other ornithischians (Fig. 11–19). Its forelimbs were much smaller than the hind. The distal bones of the rear limbs were longer than the femur, as in modern fast-running mammals. The skull is characterized by a small bone, the supraorbital, common to most late ornithischians, which extends across the opening for the eye. The teeth are small, with flattened, crenulated crowns, similar to those of modern herbivorous lizards.

The ornithischians underwent a major radiation toward the end of the Triassic, leading to several distinct lineages: the ornithopods, the armoured dinosaurs, the ceratopsians, and the pachycephalosaurids. *Fabrosaurus* is typical of primitive ornithopods. Most members of this group were more advanced than other herbivorous dinosaurs in having the tooth rows inset from the margin of the jaw. The bones of the upper and lower jaw are ridged above and below the tooth row, suggesting the pres-

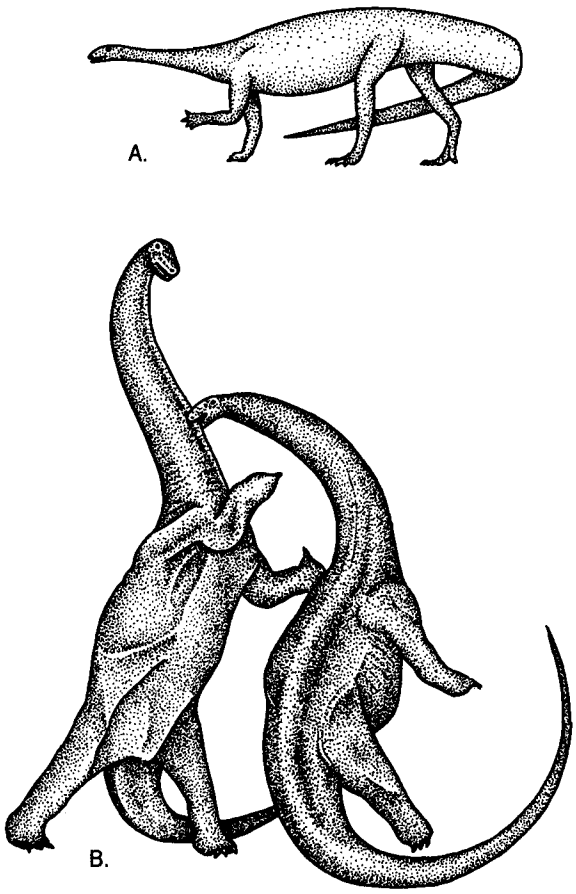


Figure 11-18 Sauropodomorpha. A. A relatively small Upper Triassic prosauropod. The great length of the rear limbs is a heritage of its bipedal ancestry. B. The gigantic sauropod *Apatosaurus* (*Brontosaurus*). Bakker's restoration suggests a very athletic posture. (A: Modified from P. M. Galton, *Postilla, Yale Peabody Museum*, v. 169. B: Courtesy of R. T. Bakker.)

ence of a fleshy cheek, as in mammals, to retain the food while it was chewed. The upper and lower teeth are worn where they moved across one another in a particular direction to insure that the food was broken into small pieces.

The iguanodontids were larger ornithopods, common in Europe and North America from the Middle Jurassic to the end of the Cretaceous. The hadrosaurs were the most common and varied of dinosaurs in the Late Cretaceous of North America and Eurasia. They were heavier than the iguanodontids, and hoofs on the forelimbs indicated that they were at least facultatively quadrupedal. Hadrosaurs had multiple tooth rows so that hundreds of shearing surfaces could be used to break up the food.

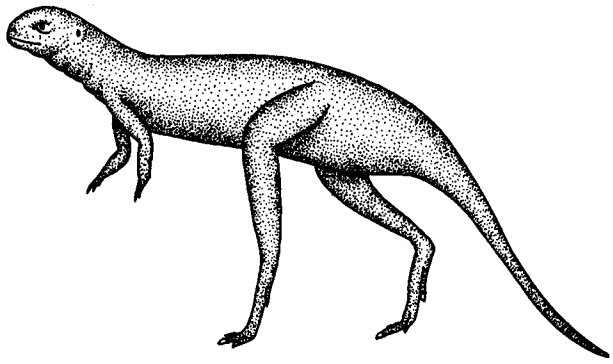


Figure 11-19 Restoration of the Lower Jurassic ornithopod ornithischian *Fabrosaurus*. This animal was approximately .5 meters tall. The short front limbs and long hind limbs indicate that it must have been bipedal. In common with *Lagosuchus* (Fig. 11-14*a*) the lower segment of the rear limb is longer than the femur. Mammals with similar proportions are rapid runners. (Modified from R. A. Thulborn, *Palaeontology*, v. 15.)

Many hadrosaurs had crests of various shapes and sizes on the skull, which were occupied by extensions of the nasal passages (Fig. 11–20). They may have been used to produce different call notes that would have been useful in species recognition (9). Jack Horner (10) has discovered the nests of many hadrosaurs that imply different patterns of parental care.

The remaining ornithischian groups appear to have diverged in the Late Triassic from a common ancestry with the ornithopods.

The pachycephalosaurids retained the bipedal stance of early ornithischians, but did not develop the complex dentition of the ornithopods. They are notable for having dome-shaped heads resulting from a greatly thickened skull. Peter Galton (11) suggested that the top of the head may have been used as a battering ram in intraspecific combat, like the horns of sheep and goats (Fig. 11–21). Pachycephalosaurids are limited to the Cretaceous but ranged through Asia, North America, and Madagascar (11).

The earliest of the armored dinosaurs appeared in Lower Jurassic rocks. *Scutellosaurus* broadly resembles *Fabrosaurus* except for the presence of bony plates along the backbone and extending over the flanks (Fig. 11–22). The stegosaurs, characterized by large, bony plates along the dorsal midline and bony spikes on the tail, lived from the Middle Jurassic into the Late Cretaceous. *Stegosaurus* is usu-

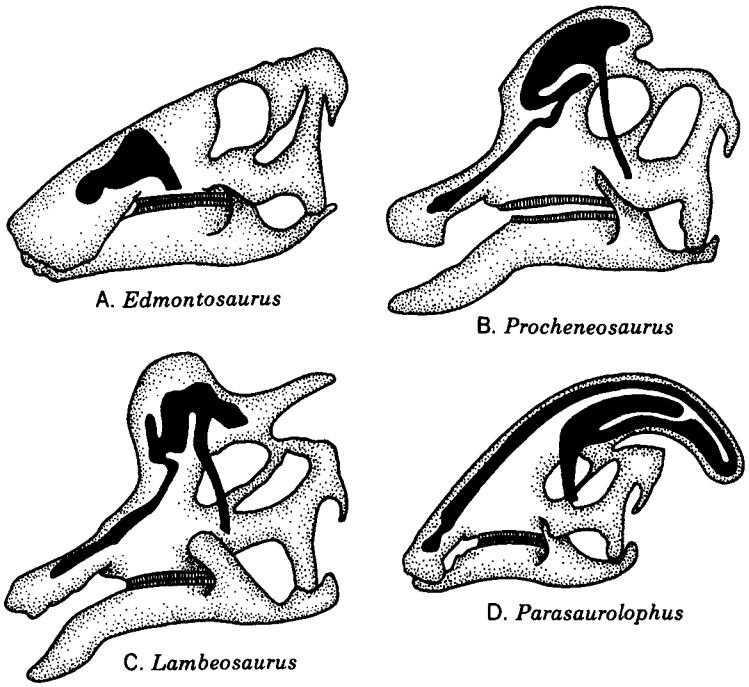


Figure 11-20 Skulls of hadrosaurs showing a variety of crests and the configuration of the nasal passages. (Modified from J. H. Ostrom, *Postilla, Yale Peabody Museum*, v. 62.)

ally restored in a quadrupedal pose, but the rear limbs were much longer than the front, reflecting their bipedal ancestry.

The most heavily armoured of all dinosaurs were the anklyosaurs, which appeared in the Middle Jurassic in Europe and were widespread during the Late Cretacous in North America and Eurasia. In addition to armor plating over the entire body, the skull was covered with dermal plates, and some genera had a massive club at the end of the tail.

Ceratopsians were among the most spectacular dinosaurs of the Late Cretaceous in North America, distinguished by their massive, commonly horned frill, extending from the skull over the neck. The frill would have offered a measure of protection but was also used for the attachment of long muscles to close the jaws and may have served for sexual display as well. The advanced ceratopsians of the Late Cretaceous were fully quadrupedal, but more primitive genera from the Early Cretaceous had long rear limbs and were probably capable of bipedal locomotion (Fig. 11–23).

Aspects of the biology and extinction of dinosaurs are discussed in Chapters 14 and 16.

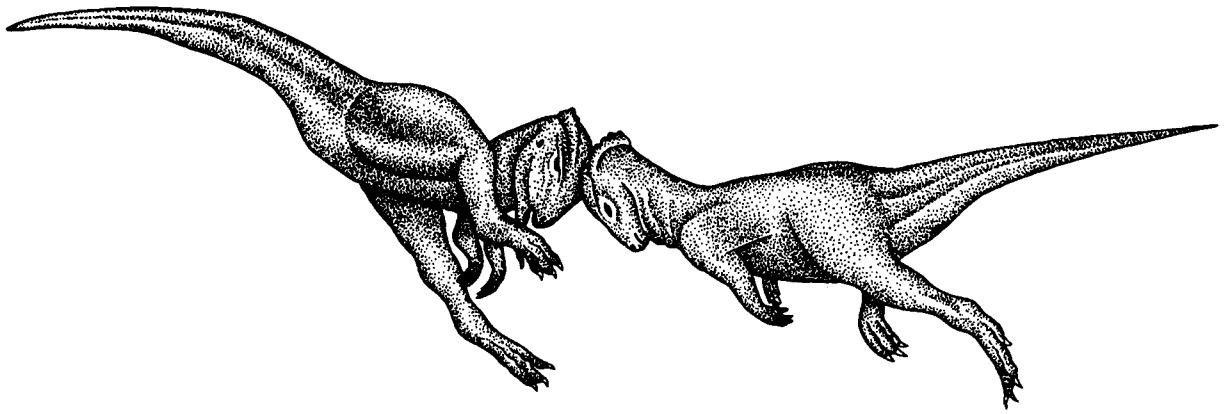


Figure 11-21 Intraspecific combat between pachycephalosaurids. Their heads are greatly thickened. This may have provided protection, as do the horns of sheep and goats in which males fight for the attention of females, about 1 m long. (Modified from P. M. Galton, *Discovery*, v. 6(1).)

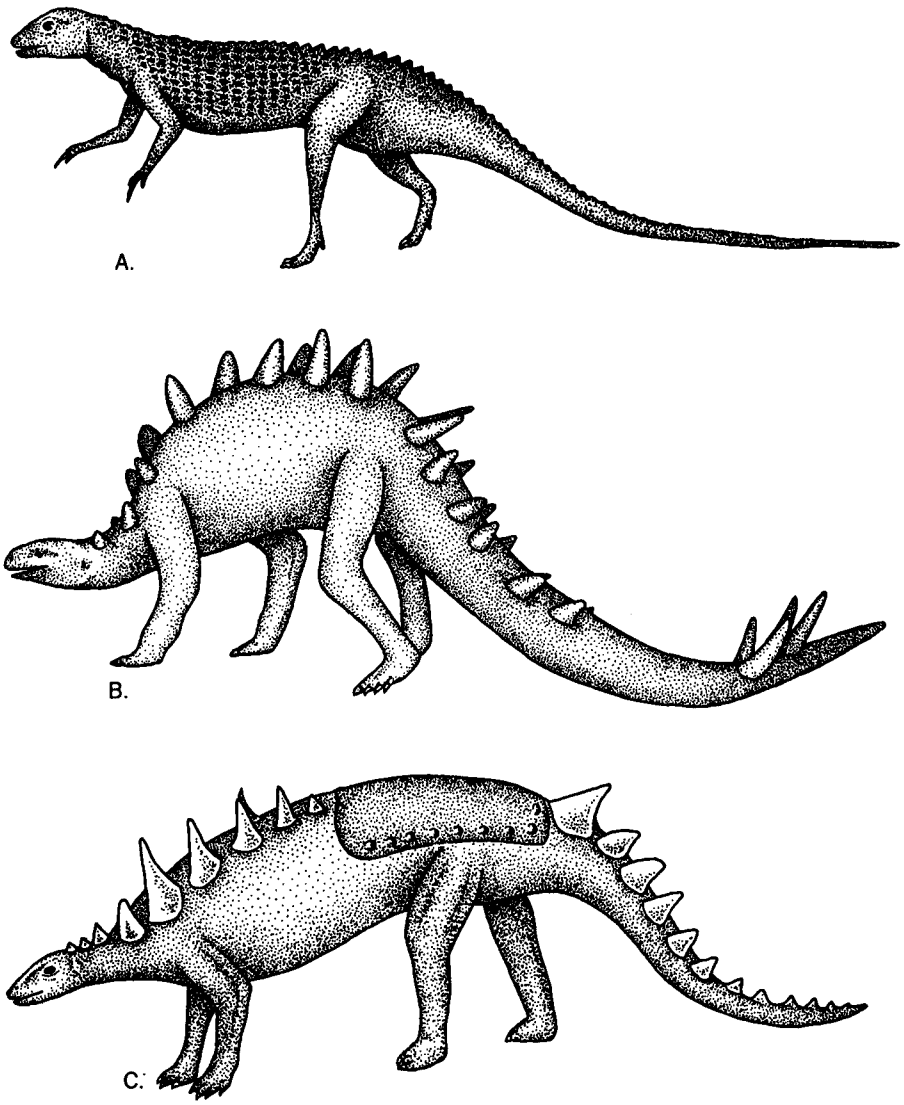


Figure 11-22 Armored dinosaurs. A. The small Lower Jurassic genus *Scutellosaurus* from North America. As in many primitive ornithopods, the rear limbs are much longer than the front limbs. Small armor plates cover the trunk region and extend down the tail. Some thecodonts and crocodiles show a similar pattern of armor. B. *Huayangosaurus*, a stegosaur from the Middle Jurassic of China. C. *Polacanthus*, a primitive ankylosaur from the Lower Cretaceous of England.

FLYING REPTILES—THE PTEROSAURS

During the Mesozoic, archosaurs were dominant not only on land but also in the air. Two groups of archosaurs became highly adapted for flight: the pterosaurs, and the ancestors of birds. These two groups evolved from different ancestors, at different times, and show different flight apparatus, but both share with dinosaurs a fully upright posture of the rear limbs, and required a high metabolic rate for active flight.

Pterosaurs differed from birds in having membraneous wings like bats rather than feathers, but unlike bats, only a single finger, the fourth, supports the membrane (13). The first three fingers retained their primitive proportions and claws. The pterosaur wing is narrow and attached to the trunk at the base of the rear limb. Early reconstructions suggested a sprawling, awkward posture, but Kevin Padian argued that the rear limbs were held vertically and moved in a fore and aft direction, as in birds (14).

Pterosaurs evolved from advanced bipedal thecodonts, near the base of the dinosaur radiation. Kevin Padian suggested that their closest relationship may be with *Scleromochlus*, a tiny thecodont of the Late Triassic. Pterosaurs were common throughout the Jurassic and Cretaceous, and recently discovered fossils show that they were al-

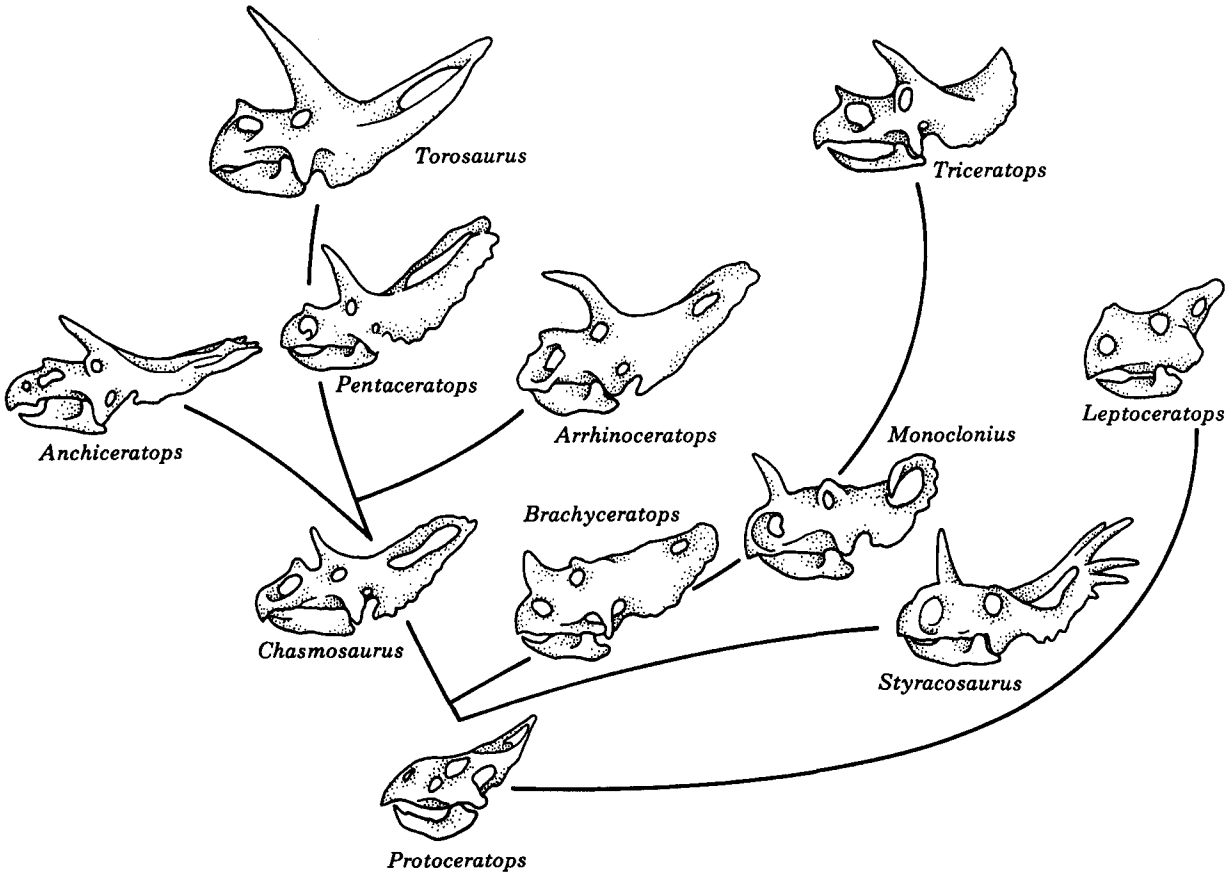


Figure 11-23 Skulls of ceratopsian dinosaurs showing a variety of patterns of horns. The bony frill extending over the neck served for the origin of jaw muscles, provided protection, and perhaps served for sexual display. (From J. H. Ostrom. Courtesy of *Discovery*, (Yale Peabody Mus. Nat. Hist.) 1(2).)

ready highly evolved in the Late Triassic (Fig. 11–24). Triassic pterosaurs were primitive in the proportionately short wings, but all the basic characters of the order were fully evident.

Pterosaurs are divided into two major groups. The primitive rhamphorhynchoids, restricted to the Late Triassic and Jurassic, and the pterodactyloids, from the Late Jurassic and Cretaceous. The rhamphorhynchoids had long tails, stiffened by ossified tendons. The skull was large, but had an open structure, with thin struts of bone between the openings for the eyes, nose, and jaw muscles. Elongate teeth were retained from the thecodonts.

Pterodactyloids had much shorter tails, as do modern birds, which provided for greater maneuverability. The teeth were reduced or lost, and the girdles were rigidly attached to the trunk.

Pterosaurs ranged in size from that of a sparrow to *Quetzalcoatlus*, with a wing span of 11 to 12 meters and an estimated weight of 65 kg (15). The remains of most pterosaurs are found in marine deposits. At Solnhofen, in the Upper Jurassic of southern Germany, the fine-grained limestone preserves impressions of the wing membranes. Because the pterosaurs are classified as reptiles, most of which have a low metabolic rate, they were thought to have been poor flyers, relying on gliding rather than active flapping flight. However, the structure of the skeleton is very similar to that of birds in many features associated with active flight including the relatively large size of the brain (indicated by endocasts), the presence of a sternum (or breastbone) for attachment of flight muscles, pneumatic foramina for the extension of air sacs into the bones, and the strong integration of the limb girdles and vertebrae. These structures would not be necessary if pterosaurs did not have flight capabilities comparable to those of birds.

Five families of rhamphorhynchoids and five families of pterodactyloids are recognized. The rhamphorhynchoids became extinct during a short period of time during the Late Jurassic, possibly as

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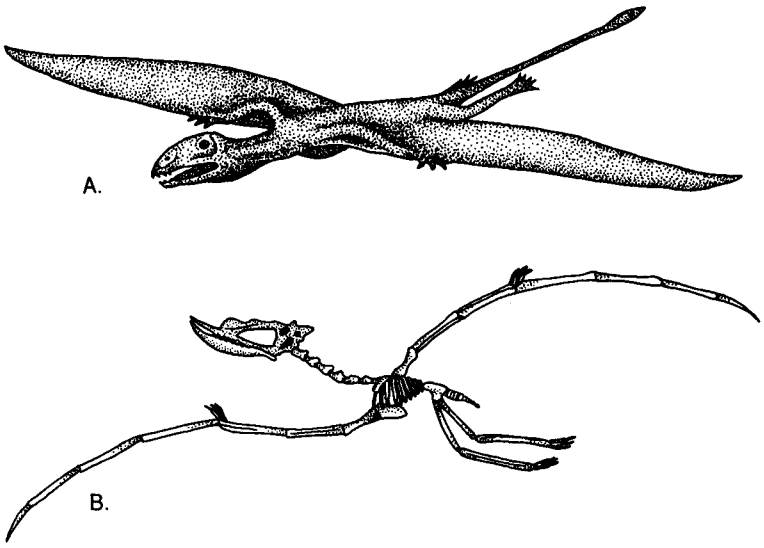

Figure 11-24 Pterosaurs. A. The Upper Triassis rhamphorhynchoid *Eudimorphodon*. B. The pterodactyloid *Dsungaripterus*, which had a wing span of 3 m. The long tail, characteristic of rhamphorhynchoids has been much reduced. (A: Courtesy of Rupert Wild. B: Modified from Dong Zhiming, *Dinosaurs from China*.)

a result of competition with their own descendants, the pterodactyloids. The pterodactyloid families became extinct gradually during the Cretaceous, but three genera, the widespread *Pteranodon* and *Nyctosaurus* and the rare *Quetzalcoatlus*, continued to the end of the Mesozoic.

AQUATIC REPTILES OF THE MESOZOIC

During the time of the dinosaurs, other groups of reptiles dominated the sea. Only a single group of amphibians, the Lower Triassic trematosaurs, managed to adapt to the marine environment. Most amphibians have such permeable skin that they would immediately lose their body fluids by osmosis if they lived in salt water. As a result of evolving a thick, more nearly impermeable skin, the reptiles were able to adapt to life in the sea. From the Late Permian on, group after group of reptiles adapted to life in an aquatic environment. The first known marine reptiles were the mesosaurs of the Middle to Late Permian (Fig. 11–25). Their remains are known from shallow marine deposits in what is now western Africa and eastern South America. Long before the idea of continental drift was accepted by geologists, this distribution suggested that these land masses might have been juxtaposed in the Late Paleozoic. Mesosaurs lack any temporal openings and apparently evolved from the ancestral reptilian stock. They are not related to any other groups of marine reptiles.

Ichthyosaurs:

The most highly specialized of all aquatic reptiles were the ichthyosaurs. They first appeared in Lower Triassic beds of China, Japan, North America, and Spitzbergen. The body was already fusiform to facilitate aquatic locomotion, but the limbs retained the elements of primitive terrestrial reptiles (Fig. 11–26). The skulls of all ichthyosaurs differ from those of other early reptiles in the great size of the quadratojugal (a cheek bone that is much reduced in other groups) and the elongation of the snout. They have an upper temporal opening like those of diapsids but lack a lateral opening. Both their origin and the length of time required for the early stages of aquatic adaptation remain unknown. During the Triassic, ichthyosaurs underwent an adaptative radiation characterized by the evolution of a variety of patterns of the limbs and body proportions. The anatomy and interrelationships of the Triassic families remain poorly known.

Fossils from the Early Jurassic show the beginning of a second radiation based on a more sophisticated pattern of locomotion. The Triassic ichthyosaurs typically had long fusiform bodies, as do moderately fast-swimming modern fish in which the propulsive force is produced by undulation of both the trunk and tail. Jurassic and Cretaceous ichthyosaurs, in contrast, have shorter, spindle-shaped bodies, and symmetrical, lunate tails similar to those of the fastest swimming of modern bony fish, including the tuna, swordfish, and marlin. This body form indicates that Jurassic and Cretaceous

Chapter 12

Cenozoic Vertebrates

The fossil record of all vertebrates groups is much more complete in the Cenozoic than in the Mesozoic or Paleozoic. The mode of life of fossil genera is also much easier to establish since most belong to living families.

The major groups of cartilaginous and bony fishes persisted from the late Mesozoic and the teleosts continued their extraordinary radiation. Even in the Cenozoic, the fossil record of amphibians is very incomplete, with only a small percentage of living species being recognized. Most of the families that are living today had probably originated by the late Mesozoic, and only a small number of families known from the early Cenozoic have become extinct.

Except for the dinosaurs, pterosaurs, and large marine reptiles, the major reptilian groups that were present in the Late Mesozoic have persisted into the Cenozoic, although the ranges of most families have been restricted as a result of the progressive cooling of the climate. Snakes underwent a major radiation in the later Cenozoic. The modern bird orders originated in the Late Cretaceous and Paleogene. Modern families and genera are known from the early Neogene.

We think of the Cenozoic as the age of mammals, for they are certainly the most conspicuous terrestrial vertebrates. Like the reptiles of the Mesozoic, mammals also radiated extensively in aquatic environments, and the bats achieved flight.

CENOZOIC MAMMALS

Although placental and marsupial mammals are known primarily from the Cenozoic, the first stages in the differentiation of the modern groups began in the late Mesozoic. Marsupials and placentals had diverged from primitive therian mammals by the Early Cretaceous, and both groups had begun to radiate by the end of the Cretaceous.

Upper Cretaceous marsupials and placentals can be readily differentiated by their teeth, which provide the most consistent fossil record. Both had five upper and four lower incisors on each side. The numbers of the remaining teeth are the same in the upper and lower jaws. Both groups had a single canine on each side, but the marsupials had three premolars and four molars, while the placentals had four (primitively five) premolars and three molars. (The last premolar of placentals may be homologous with the first molar of marsupials.) All but the molar teeth are replaced in placentals, but

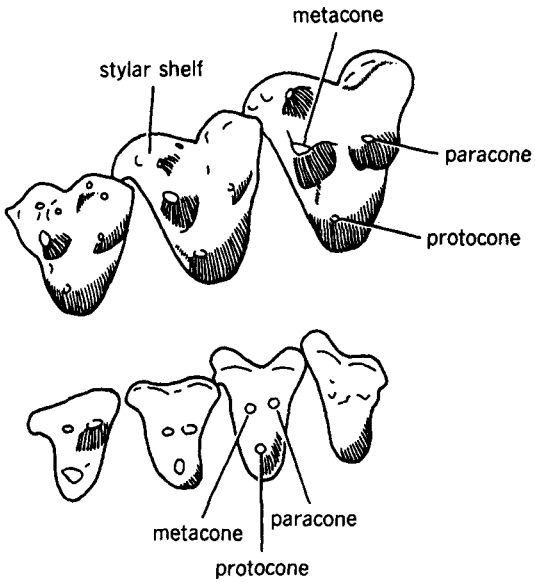

Figure 12-1 Teeth of marsupials and placentals. A. The three upper molar teeth of the Upper Cretaceous marsupial *Alphadon*. The area lateral to the paracone and metacone is wider than in placental mammals and may bear several small cusps. B. The four molar teeth of the Upper Cretaceous placental *Procerberus*.

only the third premolar is replaced in marsupials. The number of each type of tooth is typically written as a fraction (the tooth formula):

$$\frac{5}{4}\,\frac{1}{1}\,\frac{4(5)}{4(5)}\,\frac{3}{3} \text{ for placentals}$$

$$\text{and } \frac{5}{4}\,\frac{1}{1}\,\frac{3}{3}\,\frac{4}{4} \text{ for marsupials.}$$

The morphology of the individual molars can also be used to differentiate the two groups (Fig. 12–1).

By the early part of the Late Cretaceous, many placentals lived in Asia, but marsupials are absent from that fauna. By contrast, both groups inhabited North and South America in the latest Cretaceous. Marsupials radiated extensively in the early Cenozoic in South America, where placentals remained rare and little diversified.

Cenozoic Mammals, Plate Tectonics, and Zoogeography:

Late Mesozoic mammals encountered a world far different from that of their Triassic ancestors. In the early Mesozoic, the continents were still close together and rapid migration throughout the world was possible. The early mammal-like reptiles and even the Late Triassic and Early Jurassic mammals were part of a world fauna that was not separated into major endemic groups. In the late Mesozoic, the breakup of Pangaea was well advanced, and the current outlines of the continental blocks were beginning to be defined (Fig. 12–2). (See Chapter 18 for a more general discussion of biogeography.)

Continental breakup resulted in a regional differentiation of mammalian faunas that was considerably more pronounced than that of the Mesozoic biota. Separation of Pangaea into northern and southern continents had taken place by the Late Jurassic with the spread of the Tethys sea from the Caribbean through the Mediterranean region into the far east (Fig. 18–3). The North Atlantic Ocean began to form from the south about 130 million years ago, and by Late Cretaceous time (70 million years ago), Africa and South America were separating by the formation of the South Atlantic Ocean. Separation of Europe from North America was not complete in the north until late in the Eocene. South America and Antarctica were separated from one another by 35 million years ago, and Antarctica and Australia separated approximately 38 million years ago (1). North and South America were separated from sometime in the Late Cretaceous until the end of the Pliocene, approximately 3 million years ago. Africa retained some connection with Europe and Asia, but was apparently isolated to a degree from the beginning of the Cenozoic until the end of the early Miocene when a broad contact was made via the Arabian peninsula.

According to Malcolm McKenna (2), the Bering land bridge provided a broad connection between western North America and Eastern Asia from the Late Cretaceous throughout much of the Cenozoic, but it was at such a high latitude, even closer to the North Pole than today, that it was of limited use as a means of migration between the continents.

Eastern Asia was further isolated from the remainder of the world in the early Cenozoic because the Turgai Strait connected the Arctic Ocean in the north with the Tethys Sea to the south. As a result, an important endemic fauna developed in southeastern Asia, which remained in isolation until the end of the Eocene, at which time the marine barrier closed and mammals spread into North America and Europe. Europe and North America were close

Figure 12-2 Continental positions in the Late Cretaceous and early Cenozoic.

to one another in the early Cenozoic, and migration around the northern Atlantic was possible but intermittent (3).

The evolution of therian mammals was strongly influenced by the varying degrees of isolation of South America, Africa, Australia, and eastern Asia during the early Cenozoic.

MARSUPIALS

Mammalian evolution progressed in isolation in South America and Australia for most of the Cenozoic (Fig. 12–3). Both continents had a diverse marsupial fauna throughout this time—entirely without competition from placentals in Australia and with only limited interaction with placentals in South America.

There was marked evolutionary convergence between the marsupials in South America and Australia and the placentals in the other continents. This is most notable among the carnivorous forms including the wolverinelike Tasmanian devil and Tasmanian wolf in Australia and the cat, dog, and bearlike borhyaenids in South America.

There is continuing debate as to the specific nature of the relationships of the South American and Australian fauna because of the absence of any marsupials older than late Oligocene (about 28 million years ago) in the fossil record of Australia. By contrast, marsupials are known in Upper Cretaceous rocks of South America, and many genera have been described from upper Paleocene and lower Eocene beds.

Ten families of Cenozoic marsupials have been recognized from South America. They include 17 living genera and another 76 fossil genera. The Didelphidae, represented by the living opossum (a Pleistocene immigrant to North America), retain many primitive features of their Cretaceous ancestors. They are generally small, but some reach the size of a domestic cat. Most are arboreal and many are insectivorous. Twelve genera are known from Paleocene beds. These early forms may include the ancestors of all the other South American marsupials.

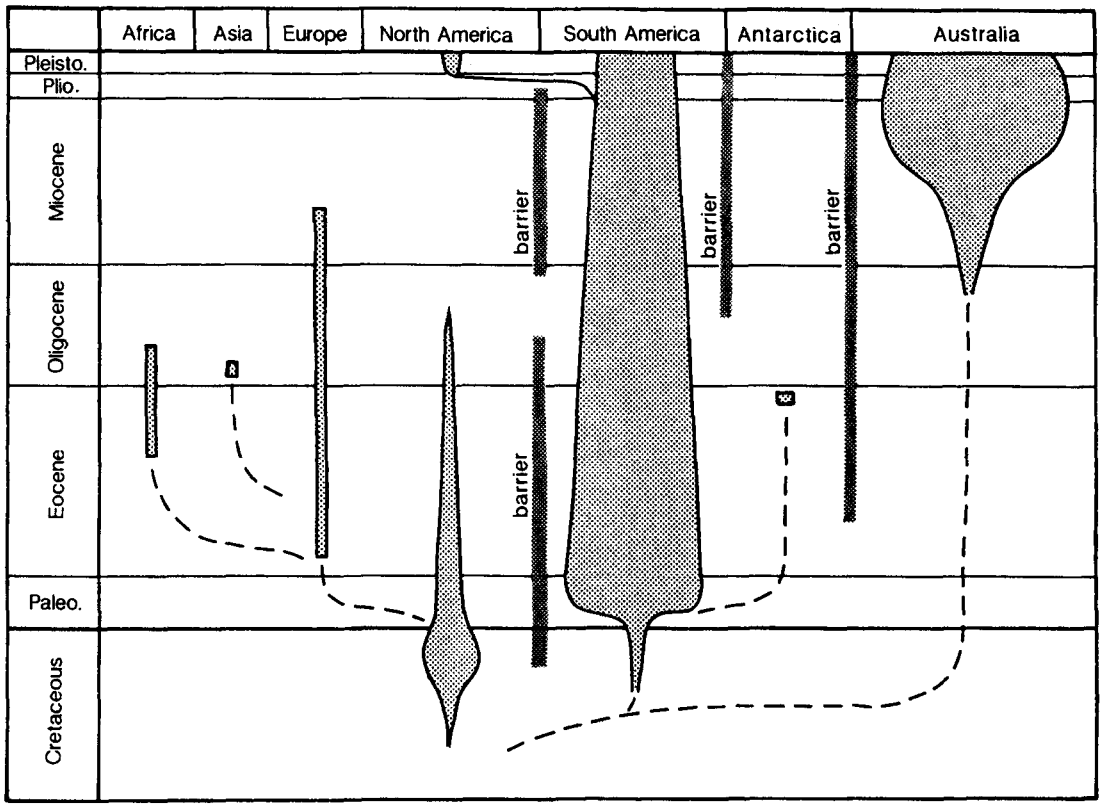

Figure 12-3 Major barriers affecting the distribution of marsupials during the Late Cretaceous and Cenozoic. (Data from A. O. Woodburne & W. J. Zinsmeister, *Journal of Paleontology*, v. 58(4).)

Infraclass—Metatheria
- Order—Marsupialia
  - (New World marsupials)
    - Suborder—Didelphoidea
    - Suborder—Caenolestoidea
  - (Australasian marsupials)
    - Suborder—Dasyuroidea
    - Suborder—Perameloidea (bandicoots)
    - Suborder—Diprotodonta
      - Superfamily—Phalangeroidea
      - Superfamily—Phascolarctoidea (koalas)
      - Superfamily—Vombatoidea

The Microbiotheriidae are known from only two, mouselike genera, one from the upper Oligocene and lower Miocene, and the other from the recent, that are characterized by a very large auditory bulla (a bony capsule surrounding the middle ear ossicles), and a foot structure resembling that of Australian marsupials. The Caenolestoidea are a large group of mouse and shrewlike forms, most common in the lower Miocene, but represented by three genera in the modern fauna. The first lower molar tooth is enlarged and bladelike, resembling the anterior premolar of multituberculates. The polydolopoids have a similar dentition, but with the last premolar modified as a shearing blade. Polydolo-

poids extend from the Paleocene into the Early Oligocene. The Eocene genus *Antarctodolops* is the only marsupial known from Antarctica.

The Oligocene to Pliocene family Argyrolagidae resemble the jumping mice in their body proportions and limb structure (Fig. 12–4). The Borhyaenidae and Thylacosmilidae evolved in convergence with placental dogs, bears, and saber-toothed "tigers." These families became extinct in the late Pliocene at the time placental carnivores reached South America from the north.

Recent analysis does not support earlier claims that one or more of the families of advanced South American marsupials had special affinities with others in Australia (4). The only phylogenetic connection that can be substantiated is between the base of the didelphid assemblage and the base of the Australian radiation.

The fossil record of marsupials in Australia began in late Oligocene, much later than that in South America, and long after their initial diversification. About 16 families are recognized in Australia. Most appear in the early Miocene and many of the early fossils resemble modern genera.

The Australian dasyuroids occupy an adaptive and phylogenetic position similar to that of the didelphoids in South America. They are generally primitive in their anatomy and include a range of mouse to cat-sized insectivores and carnivores. The Dasyuridae include the Tasmanian devil and many smaller genera. The Tasmanian wolf, which became extinct in the 1930s, is placed in the related family Thylacinidae. Its relatives first appeared in Miocene beds.

All other Australian marsupials are united by a peculiar specialization of the rear foot, termed syndactyly, in which the second and third digits are greatly reduced and united in a single sheath of tissue. The specialized digits are used for grooming. Two major groups of syndactylous marsupials are recognized: the Perameloidea, including only the rabbitlike bandicoots, and the much more diverse Diprotodontoidea. Among the living diprotodont families, the koalas, wombats, phalangerids, kangaroos, and gliding and pygmy possums can all be traced back to the Miocene. The Wynyardidae, from the early Miocene, combines primitive characters of phalangerids, kangaroos and wombats. Primitive kangaroos appear in the mid-Miocene, but the modern kangaroos and wallabies underwent a major radiation in the Pliocene, possibly associated with the spread of grasslands.

Some of the most interesting Australian marsupials are known only as fossils and have no similar modern representatives. Among the most enigmatic are the thylacoleonids (Miocene to Pleistocene). They are large relatives of the phalangerids in which the incisors are in the form of large canine teeth, and the last premolars form huge, slashing blades (Fig. 12–5). The skull appears superficially

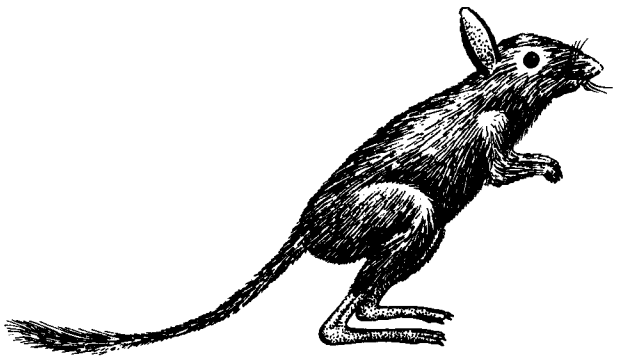

Figure 12-4 Restoration of the rat-sized jumping marsupial *Argyrolagus* from the Pliocene of Argentina.

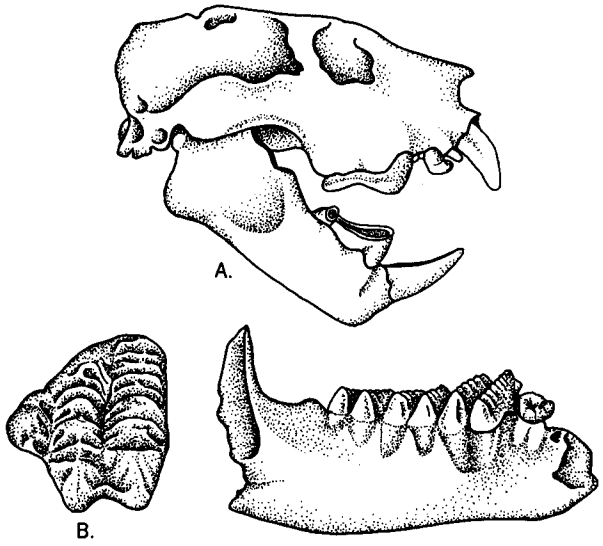

Figure 12-5 Australian marsupials. A. Skull of *Thylacoleo*, a large phalangeroid with a shearing dentition superficially resembling that of carnivorous placental mammals, B. Upper molar and lower jaw of *Ektopodon*. Little else is known of this genus which is classified among the phalangeroids. (A: from M. E. Finch & L. Freedman, *Carnivorous Marsupials*, M. Archer (ed.), pp. 553–561. B: From N. S. Pledge, *Univ. Calif. Publ. Geol. Sci.*, 131. Courtesy of University of California Press © 1986 The Regents of the University of California.)

like that of a carnivore, but most phalangeroids are herbivores. The skeleton is the size of a leopard and shows arboreal adaptations, suggesting a similar predatory habit.

The Ektopodontidae (middle Miocene to Pliocene) includes three genera known primarily from their dentition. The molar teeth are extremely bizarre. They are greatly expanded transversely and marked by numerous closely placed ridges (Fig. 12–5B). They were initially thought to be related to the living monotremes, but additional material suggests affinities with the phalangerids, although no other marsupial has similar teeth.

The largest marsupials were the diprotodonts (late Oligocene to Pleistocene), some of which reached the size of a hippopotamus. The dentition and skull shape vaguely resemble those of large grazing placental mammals. Their closest affinities lie with the wombats.

Primitive, didelphoid marsupials spread from North America into Europe, Asia, and North Africa in the early Cenozoic but all of these lineages became extinct before the end of the Miocene without further diversification. These continents were the major areas for the diversification of the placentals.

PLACENTAL MAMMALS

Placental Reproduction:

In most features of anatomy and physiology, marsupials and placentals resemble one another closely, and they have adapted to similar ways of life. In their reproduction, however, they are clearly distinct. Although no marsupial lays eggs, the young are born at an immature stage of development equivalent to that of monotremes. The young of the giant kangaroo weighs less than a gram at birth and must complete most of its development in the pouch. Small placental mammals such as shrews and small rodents also give birth to incompletely developed, blind, and hairless young, but most newly born placentals are much more advanced; the young of large placental mammals are typically able to feed and move about by themselves soon after birth.

The short gestation period of monotremes and marsupials may be related to the incompatability of tissue between the fetus and the mother. Since the fetus combines the genetic information of the father and the mother, the mother would be expected to reject fetal proteins, much as we reject transplanted organs. Rejection is not a problem in the many lizards and snakes that give birth to live young because of the lower degree of sophistication of their immune systems. Placental mammals have evolved a special embryonic tissue, the trophoblast, that forms a protective barrier between the fetus and the mother so that a rejection reaction does not occur.

Jason Lillegraven (5) points out that both the time necessary for complete development and the metabolic cost of maturation are greater for marsupials than for placentals of comparable size. Rapid maturation would give placentals a selective advantage in most environments and may explain the much greater success of placentals in the modern fauna.

Cretaceous Placentals:

The oldest placentals have been found in the Upper Cretaceous of Mongolia (Fig. 12–6). Complete skulls and much of the postcranial skeleton are known of the genera *Zalambdalestes, Barunlestes, Asioryctes,* and *Kennalestes*. They share primitive features with the most primitive living placentals, the Insectivora, and may have resembled shrews in their general appearance and way of life. The long rear limbs and feet of *Zalambdolestes* suggest that this genus hopped like modern jumping mice, but *Asioryctes* has more normal limb proportions. These early placentals lacked the specializations that characterize all the modern families belonging to the order Insectivora, and they are also excluded from all the other living orders.

Many additional species of early placentals have been found in the latest Cretaceous rocks of western North America, but most are represented by little more than jaws and teeth. These scant remains demonstrate the first stages in the radiation of the Cenozoic placental orders (Fig. 12–7). Among the fossils known from the latest Cretaceous are primates, insectivores, and ungulates (hoofed animals including the common ancestors of horses, elephants, and cattle). The ultimate ancestors of the carnivores and the common ancestors of rodents and rabbits were probably distinct by this time as well.

The precise pattern of the evolution of placental mammals in the Late Cretaceous and early Cenozoic has not been established. By the end of the Paleocene, all of the placental orders had differentiated. The exact sequence of their appearance and the groupings among the orders have not been

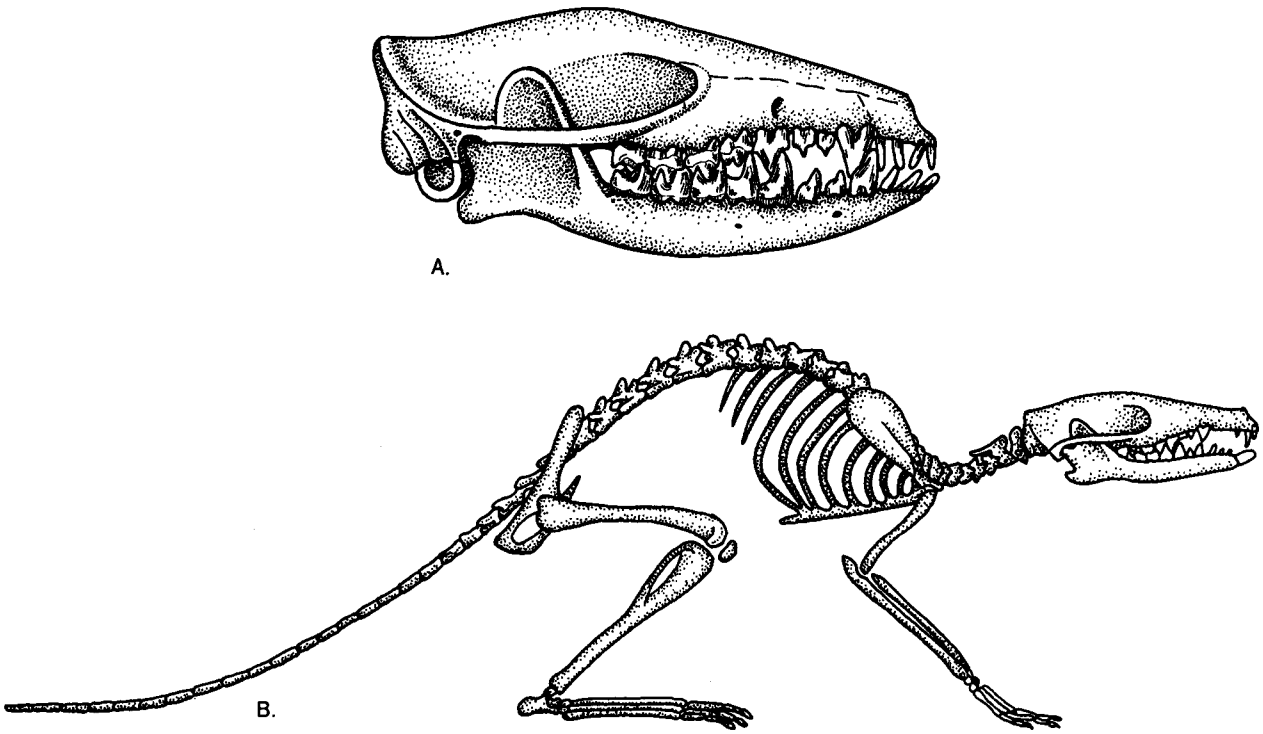

Figure 12-6 Primitive placentals from the Upper Cretaceous of Mongolia. A. Skull of *Kennalestes*, approximately 3 cm long, B. Skeleton of *Zalambdalestes*, approximately 15 cm long. (A: From Z. Kielan-Jaworowska. Courtesy of *La Recherche*, fevrier 1980, p. 152. B: From Z. Kielan-Jaworowska, *Palaeontologia Polonica*, v. 38.)

fully documented. Michael Novacek (6) has attempted a phylogenetic analysis based on a wide range of skeletal characters, but not all groups are securely assigned.

Primitive Cenozoic Mammals:

The most difficult placental mammals to classify are the primitive forms from the Upper Cretaceous of Mongolia and North America, since they cannot be assigned to any of the modern orders but might include the ancestors of all later placentals. They have been placed in a separate order, the Proteutheria. Several other early Cenozoic families are known that are sufficiently specialized to be recognized as distinct orders but show little diversity. They do not share significant derived characters with any of the better-known orders, but appear to share a common ancestry with the most primitive placentals. Some have been included in the order Proteutheria by some authors and treated as separate orders by others. These primitive placentals include the Apatemyidae, the Pantolestidae, the Taeniodonta, the Tillodontia, the Dinocerata, and the Pantodonta.

The dinoceratids (also called uintatheres) and pantodonts are large, archaic herbivores with small brains and short, heavy limbs. The uintatheres were characterized by long canine teeth and bony processes extending from the skull. They were common in Asia and North America from the late Paleocene to the end of the Eocene. Eleven families of pantodonts are known, ranging in age from the Paleocene through the early Oligocene of North America and Asia. *Coryphodon* reached the size of a rhinoceros.

Tillodonts are poorly known forms of large size with feet well adapted for digging and greatly enlarged incisors. They first appeared in the early Paleocene of Asia and ranged into the Eocene of North America and Europe.

The taeniodonts are limited to the lower Paleocene through lower Eocene beds of western North America. They increased from opossum to bear size, and evolved gigantic canine teeth for crushing. All of the teeth grew throughout the life of the animal.

The pantolestids (Paleocene to early Oligocene in North America, extending into the Oligocene in Africa) evolved a dentition and body form resembling those of the sea otter. It is probable that they fed on fish and molluscs. The apatemyids (early

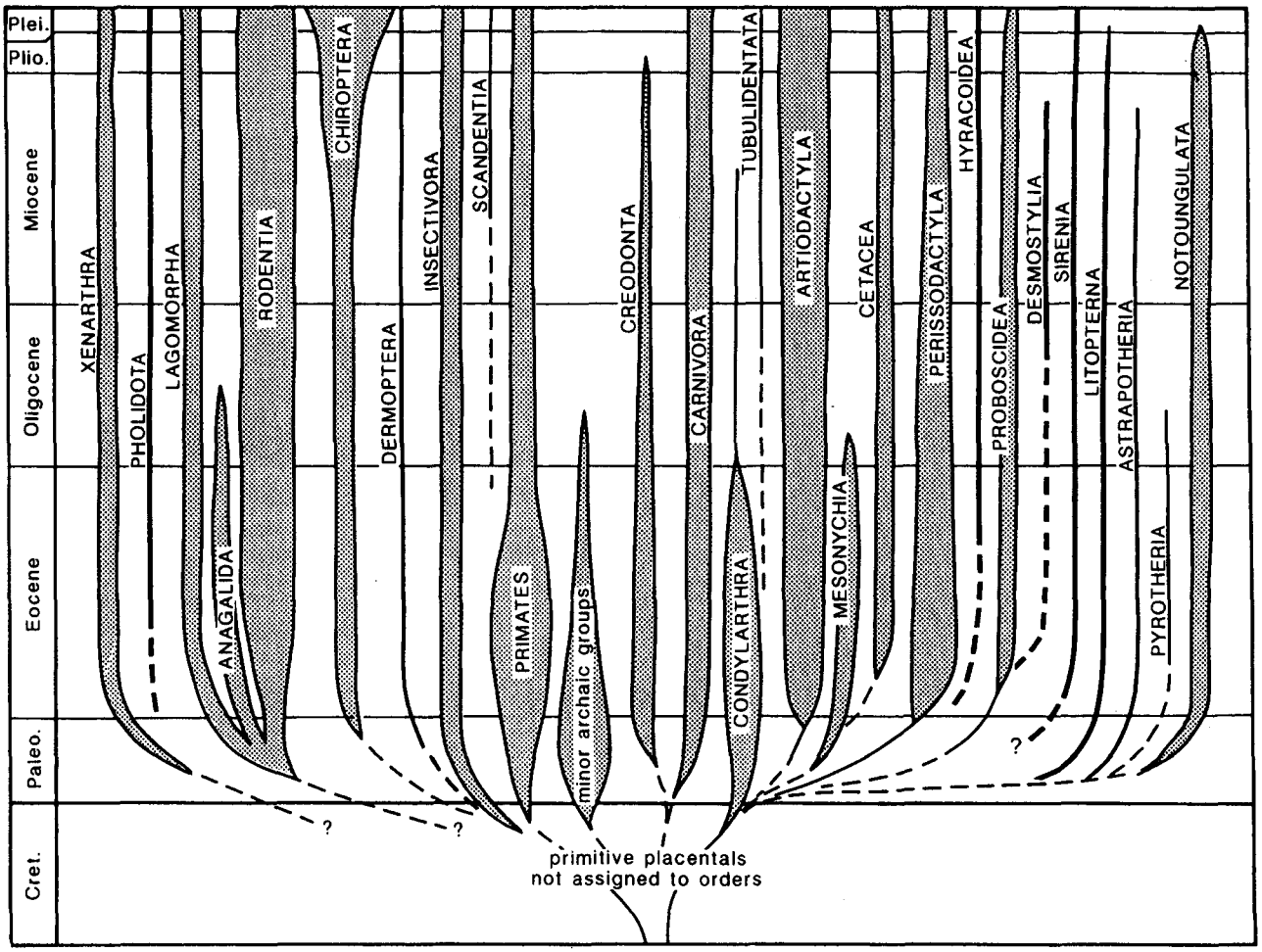

Figure 12-7 Radiation of placental mammals during the Cenozoic.

Paleocene to Oligocene in North America and Europe) had greatly enlarged incisors, suggesting a rodentlike way of life. Nothing has been known of this group except the skull and dentition, but a complete skeleton has recently been found in the mid-Eocene of Europe.

In addition to these archaic and short-lived groups, the ancestors of all the modern placental orders can be recognized in Upper Cretaceous or lower Cenozoic beds.

EDENTATES

Among the most phylogenetically isolated of Cenozoic mammals are an assemblage termed the edentates, which have much reduced or entirely lost their teeth. The edentates include three primarily South American groups: the armadillos, sloths, and anteaters; the Asian and African pangolins; and numerous genera from the early Cenozoic of North America, the Palaeanodontia.

Michael Novacek and Malcolm McKenna (6,7) argued that the edentates were the first group to diverge from the ancestral placental stock because they retain primitive features that are absent in all other placental groups, including an extra bone in the nasal region, the septomaxilla, and primitive aspects of the reproductive system. No fossils of edentates are known from the Cretaceous, and no characters have been recognized that are uniquely shared with any other placental genera that are known to have diverged in the Cretaceous.

Fossils of edentates are known as early as the middle Paleocene in South America, the upper Paleocene in North America and the middle Eocene in Europe. We do not know whether these geographically separated groups shared a common ancestry with one another, or evolved from three separate lineages of primitive placentals. The North American palaeanodonts appear to be the most primitive edentates and, according to Ken Rose (8), share some derived skeletal features with the pantolestids. The aquatic way of life of the pantolestids was, however, far different from the adaptation of the early edentates.

South American Edentates:

The South American edentates, including the living tree sloths, armadillos, and myrmecophagid anteaters, and the extinct ground sloths and glyptodonts, clearly form a natural group united by similar specializations of the pectoral and pelvic girdles and extra articulating surfaces between the vertebrae. The extra or strange (Greek *xenos* = strange) vertebral joints are the basis for the ordinal name of the group, the Xenarthra.

- Edentates
  - Order—Xenarthra
    - Infraorder—Loricata
      - Superfamily—Dasypodoidea (armadillos)
      - Superfamily—Glyptodontoidea
    - Infraorder—Pilosa (sloths)
      - Superfamily—Megalonychoidea
      - Superfamily—Mylodontoidea
      - Superfamily—Megatherioidea
    - Infraorder—Vermilingua (South American anteaters)
  - Order—Palaeanodonta
  - Order—Pholidota

The peculiar nature of the vertebrae and girdles of the xenarthrans may have evolved in relationship to digging. Many members of this group, possibly including the oldest known genera, fed primarily on such insects as ants and termites that are dug from the ground. Unlike primitive insectivorous mammals, the prey are not chewed but swallowed whole, and the teeth are reduced or lost entirely.

The oldest known armadillos are from middle Paleocene deposits. By Eocene time they had already evolved most of the characters by which we recognize the modern members of this group, although the armor was not as well consolidated. From the armadillos evolved the even larger and more heavily armored glyptodonts, which survived into the Pleistocene. Their distinctive teeth are recognized in the middle Eocene. They are thought to have fed on soft vegetation, although they had eight, very long-rooted cheek teeth that grew throughout the life of the animals. Both armadillos and glyptodonts migrated into North America in the Pliocene and Pleistocene (Fig. 12–8).

The sloths apparently evolved from ancestors resembling the early armadillos and some genera have nodules of dermal armor in their skin. Three major groups are recognized. The Mylodontoidea appeared in the early Oligocene. They were bear-sized terrestrial animals. The megalonychoids and megatherioids were common from the early Miocene. The early members were small and show arboreal adaptation. Each of these superfamilies may be ancestral to one of the two modern tree sloth genera. Other members of these two superfamilies became specialized for terrestrial locomotion and achieved large size. The terrestrial megalonychoids and megatherioids reached North America in the late Cenozoic and some genera extended as far north as Alaska. Only the small arboreal genera survive in the modern fauna.

The highly specialized myrmecophagid anteaters appeared in South America as early as the middle Miocene, but an essentially modern genus has been described from the middle Eocene of Europe (9). It is difficult to understand how this group could have migrated from Europe to South America, or vice versa, in the early Cenozoic, and there is some question as to the affinity of the European genus. This genus, *Eurotamandua*, is part of an extraordinary fauna from Messel, Germany, that is preserved in an oil seep. It includes a diverse assemblage of mammals and birds, some including such soft tissues as hair, feathers, and gut contents. Government authorities plan to use the Messel locality for a garbage dump and prevent further collecting.

The scaly pangolins (order Pholidota) are Asian and African anteaters that resemble the South American myrmecophagids in the long tubular shape of the skull and the complete absence of teeth, but lack the specializations of the girdles and vertebrae that typify the South American xenarthrans. Pan-

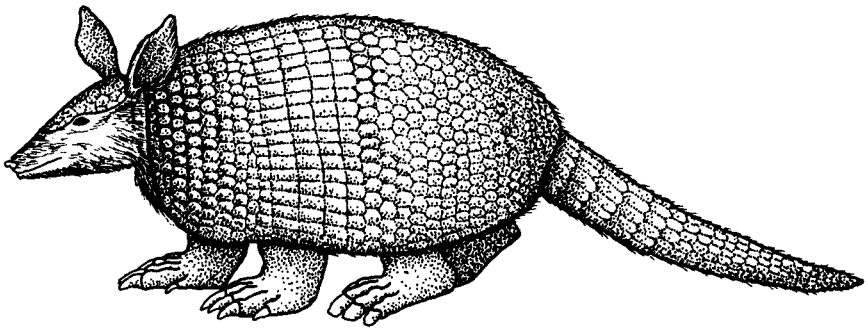

Figure 12-8 The giant armadillo *Holmesina*, approximately 3 meters long, from the late Pleistocene. (From G. Edmund, *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, G. G. Montgomery (ed.), pp. 83–93. Smithsonian Institution Press. © 1985 Smithsonian Institution, Washington, D.C.)

golins are also known from the Messel fauna (Fig. 12–9).

Two families from the early Cenozoic of North America (order Palaeanodonta) have been associated with both the xenarthrans and the Pholidota. The palaeanodonts are archaic forms, showing various degrees of digging specialization (Fig. 12–10). They have reduced but not completely lost their teeth, but they do not show the other skeletal specializations of the South American edentates.

INSECTIVORA

Modern members of the Insectivora have long been thought to be the most primitive living placental mammals on the basis of their small brain size and primitive skeleton. For a time, the concept of this order expanded to include a variety of primitive Late Cretaceous and early Cenozoic genera

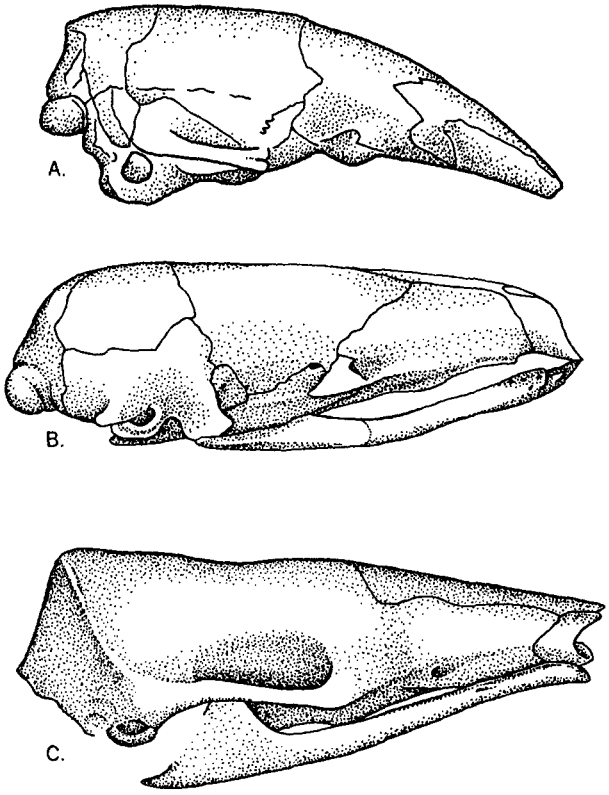

Figure 12-9 Skulls of anteaters. A. *Palaeomyrmedon*, a myrmecophagid from the Pliocene of South America. B. *Manis*, the modern Asian and African pangolin. C. *Eurotamandua*, from the Eocene of Europe. (B & C: From G. Storch, *Senckenbergiana lethaea*, v. 61.)

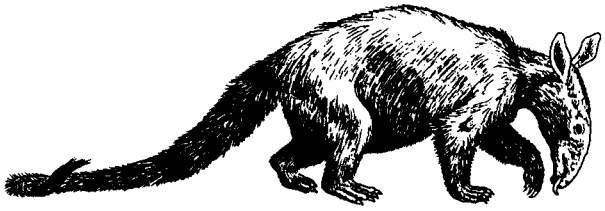

Figure 12-10 Restoration of *Metacheiromys*, a palaeanodont from the Eocene of North America. This genus may be related to the South American, Asian, and African anteaters, or represent a distinct lineage that independently specialized for feeding on subterranean insects. Approximately 1 meter long. (From G. Edmund, *The Evolution and Ecology of Armadillos, Sloths, and Vermilinguas*, G. G. Montgomery (ed.), pp. 83–93. Smithsonian Institution Press. © 1985 Smithsonian Institution, Washington, D.C.)

otherwise placed in the Proteutheria. Shrews, moles, and hedgehogs are now believed to share a common ancestry that is distinct from that of the other orders of Cenozoic placental mammals. Insectivores can be traced back to the latest Cretaceous. The ancestors of the modern families can be recognized by specialized features including the relatively small size of the eye socket, the reduction or loss of the jugal bone of the cheek, pecularities of the base of the skull, and loose attachment of the halves of the pelvic girdle. The oldest members of the group including shrews and moles, the Soricomorpha, are found in Upper Cretaceous rocks. The modern families Soricidae (shrews) and Talpidae (moles) both appear in the late Eocene. Several other extinct families are known from the early Cenozoic. These include the Geolabididae (Eocene to Miocene of North America), Apternodontidae (Eocene to Oligocene of North America), and Nyctitheriidae (Paleocene to Oligocene of North America and Europe).

Order—Insectivora
- Suborder—Erinaceomorpha (hedgehogs)
- Suborder—Soricomorpha
  - Superfamily—Soricoidea (shrews and moles)
- Suborder—Zalambdodonta
  - Superfamily—Tenrecoidea (tenrec)
  - Superfamily—Chrysochloroidea (golden mole)

The hedgehogs (Erinaceomorpha) may be represented as early as the mid-Late Cretaceous by the genus *Paranyctoides*. Its dentition is similar to that of primitive insectivorous placentals except for a blunting of the cusps and a more squared outline of the molars, suggestive of crushing and grinding rather than piercing. The Paleocene to Oligocene Adapisoricidae link *Paranyctoides* with the living erinaceids. The specific origins of other families of living insectivores remain controversial. The Solenodontidae from the Pleistocene and Recent of the West Indies may have evolved from the Apternodontidae or the Geolabidae. The tenrecs and golden moles are known as early as the lower Miocene in Africa, but even the earliest members are distinct from the other major insectivore groups.

BATS

Bats are among the most specialized of mammals in their highly developed flight capabilities and the capacity of most species to use echolocation for capture of prey and navigation in the dark. The fossil record shows that bats had already achieved a nearly modern skeleton by the early Eocene (Fig. 12–11) and the structure of the inner ear of these fossils is similar to modern bats that echolocate (10). No fossils illustrate the early stages in the evolution of their flight. Specializations of the molar teeth in early bats are similar to those of nyctitheriid insectivores which are unfortunately known from no remains other than jaws and teeth. The skeleton of bats probably evolved from those of primitive insectivores, but we have no idea how long this transition may have taken. Fossils of animals that could be the ancestors of bats are known from 8 to 25 million years before the first bats.

Modern bats are divided into two major groups, the megachiropterans or flying foxes, which feed primarily on fruit and do not echolocate, and the primarily insectivorous microchiropterans, which do. These groups probably diverged in the Paleocene. Only two fossils of megachiropterans have been found, one from the Oligocene of Europe and the other from the Miocene of Africa. There are 18 living families of microchiropterans, six of which are represented as fossils as old as the Eocene or early Oligocene. Several living genera appear in the Oligocene.

TREE SHREWS, ELEPHANT SHREWS, AND FLYING LEMURS

Several other groups of generally primitive and little diversified placentals were long thought to be descended from the base of the insectivore lineage, but no unique derived features have been recognized that unite them with the common ancestors of the modern insectivore families. All are now placed in separate orders, whose specific relationships among primitive placentals remain uncertain (11).

The tree shrews are represented by five living genera from southeast Asia that resemble tree squirrels in their general appearance, but most features of the skeleton are close to the pattern of Late Cretaceous or early Paleocene placentals (Fig.

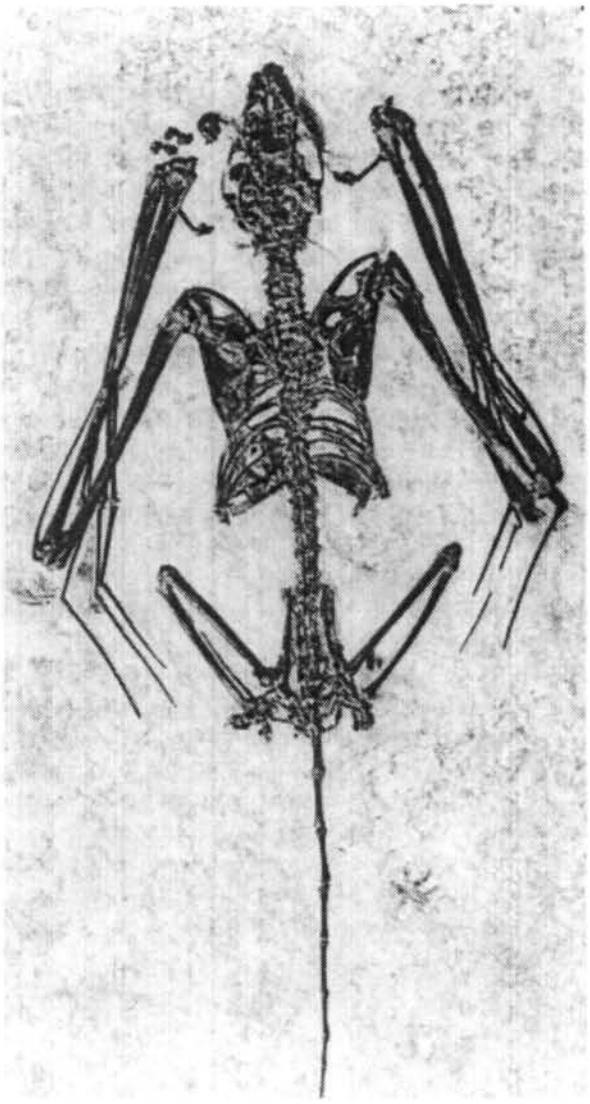

Figure 12-11 Skeleton of the Early Eocene bat *Icdaronycteris*. It is nearly identical to some modern bats. (Photograph courtesy of Dr. John Ostrom and Peabody Museum of Natural History, Yale University.)

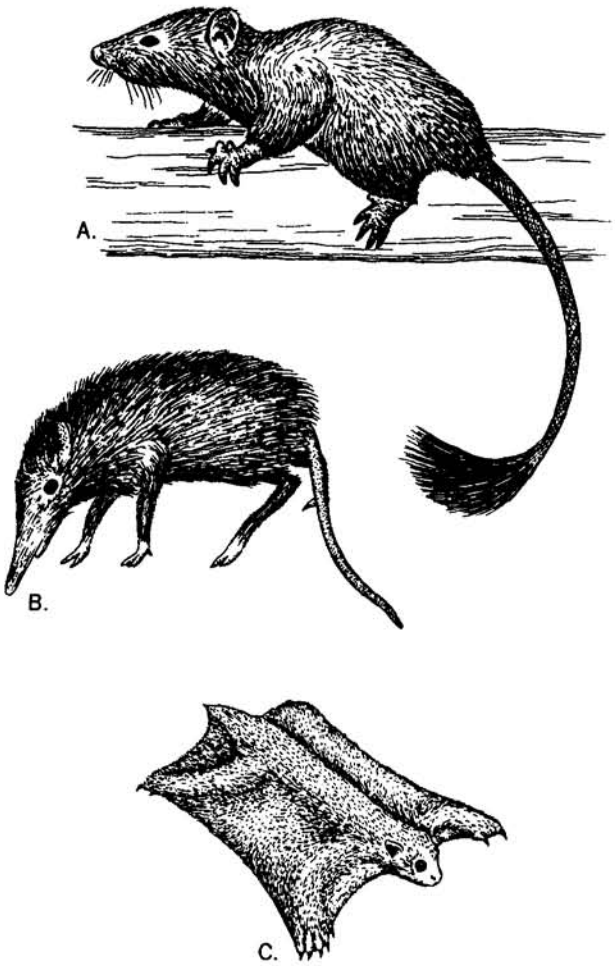

Figure 12-12 Primitive living placental mammals. A. Tree shrew, B. Elephant shrew, C. Flying lemur. All have been hypothesized as being closely related to insectivores, bats and/or primates. All retain primitive characters and cannot be allied with any of the other placental orders. Miocene fossils of tree shrews and elephant shrews resemble modern members of these groups and do not contribute to establishing their relationships. Possible ancestors of the flying lemur are known from the Eocene.

12–12). Features that were long used to suggest affinities with primates are also shared with other early placentals. Fossils of trees shrews have been found in rocks as old as Miocene, but they do not differ significantly from living genera.

The order Dermoptera consists of a single living genus from tropical Asia and Indonesia. The front and hind limbs are very long and support a gliding membrane like that of "flying" squirrels. They feed entirely on plant material and symbiotic bacteria in the caecum break down cellulose. The modern family has no fossil record, but remains from the Paleocene and Eocene assigned to the Plagiomenidae have a very similar dentition. Plagiomenids are especially common in the early Eocene of Ellesmere Island in the Canadian Arctic. Recently discovered cranial remains may make it possible to establish

the origins of this groups and test its relationship to the modern genus (12).

Elephant shrews (order Macroscelidae) have been restricted to Africa throughout their known history. They are small, mouse- to rabbit-sized insectivorous animals that are characterized by a long, flexible snout. The long hind limbs are specialized for hopping. Their fossil record begins in Oligocene beds but does not demonstrate specific affinities with other orders of placental mammals. Similarities of dentition and jaw structure suggest affinities with the lower Cenozoic Asian anagalids (discussed with the rodents), but no intermediate forms are known and their geographical separation suggests that these groups probably evolved independently since the Late Cretaceous.

PRIMATES

Because they include our own genus, *Homo*, primates are the most intensively studied mammalian group. Abundant primitive primates are known in North America and Europe from rocks ranging in age from early Paleocene into early Oligocene. The major modern groups probably originated in the late Eocene, but few of their fossils are known from rocks older than Miocene in age. The lemurs are first represented in Pleistocene rocks. No fossils are known of the living great apes from Africa, the gorilla and chimpanzee.

The irregular distribution of primate fossils in time is due to their habitat and the changing climate of the Cenozoic. Nearly all modern primates live in tropical jungles and forests. Animals living in these environments generally have a poor fossil record because sediments accumulate at a low rate, and organic decay is rapid. Collection of fossils in the tropical areas today is hampered by heavy vegetation and rapid chemical and physical weathering of the exposed sediments. In the early Cenozoic, the tropics were much more extensive than they are today, reaching far into the latitudes that are now temperate in the North. Areas that were tropical in the early Cenozoic but are now within the temperate zone have yielded most of the fossil primates. The end of the Eocene and beginning of the Oligocene was a time of increasing seasonality and decreasing temperatures, greatly restricting the tropical regions. Few primates lived in North America or Europe north of the Mediterranean region after this time.

Fossil primates have not been collected in the early Cenozoic rocks of either South America or Africa. Primates may have entered Africa from Eurasia at an earlier time to account for the very primitive genera that now live in Madagascar, but their fossil record does not begin in Africa until the Lower Oligocene. Primates appear in South America in the Middle Oligocene. Whether they reached there from North America or Africa continues to be disputed (13). South American primates evolved in isolation during the remainder of the Cenozoic.

- Order—Primates
  - Suborder—Plesiadapiformes
  - Suborder—Prosimii
    - Infraorder—Adapiformes
    - Infraorder—Lemuriformes
    - Infraorder—Tarsiiformes
  - Suborder—Anthropoidea
    - Infraorder—Platyrrhini
    - Infraorder—Catarrhini
      - Superfamily—Cercopithecoidea
      - Superfamily—Hominoidea
        - Family—Hylobatidae
        - Family—Pongidae
        - Family—Hominidae

Primates are common in the Paleocene and Eocene beds of the northern continents, and a single tooth has been described from the Upper Cretaceous. It is a lower molar, assigned to the early Paleocene genus *Purgatorius* on the basis of the distinctive pattern of the blunt molar cusps. The dominant Paleocene primates, the plesiadapiforms, are much more primitive than later primates in the structure of the ear region and the pattern of circulation at the base of the skull. Except for primitive features shared with insectivores and tree shrews, the plesiadapiforms show no features that support specific affinities with any group except the most primitive placentals. Most plesiadapiforms are specialized in the large size of the incisors and the presence of a long gap, or diastema, between them and the cheek teeth which gives them a very rodentlike appearance (Fig. 12–13). In these features they differ markedly from later primates. It has been sug-

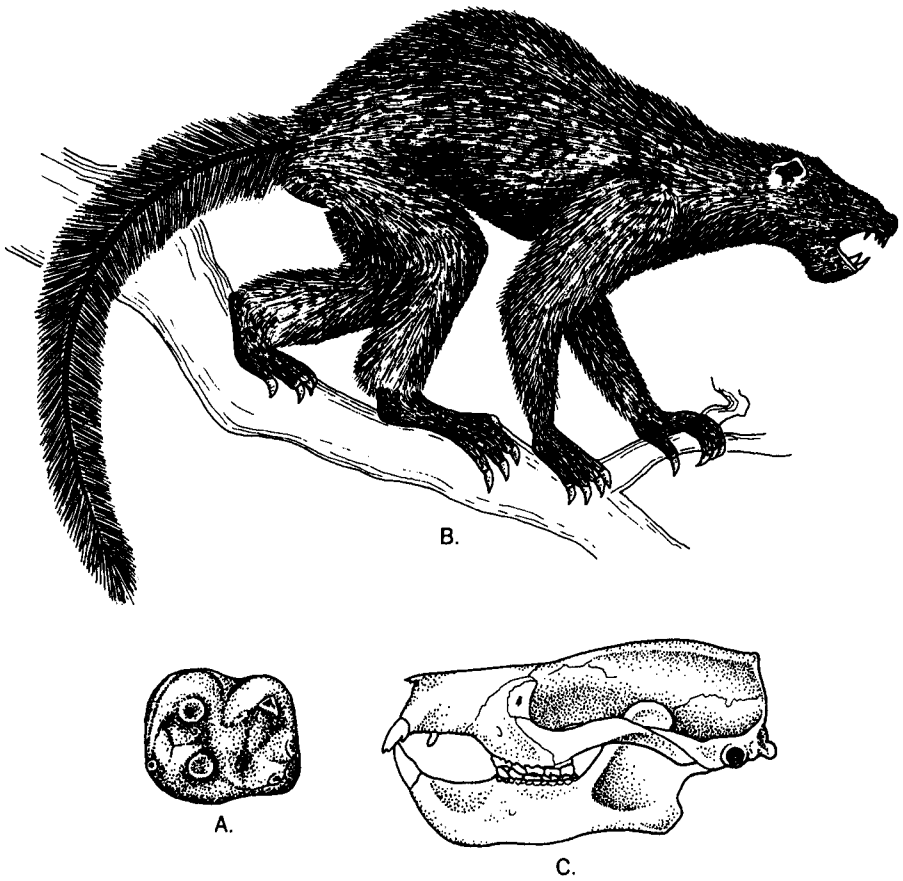

Figure 12-13 Primitive primates. A. Single lower molar tooth of a primate from the Upper Cretaceous, B. Restoration of the Paleocene primate *Plesiadapis*, C. Skull of *Plesiadapis*; the dentition resembles that of rodents in having prominent incisors and a large gap anterior to the molar teeth. (A: From F. S. Szalay & E. Delson, *Evolutionary History of the Primates*. © 1979 Academic Press. C: Courtesy of P. D. Gingerich. Reprinted by permission from *Nature* Vol. 232, p. 566. Copyright © 1971. Macmillan Magazines Ltd.)

gested that rodents evolved from these early primates, but the similarity of the dentition is almost certainly an example of convergence. The radiation of early rodents corresponds in time with the decline of the early, rodentlike primates.

In the early Eocene, two other groups of primates, the Adapidae and the Omomyidae, appeared in the northern continents. Both resembled more advanced primates in the nature of the ear region and the larger size of the brain, and showed features in the postcranial skeleton indicative of arboreal life (Fig. 12–14). The Adapidae were larger forms that broadly resembled the living lemurs and lorisids. Adapids lingered into the Miocene, but no fossils demonstrate the transition to the modern groups. The fossil record of lemurs is limited to a diverse assemblage of Pleistocene and sub-Recent remains from the island of Madagascar. Fossils of lorisids appear first in the Miocene in East Africa.

The omomyids are typically smaller than the adapids and consequently have a relatively larger braincase and a skull that more closely resembles that of advanced modern primates. They most closely resemble the tarsioids whose fossil record is limited to a single jaw from the Oligocene of North Africa.

The tarsioids, lemuroids, and their fossil relatives have been grouped as the Prosimii, and the more advanced primates (monkeys, apes, and man) termed the Anthropoidea. Teeth and jaws from the upper Eocene of Burma may have belonged to ancestors of the anthropoids, but this group is positively identified only from the Oligocene onwards. There is continued debate as to whether their ancestors were closer to the Adapidae or to the Omomyidae.

The anthropoids diversified early in their evolution; the more primitive Platyrrhini (New World monkeys) reached South America in the Oligocene. The remaining members of the Anthropoidea, the Catarrhini, remained restricted to the Old World until our own species evolved in the Pleistocene. The New World monkeys are limited to 16 living genera; eight more are known in the Cenozoic. They are more primitive than Old World Monkeys in the retention of three premolar teeth, and have greatly expanded auditory bullae.

Primitive members of the Catarrhini have been

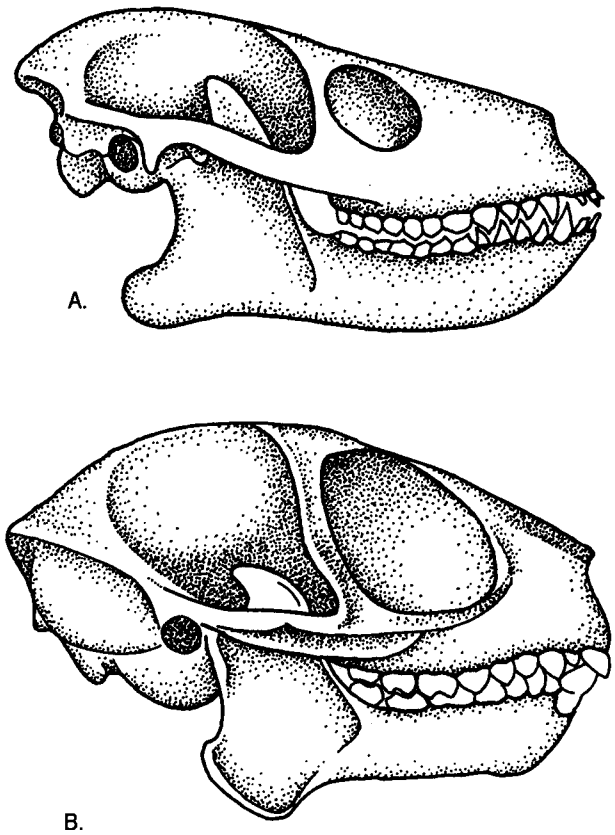

Figure 12-14 Skulls of Paleogene primates. A. The adapid *Notharctus*, B. The omomyid *Necrolemur*. Both the eye and the braincase are relatively larger in *Necrolemur*, but this may be a result of the absolutely smaller size of the skull.

found in lower Oligocene beds of North Africa. These fossils may include the ancestors of both the Old World Monkeys (Cercopithecoidea) and the great apes and man (Hominoidea). The Old World monkeys, which are distinguished by squared molars dominated by four prominant cusps, are not clearly distinct until the Miocene. The Oligocene genera from North Africa may include the specific ancestors of the gibbons (Hylobatidae) which are now restricted to southeast Asia, but this group otherwise has no fossil record before the Pleistocene.

Elwin Simons (14) has argued that the early Oligocene genus *Aegyptopithecus* may be included in the Hominoidea. It lacks the dental specializations of the Old World monkeys, and the postcranial skeleton indicates a quadrupedal, arboreal mode of locomotion. Other members of the Hominoidea are known from the early Miocene of East Africa. *Proconsul* (Fig. 12–15) probably represents the group that gave rise to both the great apes and man. It was a baboon-sized, arboreal quadruped.

In the later Miocene, primitive hominoids radiated within Africa, and in the late Miocene their descendants spread into Europe and Asia. Their Asian descendants, now placed in the genus *Sivapithecus*, are close to the ancestry of the living orangutan, *Pongo*. The contemporary genus *Ramapithecus*, which was once thought to be close to the ancestry of the hominids on the basis of the heavy layer of enamel on the teeth, is now considered to be a member of the genus *Sivapithecus*. The European branch of this radiation is represented by *Dryopithecus*.

The ancestry of our own family, the Hominidae, may stem from a poorly known East African genus *Kenyapithecus* from the mid-Miocene. Unfortunately, the fossil record of hominoids in Africa is essentially nonexistent from 4 to 14 million years ago. There is no fossil record at all for the gorilla or chimpanzee, probably because they were restricted to heavily forested habitats. Hominids appeared 4 million years ago in East Africa. The earliest known species, *Australopithecus afarensis*, is represented by several specimens, including one called "Lucy," which includes most of the skeleton (15). Members of this species were bipedal, as shown

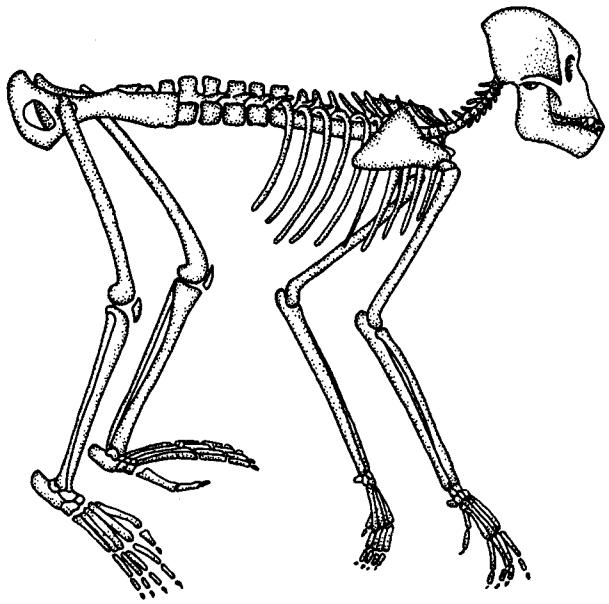

Figure 12-15 Skeleton of *Proconsul* from the Miocene of Africa. This baboon-sized primate may include the ancestors of the chimpanzee, gorilla, and humans.

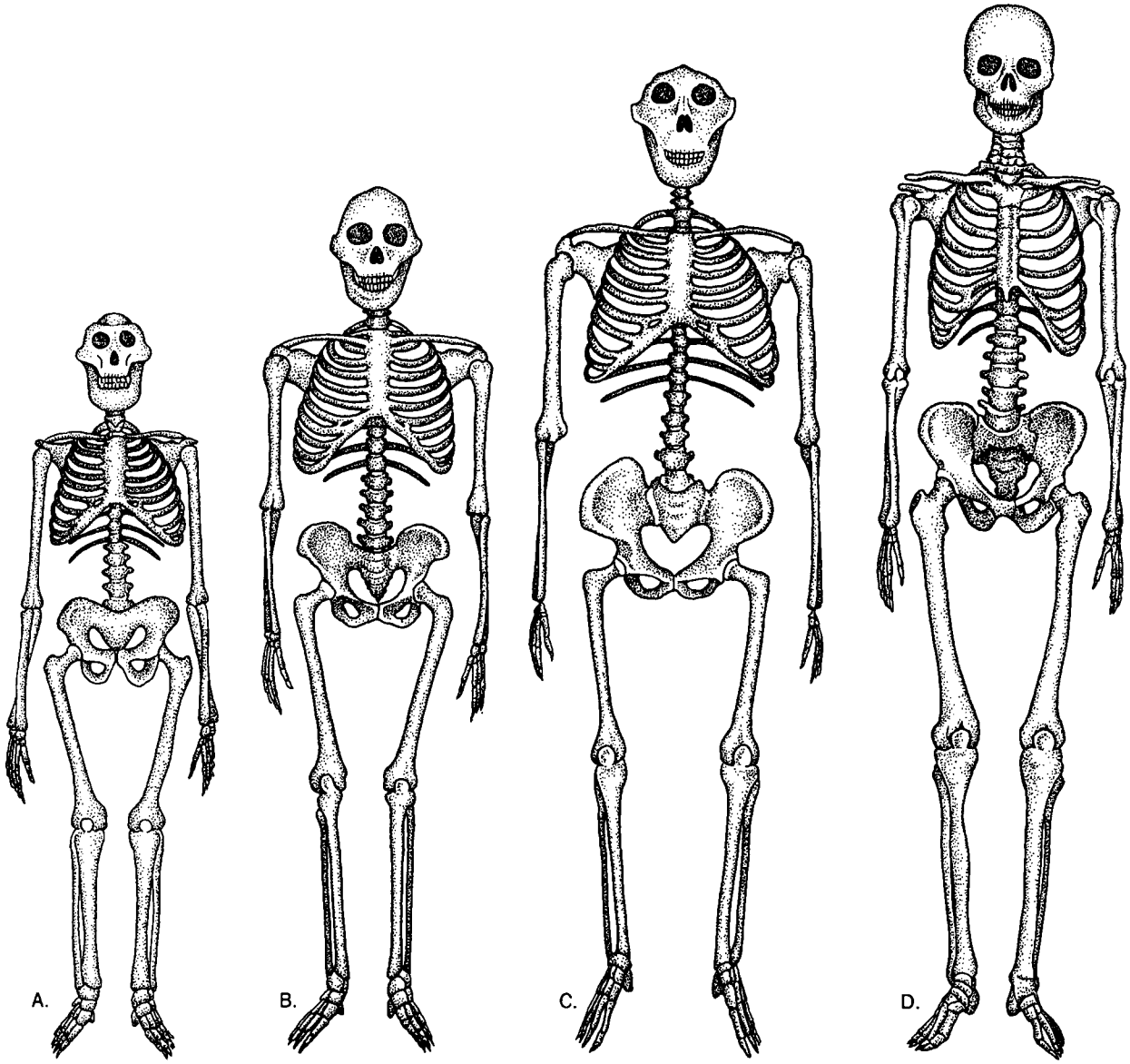

Figure 12-16 Skeletons of hominids. A. *Australopithecus afarensis*, B. *Australopithecus africanus*, C. *Australopithecus robustus*, D. *Homo sapiens*.

by the configuration of the skeleton and by contemporary footprints, although the arms were relatively longer and the legs relatively shorter than in modern humans. The bones of the hands and feet have large processes for the attachment of muscles, which suggests that they retained the capacity for effective arboreal locomotion. The brain size of approximately 500 cc is 20 percent to 30 percent larger than that of a chimpanzee with a similar body weight (25 to 50 kg). Both the front teeth and the molars of *Australopithecus afarensis* are large and apelike, suggesting that this early member of our family fed primarily on plant material (Fig. 12–16).

Several other species of *Australopithecus* lived during the next 2 million years in Africa, including *A. africanus*, *A. boisei*, and *A. robustus*. The latter two species greatly elaborated the size of the molar teeth and the area of the jaw muscles. Their massive teeth may have been used to break up hard seeds and nuts of plants that were common in the increasingly arid areas in eastern Africa where most of the fossils of early hominids have been found.

The first member of the genus *Homo, H. habilis*, appeared in the fossil record approximately 2 million years ago. The braincase had increased to approximately 700 cc and the tooth row was reduced to give a more human face. The proportions of the limbs, however, remained similar to those of the early australopithicines, with long arms and short legs. The relationship of *Homo* to the australopithicine species remains controversial. What is increasingly clear is that several distinct hominid lineages were present simultaneously in eastern Africa (Fig. 12–17).

Homo habilis was succeeded by *Homo erectus* 1.75 million years ago. *Homo erectus* is conspicuously advanced in the achievement of modern limb proportions, and the cranial capacity has increased to between 850 and 1000 cc. Approximately one million years ago, *Homo erectus* spread out of Africa into Asia. *Homo erectus* apparently gave rise directly to our own species, *Homo sapiens*, approximately 300,000 years ago (Fig. 12–18).

The term "archaic" *Homo sapiens* is applied to members of our species living between 300,000 and 30,000 years ago. The neanderthals are included in this category. They were common in Europe and southwest Asia between 70,000 and 30,000 years ago. They had the cranial capacity of modern humans (1300 cc), but heavier facial features, including brow ridges, and a shorter stature. As in the case of all the hominid species, there is not a clear demarcation between archaic and modern *Homo sapiens*, and populations from different geographical areas evolved at different rates, so that there were significant periods of overlap between forms with ancient and modern morphology. Modern cranial features were evident in some African populations as long as 100,000 years ago, while the more archaic neanderthals remained dominant in central Europe for another 70,000 years.

CARNIVORA

The carnivores—lions, tigers, dogs, hyaenas, and bears—are among the most conspicuous members of the modern mammalian fauna. Surprisingly, this group was one of the last mammalian orders to become diverse in the early Cenozoic.

The teeth of primitive placental mammals were specialized for piercing and breaking up insect cuticle, with sharp cusps and many small shearing surfaces. All primitive placental mammals were small, as are modern shrews and rodents.

With the extinction of carnivorous dinosaurs at the end of the Mesozoic and the emergence of diverse medium and large-sized mammals in the early Paleocene, an adaptive zone for large mammalian carnivores became available. The vast majority of

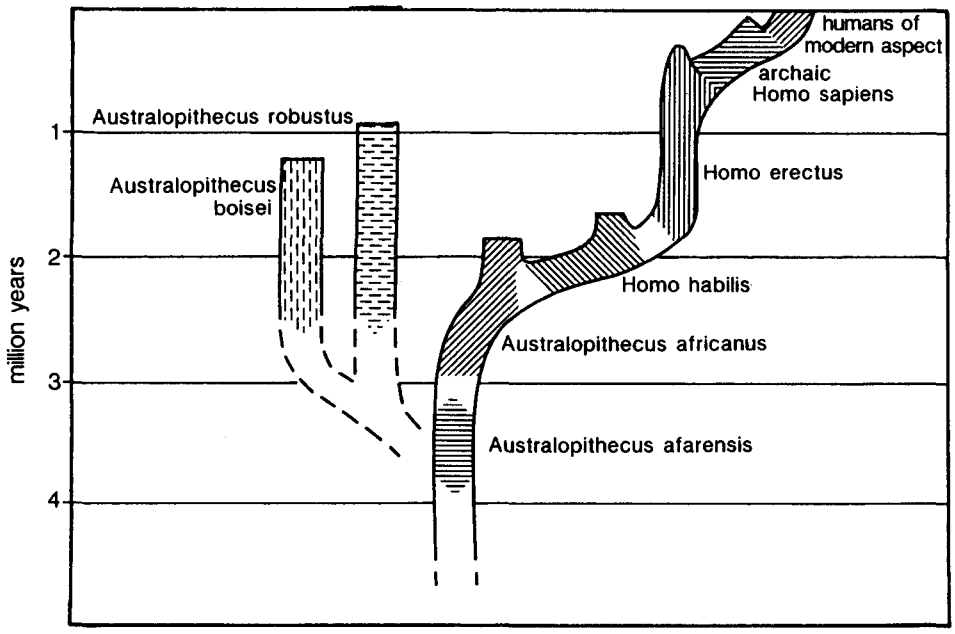

Figure 12-17 Tentative phylogeny of hominids.

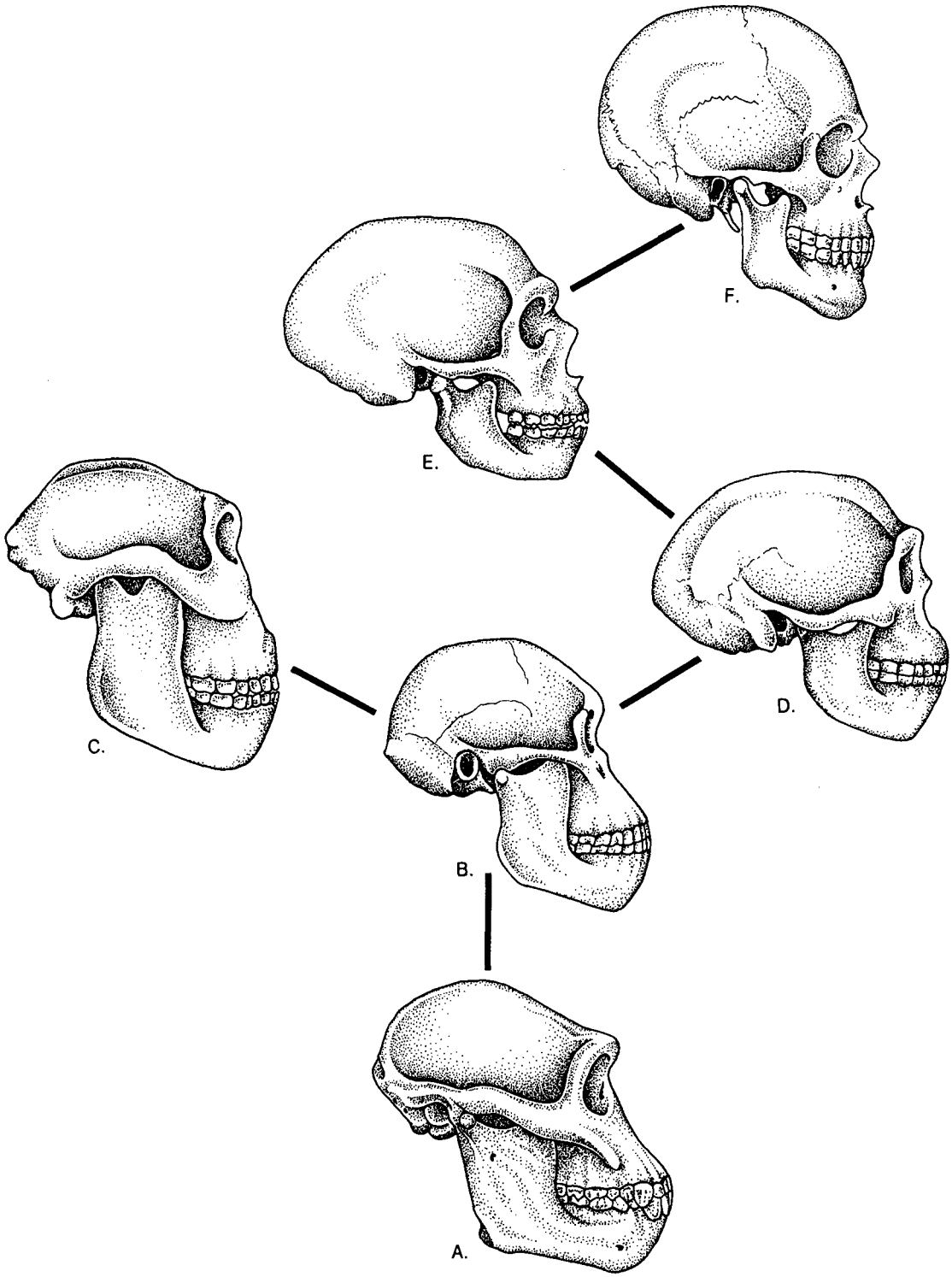

Figure 12-18 Hominid skulls. A. *Australopithecus afarensis*, B. *Australopithecus africanus*. C. *Australopithecus robustus*, D. *Homo erectus*, E. *Homo sapiens* (neanderthal), F. *Homo sapiens* (modern human).

early Cenozoic placentals show specializations of their dentition for a herbivorous diet, and large carnivores remained relatively rare. Gigantic terrestrial birds appear to have occupied a significant portion of the predator adaptive zone during the early Cenozoic of both the northern continents and South America.

Among mammals, feeding on vertebrate prey requires the evolution of teeth with large shearing surfaces to slice through the muscle fibers. This is most effectively achieved through the evolution of bladelike carnassial teeth near the back of the jaw where the muscles can be applied most forcefully (Fig. 12–19). In contrast with the transverse jaw movements of primitive mammals, the jaws of carnivores must move primarily in the vertical plane to give a scissorlike contact between the upper and lower carnassial teeth. Initiation of carnassial teeth required only a slight change from the tooth shape in the primitive insectivorous placentals that are known from the Late Cretaceous.

Two major groups of carnivores diverged from primitive placentals—the order Carnivora, which includes all the modern carnivores, and a second, now extinct assemblage, the Creodonta. The order Carnivora is characterized by the elaboration of the last upper premolar and the first lower molar as carnassial teeth. The creodonts specialized upper molars 1 and/or 2, and lower molars 2 and 3. The posterior position of the carnassial teeth in creodonts presumably provided greater leverage for the jaw muscles than that in the order Carnivora, but the specialization of the posterior molar teeth as shearing blades reduced the area available for grinding and crushing, which may have limited the type of food that they could eat.

Order—Creodonta
Family—Hyaenodontidae
Family—Oxyaenidae
Order—Carnivora
Superfamily—Miacoidea
Superfamily—Aeluroidea
Superfamily—Arctoidea
Superfamily—Otarioidea

The creodonts were never as diverse as the Carnivora. They included only two families, the Oxyaenidae and the Hyaenodontidae, and about 150 genera, compared with 400 genera of Carnivora. The Oxyaenidae, from the Paleocene and Eocene

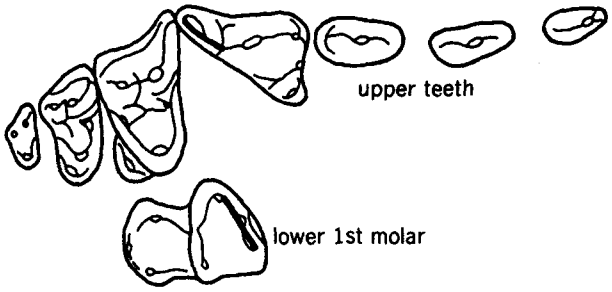

Figure 12-19 Occlusal view of cheek teeth of a primitive member of the order Carnivora. Thick lines emphasize the shearing blades of the carnassial teeth. (Reproduced with permission from R. J. G. Savage and *Palaeontology*, v. 20(2).)

of North America and Eurasia, include primarily medium-sized weasel and catlike forms, but also the bear-sized *Sarkastodon*. Hyaenodontids, which appeared in the late Paleocene and lingered into the late Miocene of Asia and Africa, may be divided into three major groups, the civit and doglike proviverines, the canid and hyaenidlike hyaenodontines, and the Machaeroidinae, which had long canine teeth resembling the saber-toothed cats. The genus *Hyaenodon* is known from North America, Eurasia, and Africa (Fig. 12–20).

The Oxyaenidae retained a primitive, plantigrade posture (walking flat on the soles of their feet), but the Hyaenodontidae were long-limbed with digitigrade posture (walking on their toes). All creodonts remained primitive in the flexible nature of the wrist joint, composed of three separate bones, whereas these bones fused in advanced members of the Carnivora. Creodonts were also primitive in the absence of ossification of the auditory bulla (the tissue that surrounds the ear ossicles).

Although the creodonts were the dominant carnivores in the Paleocene and Eocene, they were largely replaced by the early Oligocene by members of the order Carnivora. The ancestors of the modern carnivores appeared as early as the early Paleocene. The early members were small, weasel-like forms, referred to as miacids.

Two groups are included within the miacids, the Viverravidae, which appeared in the Early Paleocene but were already specialized by the absence of the last molar tooth, and the Miacidae, which appeared in the early Eocene on all the northern continents. The Miacidae may have given rise to all later members of the Carnivora. The miacids retained a primitive posture, as did the early creodonts, and lacked fusion of the carpals and ossification of the auditory bulla.

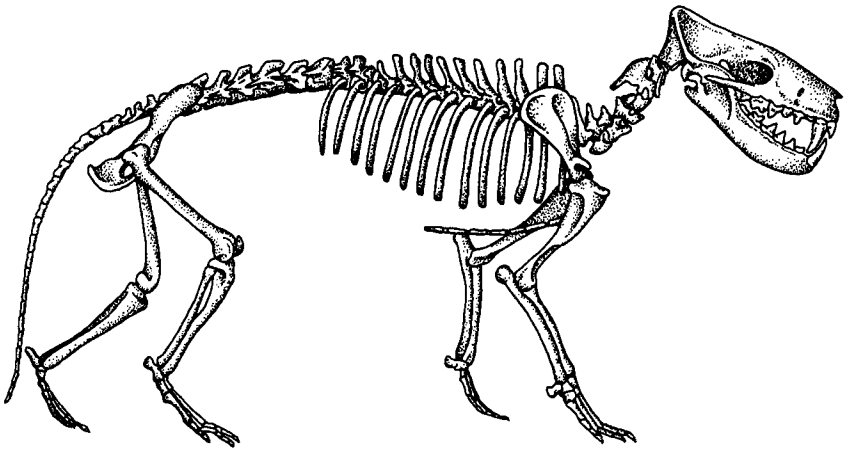

Figure 12-20 The hyaenalike creodont *Hyaenodon*. (From: W. K. Gregory, *Evolution Emerging*. Courtesy Department of Library Services American Museum of Natural History.)

All the modern carnivore families had appeared by the early Oligocene, and their ancestors may have diverged by the late Eocene. There is continuing controversy over their specific origin and interrelationships, but they are typically grouped into two superfamilies, the Arctoidea, including dogs, bears, mustelids (such as weasels and skunks), and procyonids (such as raccoons), and the Aeluroidea—viverrids (civets and mongooses), felids, and hyaenids. Unlike the miacids, the auditory bulla is ossified, but according to a different pattern in each group.

Two major groups of advanced carnivores are extinct. The Amphicyonidae or bear-dogs, which are related to the canids, were common in the late Eocene and continued into the Pliocene. They were generally short-limbed, flat-footed, and relatively large. A second extinct group are the nimravids, which were primitive, catlike forms. They have long been associated with the Felidae, but are primitive in the incomplete ossification of the bulla, and specialized in the ankle structure (16). Nimravids may have evolved separately from the miacid level, independent of both arctoids and aeluroids. They became extinct about 7 million years ago. Many nimravids (also called paleofelids) developed long, laterally compressed canine teeth. This same "saber-toothed" specialization evolved separately among the true felids, typified in the Pleistocene by *Smilodon*, which is found in large numbers in the La Brea tar pits (Fig. 12–21).

The seals, sea lions, and walruses have long been

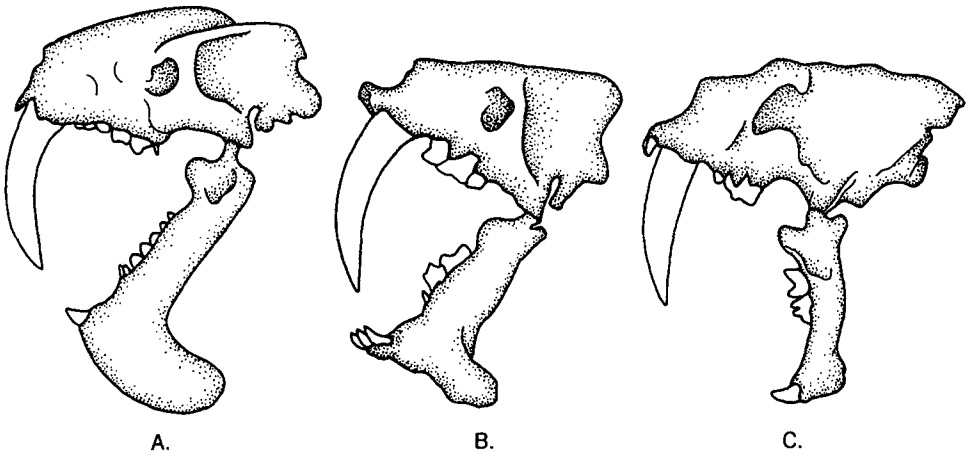

Figure 12-21 Skulls of mammals with sabershaped canine teeth. A. The marsupial *Thylacosmilus* from the Miocene of South America, B. The nimravid "cat" *Barbourofelis*, from the Miocene of North America, C. *Smilodon*, a true felid from the Pleistocene of North America.

PART THREE

LESSONS FROM THE RECORD

Chapter 13

Biostratigraphy

DIVISION OF SEDIMENTARY SUCCESSIONS BY FOSSIL RANGES

Stages and Zones:

Through the work of William Smith in Britain and Georges Cuvier and Alexandre Brongniart in France the association of specific fossils with specific layers or strata of the sedimentary record was becoming widely recognized in the early decades of the nineteenth century. Smith's work was largely practical and he does not appear to have been interested in causes, but Cuvier and Brongniart postulated that each of their faunal units represented a new creation and was terminated by an event of catastrophic proportions which they called a revolution, perhaps recalling the events that had overturned the French social system in their lifetimes. Where they worked in the environs of Paris the Cenozoic succession is an alternation of marine and nonmarine deposits and the faunas they studied replaced each other suddenly at the abrupt changes in environment. Cuvier's work was continued by Alcide d'Orbigny who called the strata bearing a distinct fauna a stage (étage) and established ten stages in the Jurassic System. D'Orbigny's stages were named after places where the fossils characteristic of that age could be collected and were defined on the basis of unique associations of fossils.

The use of fossils in dating rocks began with the succession of species found in superposed beds in a single section, such as a canal trench. The conclusion that the species found in the trench represent a succession of faunas in time, which could be inferred from their vertical superposition, was reinforced as similar sections elsewhere showed the same sequence of species without reversals of order. If their order of appearance were fortuitous and not controlled by the occurrence of the species or fauna in past time, we would expect it to be reversed or scrambled in other sections. The succession of faunas was extended in exposures that duplicate the interval of the initial section but also include beds that are younger or older, and that contain different fossils. Eventually a history of life throughout the Phanerozoic eras was built up, and its reliability was reinforced repeatedly as new sections containing segments of the history of life were described. We now recognize the sequence of life forms as being the result of the process of evolution but the outlines of the succession were established and used to organize stratigraphic knowledge long

before Darwin. During the early part of the nineteenth century, naturalists who believed that the history of life was a continuous progression from simple ancient organisms to modern complex ones were in the minority and the fossil record, as then known, did not support this view. Charles Darwin advanced this position in the middle of the century by proposing a mechanism (natural selection) that explained how the evolution of life occurred.

In the 1840s and 1850s after most of the systems of the relative time scale had been set up, Albert Oppel carefully determined the ranges of fossils in Jurassic rocks of Europe and found that they were not separated into discrete units as d'Orbigny had proposed but overlapped in time. The ranges of some fossils were short, some long, but they were not all terminated at the end of a stage. He proposed to divide the stages into zones characterized by sets of fossils whose ranges overlapped in that interval and whose boundaries were drawn where new species appeared. Oppel named zones after the species of fossil that occurred within the zone, but the named species were not necessarily confined to their zone.

This work of paleontologists in northern Europe developed a scheme for the division of stratigraphic successions into stages and zones on the basis of the vertical or time ranges of fossils. It is a biostratigraphic classification because it divides rock strata into units on the basis of the life-forms contained

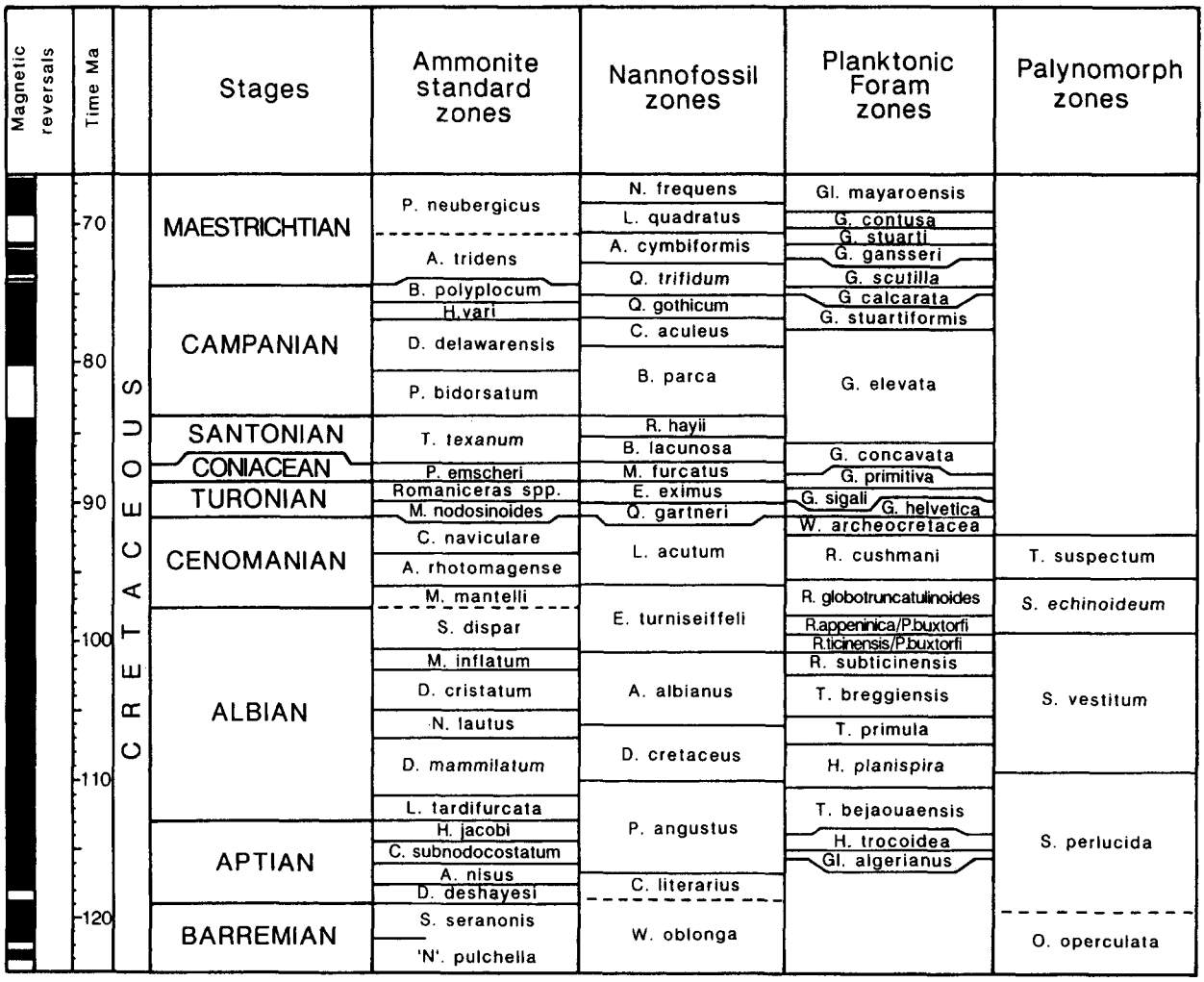

Figure 13-1 Biostratigraphic zonation of the Upper and part of the Lower Cretaceous on the basis of ammonites, nannofossils, foraminiferans and spores. (*Source:* Modified from D. V. Kent and F. M. Gradstein, *Bulletin of the Geological Society of America*, v. 96, pp. 1424–1425.)

in them. Because the ranges of fossils can be used not only for subdivision but also for estimating whether beds in different regions were deposited at the same time (that is, for correlation), these divisions could be extended from northern Europe to other continents as knowledge of the stratigraphic record of the world expanded. The systems that are the basis of major divisions of the standard time scale were originally proposed as successions of rocks of distinctive character, but away from the areas where they were first described, they could only be identified by their fossil content. Systems and stages were based on successions of rocks at localities where they were first distinguished and where their fauna was thought to be typical of that interval. Zones were defined on the basis of fossil ranges only.

The biostratigraphic division of the Upper and part of the Lower Cretaceous System as it is now accepted is shown in Figure 13–1. In this system ammonites are the most useful fossils for defining zones, and the standard divisions of the system into stages depends on the ammonites' ranges. Zonal schemes using other groups, as shown in the chart, are used for strata that do not contain ammonites.

At present the term zone is used in several ways and modifiers are necessary to distinguish them. Interval zones have boundaries based on the first and last appearance of fossils. If the boundaries are based on the first and last appearance of a single fossil taxon, then the interval zone is a range zone. If the interval is defined on the overlap of the last appearance of one taxon and the first appearance of another, it is a concurrent range zone. Usually zones are based on the overlapping occurrence of three or more species and their boundaries are not fixed by first or last appearances. Such zones are called assemblage zones or, more formally, coenozones.

Controls on Fossil Ranges:

The total interval in rock strata in which a fossil species occurs from the time it evolved from its ancestor to its extinction, or its passage into one or more descendant species, is its biozone.

An example will illustrate the problems faced by paleontologists in defining biozones of fossil species (Fig. 13–2A). In a marine succession of limestone, sandstone and shale most species are confined to a certain lithology because organisms are adapted to specific environments and each environment on the seafloor is represented by a type of sediment. We deduce that species b is probably a swimming or floating animal because it ranges through the succession, and its occurrence is independent of changes in lithology that signal changes in bottom conditions. Species c, d, and e are confined to the thick limestone unit I, and the ranges of d and e end abruptly at its top. Did they become extinct at this level owing to the environmental change or did they migrate to follow the limestone environment elsewhere when it was replaced by the muddy bottom on which the shale was deposited? The question can only be answered by looking for other sections of the same age in which limestone deposition continued into the time represented by the shale unit II in this section. We cannot define the top of the biozones of a species from this section alone but as its ranges in other sections are examined, we can come closer to defining it. We can never be sure that another section will not be found where its range extends higher than current findings indicate, some place where it continued to live after most of the individuals of the species became extinct.

The term facies means aspect and refers to the sum of the characteristics of a rock that relates to its origin. The term is also used with the prefixes litho- and bio-. Different lithofacies are distinguished on the basis of the physical aspects of rocks, and biofacies, on the fossil content. Stratigraphers would recognize unbedded porous limestones and dolomites as the reefal lithofacies. Paleontologists would recognize an assemblage of corals, stromatoporoids, and algae as the reefal biofacies.

In Figure 13–2A species such as g, a mud lover occurring only in shales, and h, a sand dweller found only in sandstones, are called facies fossils because they are confined to a certain facies. The occurrence of species g in this local section tells us little about its biozone. For species like g and h we can be certain that their comings and goings are migration events dependent on changes in local conditions. Their appearance may still be useful for correlating rocks or placing them in the relative time scale but the boundaries of their local ranges are unlikely to be origination or extinction events.

The ranges of such species as a and b that are not bounded by lithologic changes may be controlled by a variety of factors. Not all changes in environment will leave their mark; a change of temperature might have little effect on the accumulating sediment yet control the appearance or disap-

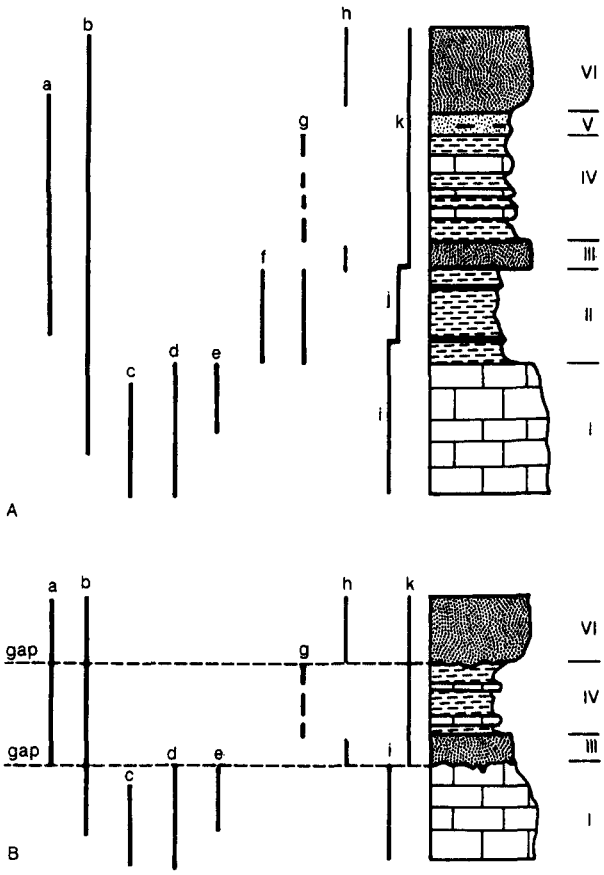

Figure 13-2 Hypothetical example to show the influence of lithology and gaps in sedimentation on the ranges of fossils. A. A section of nearly continuous deposition. B. The same section interrupted by two disconformities.

pearance of a species. A barrier that prevented a species from reaching this area could have been cleared away to allow immigration. For land animals such a barrier might be a strait of water that was blocked by rising land; for marine animals, an isthmus of land that became submerged.

If, in a section of continuous deposition, such as Fig. 13–2A, the paleontologist can identify a series of ancestors and descendants, then biozones of species, such as species j, may be precisely defined. Within the shale unit II, j evolved from its ancestor species i, and at the beginning of unit III it evolved into its descendant species k. Because such evolutionary events are thought to have occurred in small populations occupying limited areas, the chances of such an event being preserved in the record is very small. Ideally the division of strata into zones and stages should be on the basis of ranges established from such evolutionary successions, but unfortunately such successions can be recognized only rarely. Zones established in such successions have been called phylozones.

In Figure 13–2A continuous deposition was assumed, but few sections are uninterrupted by pauses in deposition or times of erosion called disconformities. In Figure 13–2B two gaps in deposition that eliminate units II and V are identified. The effect of the gap between I and III is to concentrate the tops and bottoms of the ranges of species a, h, i, and k at this level giving it an apparent significance in the evolution of the fauna that is unjustified. Species f and j are entirely eliminated and the transition from i to k is no longer evident. On the other hand, the gap between IV and VI makes little difference to the ranges of species.

Most of the beds from which the marine invertebrate record has been collected were deposited in seas that flooded the interiors of continents. Because deposition in these epicontinental seas was discontinuous, more time is represented by the erosional and nondepositional gaps between beds than by the sedimentary layers themselves. In the alluvial deposits that contain much of the vertebrate record, deposition is also episodic and interrupted. Such gaps obviously affect our knowledge of the ranges of species determined from a succession of sedimentary rocks. Because most of these gaps in the record are of local extent and are filled by sediments at some other location, the discontinuities in the ranges of fossils can be filled by patient regional work. Over the past 150 years this type of work has produced such detailed zonal schemes as illustrated in Figure 13–1.

Paleontologists who work with samples from the drilling of oil wells have several problems in the recognition of zones. The fossils are contained in fragments of rock commonly less than 1 cm across that are chipped from the rock at the bottom of the hole and brought to the surface by mud that is circulated in the hole. In the cuttings brought up in the mud the paleontologist encounters new fossils from the top of their ranges, not as they appeared successively in time. Most stages are defined by beginnings of ranges but subsurface samples can rarely define these beginnings, which would be signalled by the absence of a fossil found higher in the hole. This is because fragments of fossils from higher in the hole mix with newly cut chips as they are flushed to the surface. The paleontologist learns to look for new kinds of fossils appearing in suc-

cessive samples as the top of the fossil zones are penetrated and ignores fossils that have already been recorded from higher in the hole whose presence or absence may be fortuitous.

CORRELATION

General Principles:

Nearly all stratigraphic information is available only in geographically separated areas that are isolated successions of sedimentary beds exposed at the surface or encountered in drilling wells. Within an ancient basin where the sedimentary beds were deposited, the strata were originally laterally continuous, but subsequent erosion removes parts once deposited and later deposits limit our access to lower layers to wells drilled considerable distances apart. To determine ancient environments of deposition, stratigraphers must take the digitized data provided by wells and outcrop and compare lithology, fossil ranges, and other features that indicate that sediments were deposited contemporaneously to reconstruct the original continuity in the depositional setting. This comparison is known as correlation.

The word correlation is used by paleontologists and stratigraphers in several different senses and its precise meaning is not always obvious. We can distinguish three types of correlation. Lithostratigraphic correlation is the comparison of lithofacies between outcrop sections and wells to establish the depositional continuity of these units. The units of lithology, or formations, are traced from well to well or outcrop to outcrop. Time correlation is the comparison of successions in order to establish equivalence in time Sets of strata laid down in the same interval are said to be time correlative. Biostratigraphic correlation is the comparison of the ranges of fossils in successions to determine time correlation. In most stratigraphic studies, biostratigraphic correlation is as close as a stratigrapher can get to time correlation because few criteria of contemporaneity are preserved in sedimentary rocks. Sedimentary beds that were deposited in a short time over a large area, such as the ash layers that result from a volcanic eruption, are invaluable for establishing time correlation in both marine and nonmarine successions but are relatively rare in many depositional environments. They have the additional advantage that they can be dated isotopically in years. The value of fossils as time indicators is limited by factors discussed below but in most sections they are the best criteria available. In most stratigraphic studies time correlation is an unattainable ideal.

Since the end of the eighteenth century when faunal succession was discovered, similarity of fossils from two locations has been taken to indicate that beds containing the fossils were deposited at the same time. The precision of the correlation will depend on the accuracy with which the ranges of the fossil species are known and the length in time of those ranges. Species that lived for a short time and are abundant enough that their ranges have been confirmed in many areas are more valuable for establishing precise correlation than are species that lived for a long time or those that are so rare that the tops and bottom of their ranges have not been confirmed.

Lack of similarity of fossils does not indicate that the rocks were laid down at different times. The kinds of fossils in a bed depend on the environment in which they were deposited as much as on the time of deposition. Contemporaneous beds of shallow-water limestone and deep-water shale may contain no fossil species in common. Attached, crawling, and burrowing organisms are dependent on bottom conditions and sediment, but swimmers and floaters can live above many different bottom environments and fall onto them when they die. The fossils of such organisms occur in many different facies and can be used to correlate rocks of different lithology. With few exceptions, bottom-dwelling organisms are facies fossils, associated with a specific rock type but nonetheless useful for correlating beds of that facies.

Relative Value of Fossils:

The most useful fossils for correlation are those that are abundant, widespread, rapidly evolving (and therefore of short range), and distributed in a variety of facies. For different times in the past different groups are useful. In the Cambrian, trilobites were the only organisms that fulfilled these requirements and within that system, division into zones and correlation of these zones is based on trilobite ranges. Graptolites and conodonts are the most useful fossils for correlating rocks of Ordovician, Silurian, and Devonian ages. The ammonoids appear in Upper Devonian rocks and between that series and the top of the Cretaceous System they

have proved to be invaluable for correlation and zonation. Foraminiferans are useful zone fossils for the late Paleozoic when the fusuilines were abundant and for post-Jurassic time when planktonic foraminiferans spread widely through the oceans.

This short list should not give the impression that other fossils are useless. Practically every group has been used for the division and correlation of some group of rocks. Almost all fossils are of some use in dating but relatively few, because their ranges are short and our knowledge of their succession in time is extensive, are capable of giving precise ages. The precision in years attained by fossil dating varies widely in time and place but for the Jurassic and Cretaceous rocks whose fossils have come under the closest scrutiny for the longest time, a precision of a few hundred thousand years is possible.

Dispersal and Migration:

If dispersal of organisms from their site of first appearance is slow, new species will appear in the sedimentary record at successively later times away from the population from which they evolved. Paleontological correlation is based on the assumption that dispersal rates are rapid, in fact essentially instantaneous, when compared to the units of time that can be distinguished by fossil ranges. How valid is this assumption?

If dispersal rates were measurable in millions of years, the order in which species appear in widely separated sections of a given time interval would be different. Starting from various dispersal centers they would arrive at distant sites in different sequences (Fig. 13–3). In fact this is not observed. Reversals in order of appearance of fossil species are uncommon enough to require special investigation, such as the search for environmental barriers that may have retarded the arrival of a species in one region to a time after its appearance in neighboring regions.

Marine animals that live in the water rather than on the bottom can disperse rapidly on currents or through their own swimming power. Most bottom-dwelling invertebrates pass through a larval stage in which they are free-swimming or floating. During this stage they may be dispersed widely depending on its length and the strength of currents. Although most invertebrate larvae must find a site to settle on the bottom within a few days or weeks, some can postpone settlement if no suitable substrate is available. Larvae that feed on plankton are capable of more extensive dispersal than those that do not feed during the larval stage. Such larvae can travel for several months without settling to the bottom. These larvae are capable of crossing large stretches of deep water such as the North Atlantic Ocean on currents. The rate of spreading of molluscs along coastlines to which they have been introduced by shipping or currents in historical times has been traced by shell collectors. At these rates they would disperse around the world in a few hundred years. Marine organisms are not universally dispersed because their larvae face barriers in their search for a place to grow to adulthood. They have the potential for geologically instantaneous dispersal, but dispersal may be blocked by ecological or geographic barriers that delay or prevent their appearance in all areas at the same time. For correlation those animals that are likely to be least subject to such barriers are therefore preferable.

Quantitative Correlation:

Two collections of fossils from different areas are unlikely to contain exactly the same species; some will be common to the two collections, others will be found in only one. Some paleontologists have argued that the reliability of the correlation or the closeness in age of the two collections can be estimated by the proportion of species that are common to those that are different. Expressions the degree of difference between collections are used in many statistical procedures. Several similarity coefficients for comparing collections are listed below. They are improvements on simple counts of the number of species common to the collections in that they take account of the difference in size of the collections. In all of these C is the number of items in common, N_1 is the number of species in the smaller sample, and N_2 is the number in the larger sample.

SIMILARITY COEFFICIENTS

Simpson coefficient $= C/(N_1 + N_2)$
Jaccard coefficient $= C/(N_1 + N_2 - C)$
Dice coefficient $= 2C/(N_1 + N_2)$
Otsuka coefficient $= C/\sqrt{N_1 N_2}$

The larger the values of the coefficients calculated from two faunas being compared, the closer

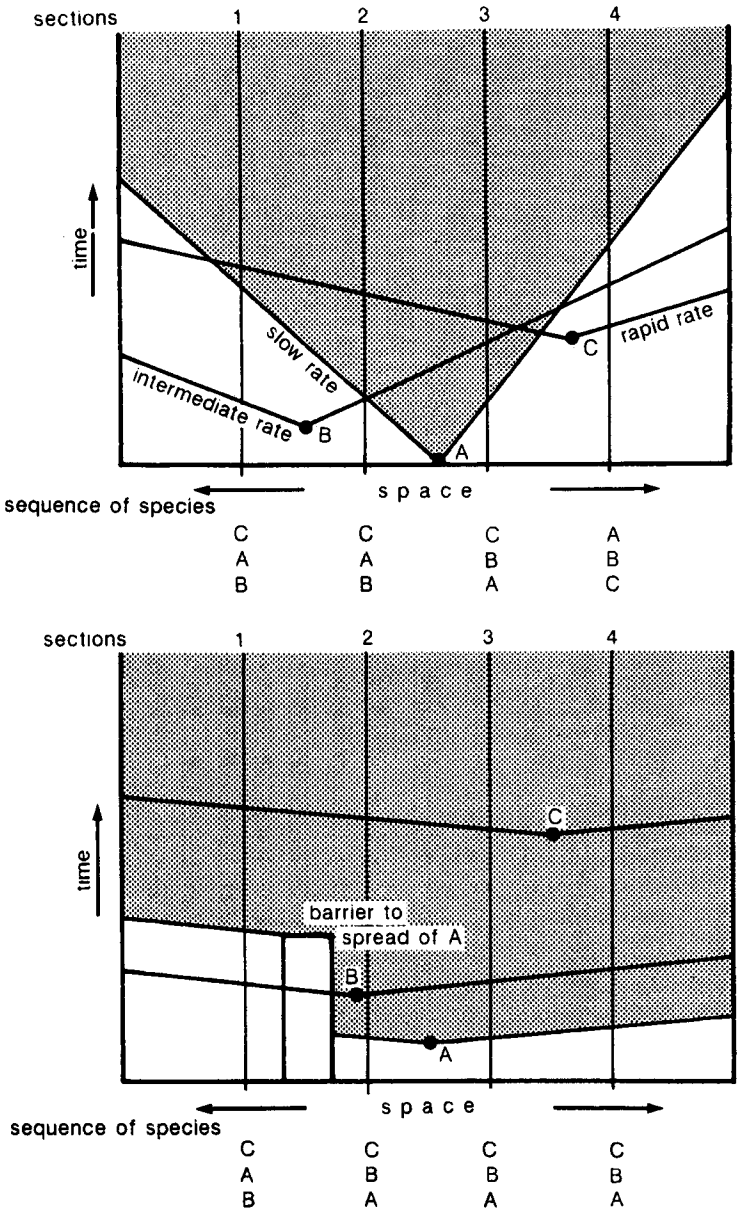

Figure 13-3 Hypothetical example to show the effect of the rate of dispersal on the order of appearance of fossil species in four sections (1, 2, 3, 4). The species originate at the dots marked A, B, and C, and their dispersal outward from these points is represented by the upwardly diverging lines. The increasing area occupied by species A is shaded for emphasis. When the rate of dispersal is slow, these lines form an acute angle with the apex of origin; when it is fast, the angle is obtuse. The order in which the species appear is listed below each section. If some species disperse at relatively slow rates, the species will appear in different orders in the different sections (top diagram). As this is not commonly observed in the paleontological record, we deduce that rates of dispersal were rapid, as in the lower diagram. This lower diagram shows that a barrier to the spread of one species (species A), which is present for a limited time, may block its spread into section 1 and delay its appearance there until after the appearance of a later evolved species B.

in age they are considered to be. In merely summing matches and mismatches the paleontologist is assuming that all species affect the accuracy of the correlation equally. From what has been indicated in the discussion above this is obviously not true; species with short ranges are more valuable than others and species with very long ranges are practically valueless. Attempts have been made to apply a weighting factor that would modify the impact on the similarity coefficient of each species on the basis of its geographic and stratigraphic range but these factors inevitably have subjective aspects. Paleontological correlation has so far resisted reduction to a mathematical expression, and fossil biotas must be compared by an expert who knows the value of each fossil as a time indicator before correlations can be made.

Depth-Controlled Communities and Correlation:

Sedimentary successions all over the world record episodes of sea level rise and fall. The magnitudes of these oscillations range from those that caused

oceans to become a few meters deeper to those that inundated large parts of continents. The larger changes in sea level, such as the one that caused extensive continental seas to flood the continents in Late Cretaceous time, have been known for many years to have affected much of the earth. Only recently have many stratigraphers become convinced that the smaller variations that occurred 10 to 20 times during a geological period are also worldwide. Once the times of these sea level changes have been established on the basis of normal techniques of paleontological dating, the changes become useful for correlation. Large-scale sea withdrawal will be marked by erosion surfaces in the sedimentary succession, and large-scale transgression by the appearance of deep-water sediments in areas of shallow-water deposition, but smaller changes may be reflected only in fossil faunas that are sensitive to water depth.

The composition of modern and fossil invertebrate communities changes with depth. For an interval in the past, the sequence of fossil communities can be established from the reconstruction of an offshore, downslope gradient at the margin of ancient continental platforms. The vertical (temporal) changes in communities in stratigraphic sections can be interpreted in terms of changes of sea level and transgressive and regressive episodes can be identified. An example will illustrate the method. In England and Wales a transition can be traced in Lower Silurian rocks from shallow-water environments to the deep-water graptolitic shales of a marginal trough. The transition is marked by changes in fossil faunas that have been divided into five depth-controlled communities. Alfred Zeigler and his co-workers distinguished them on the basis of distinctive brachiopods (1) (Fig. 13–4). Markes Johnson and his co-workers have used a wider spectrum of organisms to identify similar depth-controlled communities (2). Deep communities are recognized by the occurrence of pentamerid brachiopods, intermediate ones by corals and algae and shallow-water ones by stromatolites and ostracodes. When the sequence of these communities is recognized in stratigraphic sections, a curve showing the relative change of sea level during the deposition of the section can be constructed (Fig. 13–5). The curves of many sections show four periods of deepening water in Early Silurian time. If these deepening events can be identified in new areas, correlation between two sections can be established without the use of the ranges of fossils. The fossils themselves are not matched from section to section and sections can be correlated that have no communities in common.

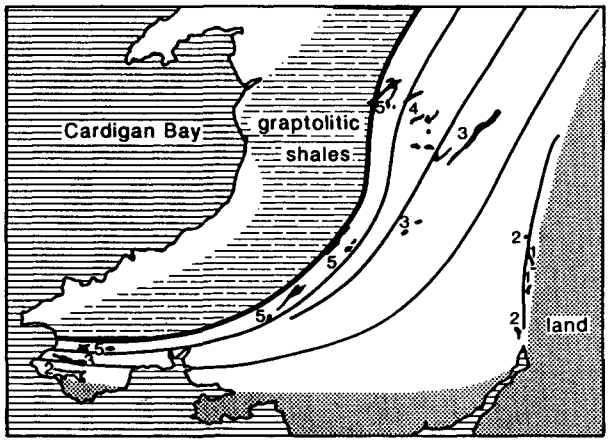

Figure 13-4 Depth-controlled assemblages of Early Silurian brachiopods in southern Wales. The shelf between the deeper water graptolitic shales and the land has been divided into 5 assemblages indicated by numbers. 1: *Lingula* assemblage; 2: *Eocoelia* assemblage; 3: *Pentamerus* assemblage; 4: *Stricklandinia* assemblage; 5: *Clorinda* assemblage. The areas in which the shelf assemblages are exposed and identified are indicated by the irregular black patches. (*Source:* Modified from A. M. Zeigler, *Nature*, v. 270, p. 271.)

Transgression and regression of seas not only change depth communities but influence, and may control, the evolution of new species and the extinction of old. The bases of zones marked by the introduction of new species of ammonoids in the Carboniferous correspond to times of sea level rise and transgression (3). Events that expanded or contracted the living space of marine organisms can be expected to have had a profound effect on their rate of evolution and extinction. Within the last decade stratigraphers have established that worldwide changes of sea level occurring in superposed cycles of as many as five or six orders have affected the transgression and regression of the sea and presumably also the life of the sea. The subject is discussed further in Chapter 16.

STRATOTYPES: DRIVING THE GOLDEN SPIKE

Type Sections:

The stratigraphic sections from which the systems were originally described became standards for the recognition of these rocks and fossils because they

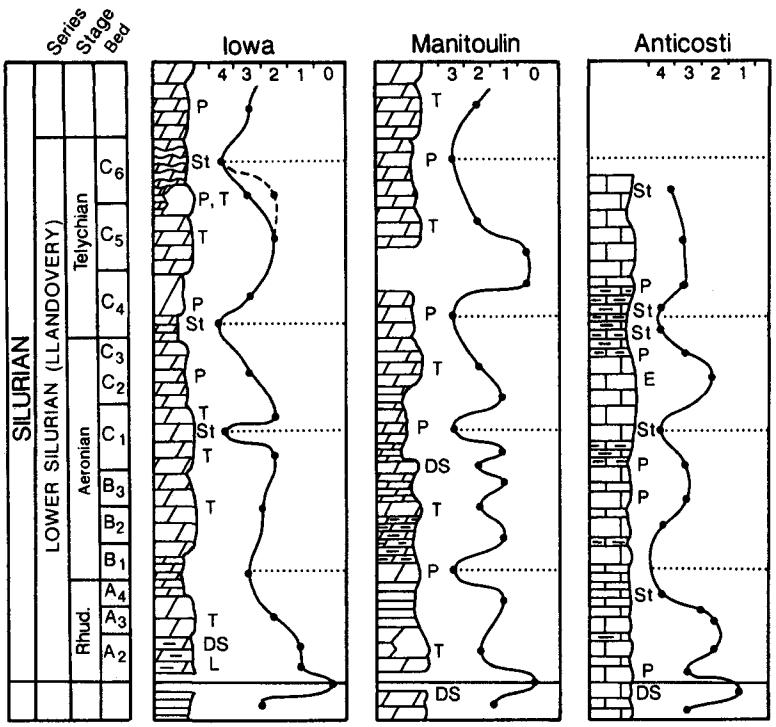

Figure 13-5 Correlation of three stratigraphic sections on the basis of change of water depth, as deduced from depth-associated fossil communities in the Lower Silurian of central and eastern North America. The four benthonic assemblages are scaled at the top of the graphic sections in order of increasing depth (1-4). The fossil assemblages indicating depth are indicated by the letters to the right of the graphic sections as follows: L = *Lingula* assemblage (assemblage 1); DS = domal stromatolites or stromatoporoids (assemblage 2); T = tabulate corals (assemblage 2); Eo = *Eocoelia* fauna (assemblage 2); P = pentamerid fauna (assemblage 3); St = stricklandiid fauna (assemblage 4). The continuous sinuous line represents the inferred relative rise and fall of sea level and the dotted lines join correlative levels of high water. (*Source:* Modified from Markes Johnson, *Geological Society of America Bulletin*, v. 96, pp. 1484–1497.)

were at first the only ones available. For example, in North America rocks were recognized as deposited during the Silurian Period by comparison with fossils that had been collected by Roderick Murchison when he set up the Silurian System in Wales. When d'Orbigny set up the stages as subdivisions of the Jurassic System, he gave them geographic names from localities where the units could be examined and the fossils that defined their place in the geological time scale could be collected. The Bathonian Stage was typically exposed at Bath in England and the Hettangian Stage at Hettange in France. Unfortunately d'Orbigny did not always locate his type sections at the locality that gives its name to the stage; for example, the Oxfordian Stage is defined by cliff sections in Yorkshire, not at Oxford. Biostratigraphic units must have a type section where their boundaries are designated and displayed not only by fossil ranges, but also at specific levels in the section. These sections are called type sections, or stratotypes.

Because the systems were described originally from various areas across northern Europe at a time when paleontological correlation was in its infancy, there was no way of knowing whether time gaps existed between the systems or whether they overlapped. For example, when the Permian System was first described in Russia it inappropriately included in its base rocks of the same age as those that had already been assigned to the Carboniferous System in England. Detailed correlation on the basis of fossils brought gaps and overlaps (such as the Carboniferous–Permian one) to light, and international commissions of paleontologists were set up to make decisions on where the boundaries should be placed.

Some of the regions where the systems were first described were far from ideal as standards for worldwide correlation. The Devonian rocks of Devon are complexly folded and faulted, and the stratigraphic succession there is still uncertain. As a result the rocks of the Ardennes region of Belgium have been used since the last century as a standard for Devonian correlation.

Boundary Stratotypes:

Recently commissions of the International Union of Geological Sciences have concentrated on designating boundary stratotypes, that is, sections to act as standards in correlation of boundaries between biostratigraphic units. If the boundaries of the unit are well defined in terms of fossil ranges, then the whole unit is precisely defined as the rocks lying between these boundaries. Recently a commission has designated a section at Klonk in Czech-

oslovakia as the stratotype of the Silurian–Devonian boundary and the horizon at the top of the zone of the graptolite *Monograptus uniformis* as the boundary itself. The boundary between the Ordovician and Silurian systems has recently been set by the vote of a committee at Dobb's Linn in Scotland at the base of the *Parakidograptus acuminata* graptolite zone.

Informally the process of choosing boundary stratotypes has been called "driving the golden spike." By setting for all time the plane of the boundary, the commission figuratively drives a marker into the section. Such boundaries should be in sections that are accessible, rich in fossils, and of essentially uniform lithology so that changes in fauna cannot be ascribed to local changes in environment. Although the boundary position is usually chosen at the base of some fossil zone, the boundary is defined as a position in the rock sequence, not the base of the zone.

The Stratigraphic Code:

Efforts to codify stratigraphic procedure culminated in the publication of the International Stratigraphic Guide in 1976, and the North American Stratigraphic Code in 1983 (4,5). Although not all the recommendations on biostratigraphic units are accepted by all stratigraphers and paleontologists, most follow their major recommendations. The American code makes the distinction between stratigraphic units defined by time criteria, such as isotopic ages (chronostratigraphic units), magnetic reversals (magnetopolarity units), and those defined by fossils (biostratigraphic units). Systems and series are considered by those that drafted the Codes to be chronostratigraphic units and only biozones are biostratigraphic. For most sedimentary rocks, however, fossils are the only means available to tell time, and the original divisions of sedimentary rocks into systems and series were originally, and continue to be, on this basis. In stratigraphic studies, paleontologists "hold the watch" (6).

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Chapter 14

Adaptation and Functional Morphology

ADAPTATION

Stephen Gould and Richard Lewontin defined adaptation simply as the "good fit of organisms to their environment" (1). In another place Lewontin described adaptation as the process by which organisms provide better and better solutions to the problems posed by the environment (1). The term *adapt* implies movement towards an appropriate or apt relationship to environmental demands and is commonly linked to the term *fitness* in discussions on the relationships of organisms to their environments. Evolution has been explained in terms of the "survival of the fittest," meaning the best adapted organisms.

The concept of the good fit of organisms to their environments can be traced back to antiquity. It was most clearly stated by the natural theologians of the eighteenth century. The world and its inhabitants were regarded by natural theologians as expressions of the perfection of their Creator and therefore in themselves perfect. The Creator perfected the form and behavior of organisms to fulfill their functions in the world and His creation could be no less perfect than Himself. Charles Darwin asked "How have all those exquisite adaptations of one part of the organization to another part, and to conditions of life, and of one organic being to another being been perfected?" and answered that it was not by God but by competition, natural selection, and the survival of the fittest (2).

If only the fittest survive in the competition, levels of fitness must exist among the competitors. Several possible measures of fitness have been proposed among which are survival, reproductive success, and breadth of environments successfully occupied. The organism that survives when its competitors die for other than chance reasons must be considered better adapted to its environment. The organism that produces more offspring than its competitors will in time displace the competitors in their home range. Their greater fecundity will then give them the opportunity to spread to adjacent areas to increase the range of the species. Those organisms that are more fit can be described as those that are more successful under natural selection. Fitness then becomes a description of the biological properties of an organism that result in its survival and perpetuation.

To some evolutionists only whole organisms can be considered as adapted to their environments; to others, the features or parts of the organisms are

adaptations. One method of studying adaptation is to divide the organism into traits, either morphologic features or patterns of behavior, and to consider separately how each of these is related to environmental factors. Those who take a more holistic approach say that the traits of an organism so interact that the organism cannot be reduced to its component parts but must be considered as a whole (1). Paleontologists are concerned with adaptation because they need to know how ancient organisms lived. Most of the evidence they use is confined to the preserved parts of the body. Body parts adapted to fit the environment should in their design give evidence of their use and help us to interpret the lifestyle and habitat of the organism.

Becoming Adapted:

Darwin's concept of competition among individuals leading to progressively better adaptation implies that an organism is never completely or perfectly adapted and that its gains in solving the problems of the environment are at the expense of other organisms. Darwin used the metaphor of a group of wedges driven into a limited space. Each species is a wedge hit occasionally by a hammer but it can only make progress into the hole by squeezing out other wedges. Leigh van Valen (3, 4) formulated a similar idea as the Red Queen hypothesis. In "Through the Looking Glass" the Red Queen told Alice that in her country you had to keep running just to stay where you are. Van Valen postulated that, because a species competes for resources with other species, even in a stable environment its relationship with the environment steadily deteriorates unless it is continuously improving its adaptation. Those that fall behind in this race become extinct.

The Red Queen hypothesis assumes a stable physical environment but geologists know that in the long run no environment is entirely stable. Paleontologists conceive of evolutionary changes as repeated responses by organisms adapting to changes in their physical and biological environments. Major steps in evolution discussed in the next chapter may involve other mechanisms, and mass extinction events that cause major shifts in the history of life also disturb the process of adaptation. If adaptation is viewed from this longer geological perspective, better adaptation can be measured in terms of survival of the species through the greatest number of environmental changes or the greatest length of geological time. To achieve maximum capacity to adapt according to this longer time scale, a species would have to maintain a large stock of genetic variability within the population in order to be able to respond repeatedly to changes in the environment, with morphologies that were successful in terms of short-term survival of the individual. Alternatively, species may be able to survive for millions of years as a result of extensive capacity for physiological adaptation that is not based on genetic variability.

Imperfection of Adaptation:

Animals of different ancestry adapted to the same environment may have similar forms. This is the phenomenon of evolutionary convergence, and it is good evidence of the reality of adaptation. A classical example of convergence from the paleontological record is that of the ichthyosaur of the Mesozoic and the dolphin of today. One was, and the other is, a pelagic, fast-swimming predator. They have in common streamlined bodies, the arrangement of fins, and a pointed snout with teeth (Fig. 14–1). Yet the first was a reptile with reptilian skeletal structures and physiology and the second, a mammal with mammalian skeleton and reproductive system. Although molded by the requirements of the environment to superficial resemblance, they maintain many internal features of their ancestors. That is, their adaptation to the same environment at different periods of life history through natural selection has not produced identical organisms.

Even casual observation shows that parts of complex organisms are used for a variety of functions and usually are not adapted for a single particular function. In birds the beak may be used to obtain a certain food but, since it must serve also for feeding the young, grooming, fending off rivals, etc., its shape must be a compromise between the forms that are ideal adaptations for each of these uses. The study of adaptation is simpler for invertebrates that live attached in one place utilizing one special food resource, but the organs of even these simple organisms cannot be optimized through natural selection for a single feeding condition because they are likely to encounter a range of conditions that follow each other in time.

The constraints of ancestry and the multiple use of organs are two reasons why traits or individuals

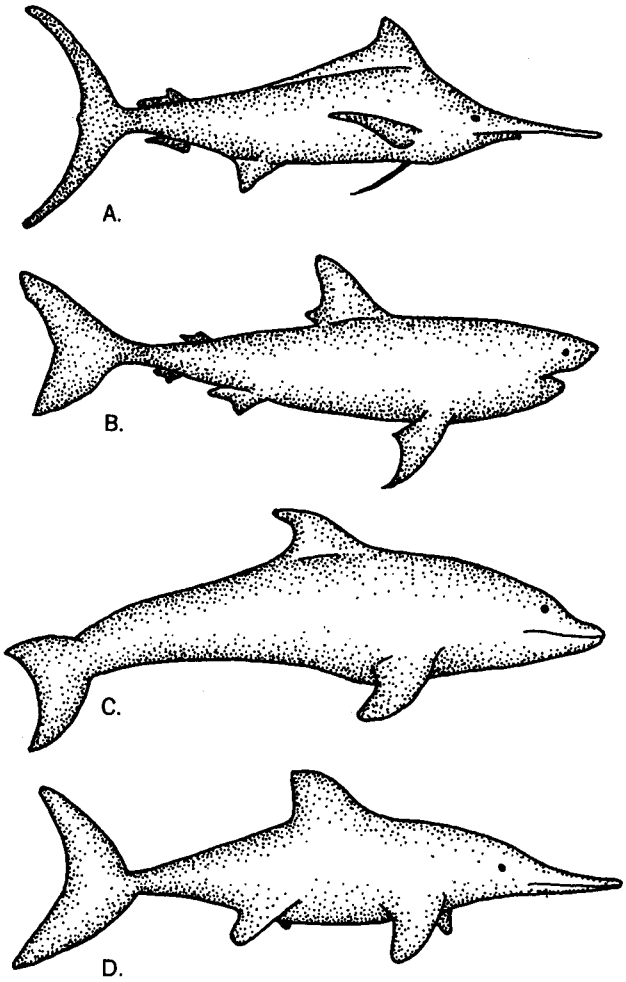

Figure 14-1 Evolutionary convergence illustrated by adaptation to fast swimming. A. Swordfish (a bony fish). B. Shark (a cartilaginous fish). C. Dolphin (a mammal). D. Ichthyosaur (a reptile). Each of the groups independently evolved a spindle-shaped body and a high lunate tail which enables it to swim rapidly (approximately 40 km/hour). Dolphins and ichthyosaurs evolved from terrestrial ancestors. Primitive bony and cartilaginous fish had elongate bodies and were only capable of swimming at much slower speeds. In contrast with their similar body shapes, details of their skeleton reveal their distinct ancestries. Typical of bony fish, the swordfish has a large operculum covering the gill region; sharks have several separate openings for the gills. Both dolphins and ichthyosaurs breathe through nostrils. The vertebral column of sharks supports the dorsal lobe of the tail; in ichthyosaurs, it supports the ventral lobe. The vertebral column does not extend into the tail in bony fish. In contrast with all other groups, the tail of the dolphin is horizontal, not vertical.

cannot be fully optimized by natural selection to take advantage of their environments (5). Three other reasons, among many, can be mentioned here briefly.

1. Features that are nonadaptive for everyday life may be essential for attracting mates. Flamboyant plumage in male birds may attract hawks but also attracts females and is therefore essential to the survival of the species.
2. Natural selection operates in a world where chance events—storms, earthquakes, and droughts—may carry away the fittest and leave the less fit, thereby interrupting the selective processes that tend to optimize adaptive features.
3. If the adaptive value of a trait is neutral or even slightly deleterious, the genes that determine its appearance in a population may still become widespread in a small population, not by selection, but merely by chance interbreeding. This phenomenon, called genetic drift, may perpetuate traits that are of relatively low selective value to the organism.

FUNCTIONAL MORPHOLOGY

Functional morphology is the study of the relationship of form to the functions that organisms or their component parts perform. To determine how a fossil organism lived the paleontologist analyzes the possible functions of the parts that are preserved. Adolf Seilacher (6) proposed that form can be understood in terms of the interaction of three factors: adaptation, growth, and phylogeny (Fig. 14–2).

Phylogeny:

Organisms do not have unlimited capacity to generate new adaptations. They modify for new functions the structures that they have inherited from their ancestors. The inherited structures were selected to meet environmental demands which were faced by ancestors but are possibly irrelevant to the way of life of the descendant as it has entered new environments. Each organism must use imperfect modifications of the adaptations of its forebears to meet its own environmental challenges. Stephen

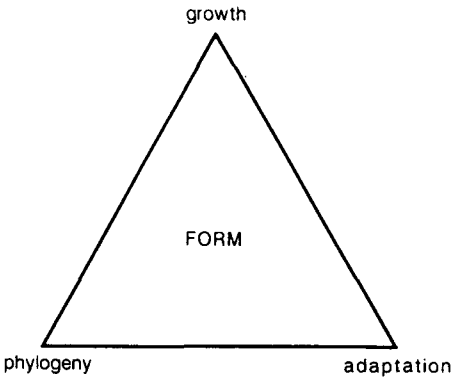

Figure 14-2 The three factors controlling morphology suggested by Adolf Seilacher.

Gould (7) has pointed out that these types of imperfect adaptations are strong evidence for evolution. His favorite example is the panda's thumb, which is used to strip leaves from young bamboo shoots—the panda's only food. The panda is descended from bears whose front feet were specialized for running and were not able to grasp objects between their thumb and other fingers as primates do. The panda inherited five digits but the thumb was not opposable or useful for stripping bamboo. In adapting to the bamboo diet, the panda developed a thumb-substitute by a modification of one of the bones that is normally a small part of the wrist (Fig. 14–3). Although this sixth digit is not an ideal adaptation, it evolved to become an efficient leaf stripper because the panda was constrained by inherited fore-foot anatomy in its adaptive pathways.

The basic designs of the invertebrate phyla were established at the beginning of the Paleozoic Era as organisms diversified into different habitats in the oceans. Specialization within, and progression beyond, these original adaptations may have obscured the original adaptation, but the potential to develop new adaptations has since been constrained by these early events. When a group of bivalves, the scallops, diversified into the swimming niche they did not have the materials to grow fins as did fish but could only modify the shell and mantle inherited from distant ancestors adapted to burrowing in sediment. The scallop's adaptation to swimming is not comparable in perfection to that of fish or squid, which from their early history entered this niche, but it is apparently an effective method of escape from predators. The form of the scallop is based in its history but was modified by

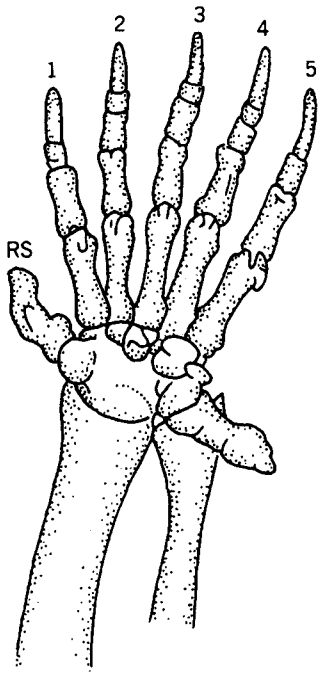

Figure 14-3 The bones in the panda's forelimb. In addition to the five digits (numbered), the panda has a "thumb" formed by modification of the radial sesamoid bone (RS) used for stripping leaves from bamboo. (*Source:* Modified from S. J. Gould, *The Panda's Thumb.* 1980 New York, Norton)

adaptation to a lifestyle much different from that of its ancestors.

Growth and Allometry:

The form of the fossil skeleton will be a product of how it grows. Some organisms form a skeleton on the exterior of their bodies (bivalves, brachiopods), others within the tissue (vertebrates, echinoderms). In some it grows continuously (sponges), and in others it is periodically molted (arthropods).

If, in the growth of an individual, the parts all grow at the same rate, their proportions will be in the same in the adult as in the juvenile form. Such growth is said to be isometric but this is not a common mode of growth. In most higher organisms, some parts grow faster or slower than others so that as the organism increases in size its proportions change. This is allometric growth. The relation between the size of a part and the whole organism can commonly be expressed in an equation of the following type:

$$X = a\,Y^b,$$

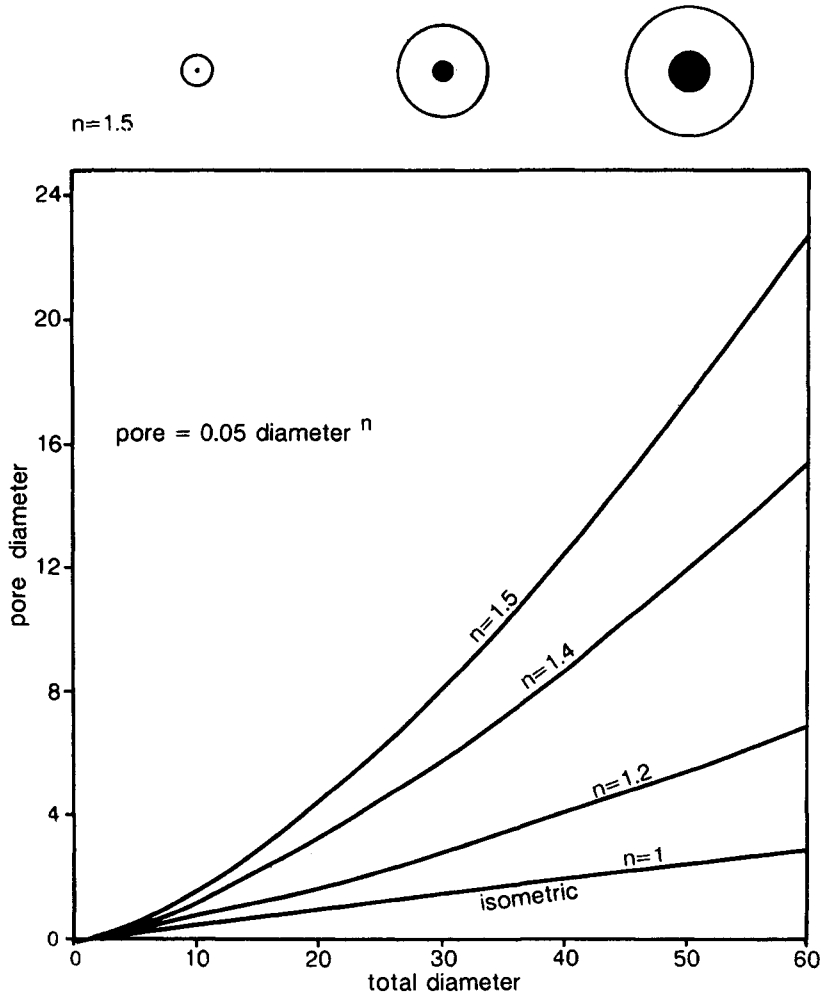

Figure 14-4 Allometric growth. A hypothetical round organism with a central pore whose growth can be expressed according to the allometric equation. Growth curves for various values of the exponent n are shown. The proportions of the organism during growth if n = 1.5 are shown at the top of the graph. If n = 1, as illustrated by the bottom line, the growth is not allometric but isometric.

where X is the dimension of the part growing allometrically, Y is a measure of the size of the organism, and a and b are constants (Fig. 14–4). If the exponential constant b is large, the increase in X for a small change in size (Y) may be very large. If b is 1, growth is isometric. Parts that increase in size faster than the animal grows are said to have positive allometry and b is greater than 1. An example is the head of the human foetus, which grows faster than the body. Those that decrease relatively in size (b is less than 1), have negative allometry. After birth the human head grows at a rate slower than that of the body and is therefore an example of both positive and negative allometry at different times of its development.

Allometry has been used to explain features that are not only nonadaptive but apparently harmful. The most famous example of this supposed relationship is the extinct Irish Elk (more properly, a deer) whose antlers are found in abundance in Pleistocene peat bogs in northern Europe (Fig. 14–5). The antlers of this deer reach spreads of 3.5 meters and weights of 40 kg. They are so large that many students of evolution have thought that they must have impeded the mobility of the animal and drained its energy as they were formed each year only to be discarded after the mating season. In the deer family (Cervidae) antler length (A) is allometrically related to the overall size expressed as the height at the shoulder (H) by the equation:

$$A = 0.0754H^{1.63}$$

In the skulls of fossil Irish Elks the relationship between the antler's length (A) and the basal length

Figure 14-5 Reconstruction of the extinct Irish Elk *Megaloceras*. (Source: J. G. Millais, British Deer and Their Horns, 1897.)

of the skull (L, used as a measure of overall size) is shown by the equation:

$$A = 0.00025L^{2.115}.$$

Both in deer in general and in the Irish Elk small increases in overall size led to large increases in the size of the antlers. Possibly increase in overall size was so advantageous to the elk that the harmful effect of the large antlers was tolerated or possibly the antlers were even, at their largest, adaptive in the competition for mates (8).

THEORETICAL MORPHOLOGY

Paradigm Method:

The term *paradigm* means a model, a pattern or example in general usage. In science, it has come to mean a way of thinking about, or solving, a problem. The paradigm method can be applied to problems of functional morphology through proposing a model for the function of a structure in question. For example, the zigzag folding of some brachiopod shells, particularly rhynchonellids, could be postulated to have evolved to strengthen the shell (Fig. 6–53). A paradigm or model is then defined which is the structure that would be capable of fulfilling the supposed function with the maximum efficiency under limitations imposed by the nature of the materials. In this case the paradigm could be a surface repeatedly folded, or corrugated, along axes perpendicular to the line along which it might break or deform; a surface like a corrugated sheet of iron. In brachiopods, because the stress is along the roughly semicircular open margin where the valves are pressed together, the corrugations would ideally be in the form of a fan. The fossil shell is then compared with the model and the extent of their similarity determines the degree of confidence that the true function of the feature has been discovered. Because the radially folded brachiopod shell does closely resemble a sheet corrugated to increase its resistance to bending, the conclusion that the shell evolved this shape to resist breaking or bending is logical.

The example can be used to illustrate some difficulties with the method. The zigzag shape of the aperture has also been interpreted as adapted either for directing feeding and respiratory currents to the lophophore within, or to preventing sand grains from entering with the incoming current. It is effective in keeping out sand because the brachiopod does not need to open such an aperture as widely as a straight one. A zigzag aperture lets in the volume of water required by the animal at a smaller gape than a straight one because it is longer. The folding of the brachiopod shell could be an adaptation for one or all of these three requirements. Most parts have more than one use and their form is not specifically engineered for any one function.

The paradigm approach can also be applied to exploring the function of astrorhizal systems of Paleozoic stromatoporoids. Stromatoporoids commonly have on successive growth surfaces radially arranged canals that lead to a central opening (Fig. 6–19). Different paleontologists have proposed that these canal systems, called astrorhizae, housed the exhalent canals of an encrusting sponge, canals for diffusion of nutrients between polyps, filamentous

juveniles of cyanobacteria, and parasitic animals. Their interpretations were based on the different phyla to which each assigned the stromatoporoids. The canals join and increase in size toward the center. Michael LaBarbera (9) has pointed out that if water was gathered from two smaller canals into a larger one and the flow was laminar in nature, the laws of fluid flow indicate that the sum of the cubes of the radii of the tributary canals should equal the cube of the radius of the canal to which they lead (that is, $R^3 = r_1^3 + r_2^3$). This ideal relationship or paradigm can be tested in stromatoporoids in which the canals are empty and can be filled with plastic to make internal molds, released from the skeleton by dissolving it with acid, and measured. The average difference between the expected and the observed values derived from the equation was 13 percent. The closeness of this value to the one predicted by the flow equation suggests that the tubes were capable of carrying a current of water. The geometry of the canal system would therefore allow its use as an exhalent system of an encrusting sponge and the similarity of its form to the canals of living sponges suggests that this is how it was used (Fig. 6–20).

Computer Simulation of Fossil Form:

The growth of some organisms and their shells is simple and regular enough to be expressed by a mathematical equation. For such organisms variations in morphology can be expressed as changes in the parameters of the growth equation. The growth formula can be programmed for a computer and the machine can be asked to draw the range of forms that result from changes in the parameters. Such studies help paleontologists to understand the factors that determine form and the relation between animals of different forms. The method works best for invertebrates of simple skeletons; the growth of complex skeletons and shells cannot be reduced to equations.

Many simple invertebrates, such as bivalves, gastropods, cephalopods, brachiopods, and foraminiferans, secrete a shell in the form of a logarithmic spiral. Although the correspondence of the gross form of their shells to the spiral was recognized early in the last century, David Raup was the first to use a computer to illustrate the range of forms that can be generated by varying the parameters (10). The logarithmic spiral growth pattern provides for growth of the shell without change in its shape.

The basic form of all these shells is a coiled cone growing and expanding at its aperture. The various shapes of cones in cross section are not easily expressed mathematically. However, variations in gross shell form can be studied by making the cone circular in section. If this is done, the shell form can be described in terms of three parameters: (1) the whorl expansion rate (W), which expresses the amount that the tube expands during one turn (whorl) of the spiral (Fig. 14–6); (2) the distance from the coiling axis of the tube (D); 3. the translation rate down the axis of coiling in one whorl (T). Shells in which the translation rate is high will have high spires, like many gastropods, and those in which it is zero will be planispiral, like most ammonites. Shells in which the distance from the coiling axis D is large will be loosely coiled with central cavities, and those in which it is low will have overlapping whorls that cover older parts of the shell. Variations in the three parameters can be plotted on the three dimensions of a cube (Fig. 14–7). The plot shows that not all possible shell variations have

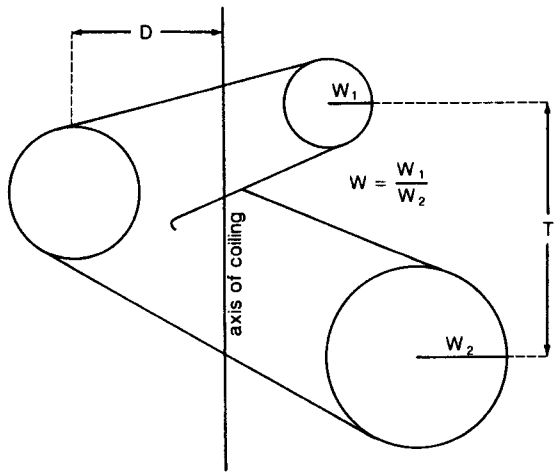

Figure 14-6 Parameters of the geometry of spiral shells. W = whorl expansion rate, the ratio between diameters of the expanding cone at the beginning (W_1) and end of one whorl (W_2). T = translation rate, distance along the axis of coiling travelled in one whorl. D = distance of the center of the cone from the axis of coiling. (*Source:* Modified from D. M. Raup, *Journal of Paleontology*, v. 40, pp. 1178–1190.)

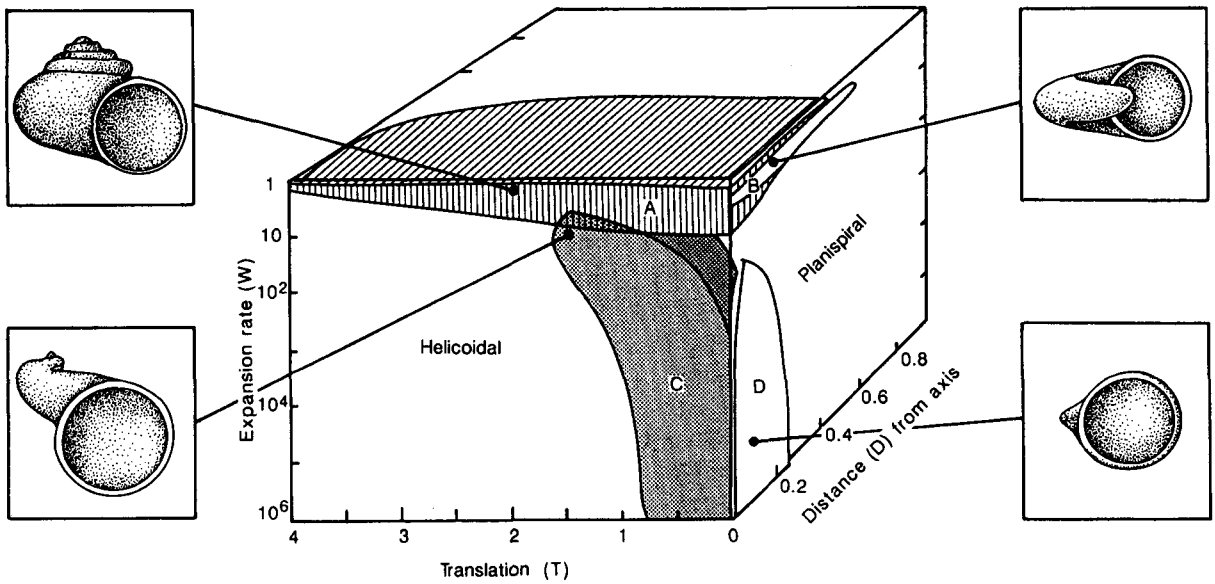

Figure 14-7 Block diagram defined by the three parameters of a spiral shell showing the areas occupied by gastropods (A), coiled cephalopods (B), bivalves (C), and brachiopods (D). The form of the shell represented by the four points marked by dots is shown in the four boxes around the block. Helicoidal shells plot on the front face of the block and planispiral shells on the side face. (*Source:* Modified from D. M. Raup, *Journal of Paleontology*, v. 40, pp. 1178–1190.)

evolved, for parts of the solid are not represented by known shells, and also that certain forms are favored by certain animal groups. Most gastropod shells are represented by the upper forward part of the cube where expansion rate is low and translation rate is moderate. Ammonite shells occupy an area on the right face where translation rate is zero, expansion rate is low, and distance from the axis (*D*) is variable. If *D* is low, the adult whorls completely overlap earlier ones as in *Nautilus* (Fig. 7–3); if it is high, all the inner whorls can be seen in adult shells (Fig. 10–2). Bivalves and brachiopods have shells with such high expansion rates that they are bowl-shaped. Shells of this form have such wide apertures that they are of little use to the animal for protection unless the aperture is closed either by another similar shell, as in bivalves and brachiopods, or by clamping it against a rock surface as in limpet gastropods. In all bivalved shells the expansion rate for each valve must be more than 10 and additional growth must take place on the side of the aperture near the apex if the shell is to open without the apexes interfering with each other (Fig. 14–8).

Richard Fortey and Adrian Bell (11) have simulated graptolite colonies by a computer program. They have shown that the form and branching pattern of colonies depended on the even placing of

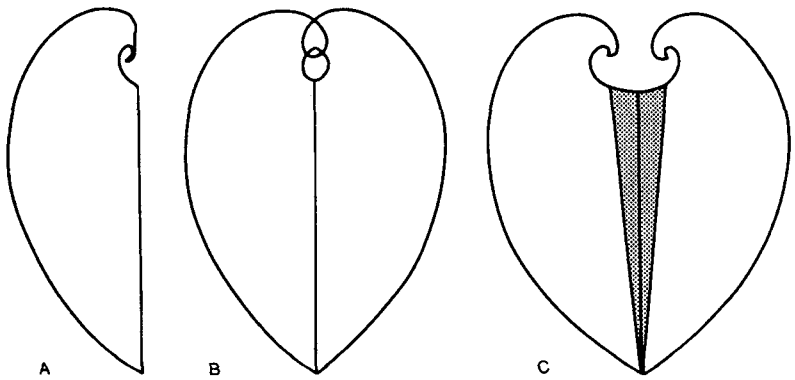

Figure 14-8 Cross sections of hypothetical bivalve showing the necessity of interumbonal growth if the valves are of equal size. A. A single valve with whorl expansion rate of 10. B. If two similar valves are placed together their umbos overlap, an impossible relationship. C. By growth of the shaded part of the valves, a functional bivalve shell can be formed. (*Source:* Modified from D. M. Raup, *Journal of Paleontology*, v. 40, pp. 1178–1190.)

individuals on a horizontal plane so that they could efficiently harvest planton.

COMPARISON WITH LIVING ORGANISMS

The adaptations of fossil organisms may be understood by comparisons with living relatives whose habitat and behavior are known. The most reliable inferences can be drawn from structures in related animals that are derived from the same organ. Such structures are said to be homologous. The septa of ammonites and living *Nautilus* are homologous structures. Structures that serve the same function but are derived from different body parts are said to be analogous. The panda's thumb is analogous to the thumbs of primates.

Functional Morphology of Ammonoid Cephalopods:

Extensive studies have been made of *Nautilus* to help paleontologists understand the adaptations of the extinct nautiloids and ammonoids. *Nautilus* secretes a coiled shell divided into gas-filled chambers by septa (Chapter 7). The animal lives in the last, or living, chamber and communicates with all the others through a thread of tissue bearing arteries and veins that passes through each one in a tube called a siphuncle. Before a septum is secreted the body moves forward, water enters to fill the space between the body and the last septum, and the back of the body secretes a new septum, partitioning off a new chamber filled with water (Fig. 14–9). This water is then slowly pumped out of the chamber through the siphuncle using an intracellular mechanism based on osmosis. The pumping action may take weeks and during this time the shell buoyancy slowly increases. Displacement of the water from the chambers compensates for the growth of body and shell weight, maintaining the whole animal at near neutral buoyancy. Some of the water is out of contact with the siphuncle and may stay in the corners of the chamber for some time. The chambers are filled with gas at less than 1 atmosphere pressure by diffusion from the siphuncle. When the animal reaches the adult stage after several years of growth, new chambers are no longer added.

In addition to compensating in juvenile stages by long-term changes in buoyancy for the growth of the animal, the shell of *Nautilus* allows the animal to migrate vertically in the water in youth and adulthood. *Nautilus* lives at 200 and 300 meters during the day and rises to about 150 meters at night to feed on the coral reefs of the South Pacific. Its movements have been directly observed and individuals tagged with electronic devices have been traced by radio. In this depth range the ambient pressure changes by about 15 atmospheres. A flexible cavity with gas at 1 atmosphere pressure would be collapsed as the animal descended by an increase

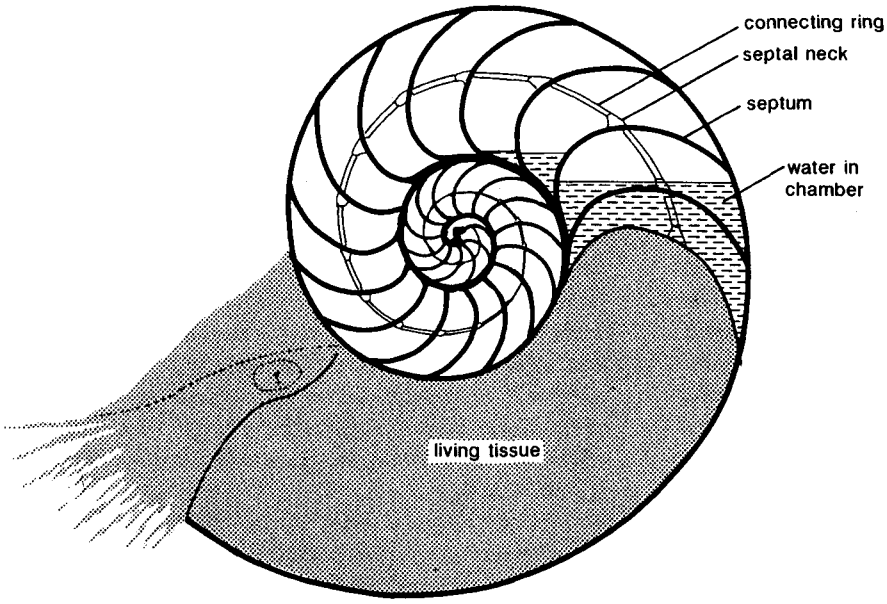

Figure 14-9 Juvenile *Nautilus* in cross section, showing the last chamber filled with water and recently formed chambers still containing some water. (*Source:* Modified from E. J. Denton, *Proceedings*, Royal Society, London, v. B185, p. 288.)

in pressure of this magnitude, but the *Nautilus* shell is a rigid pressure vessel and, until the seal is broken, will maintain constant buoyancy. The depth at which the animal can live over a prolonged period is limited by the ability of the permeable siphuncle to pump out the chambers against the ambient hydrostatic pressure as they form and, after they are all formed, to prevent seawater from forcing its way into the chambers against the osmotic pump. This limit is at about 300 meters where the pressure is approximately 30 atmospheres.

The depth to which the animal can penetrate for short periods is theoretically limited by the strength of its shell to resist hydrostatic pressure. Animals forced to depths of over 750 m in cages implode and die. Although failure of the shell might be expected at the siphuncle, it is as resistant to short-term stress as the rest of the shell and failure in pressure tank experiments commonly occurs in the septa, in the walls, and the body chamber. Gerd Westermann estimated the strength of the septa of fossil cephalopods on the basis of simple measurements of thickness and curvature and deduced that Paleozoic cephalopods with wide apical angles and septa of low curvature would have imploded at depths of 250 meters. Long shells with lower apical angles and thicker, more widely spaced septa could have lived at greater depth (12, 13).

We can apply lessons learned from observing *Nautilus* and experimenting with its shell to its extinct relatives. Several features of ammonite shells appear to be adaptations to living in an environment of changing pressures as the animal rose and fell in the sea. The intricately folded sutures of ammonites must have strengthened the line of potential failure between septum and wall and also buttressed the wall itself against outside pressure by extending the line of contact with the septum. Shells strengthened in this way would have allowed the animal to live over a much larger depth range than animals with weaker shells. For a given strength and shape the shell could be lighter and therefore more easily moved and easier to secrete. The cross section of the whorl can also be interpreted in terms of pressure resistance. Cross sections that approach a segment of a circle would have been more effective in resisting pressure changes than those with flat sides because a sphere is the most efficient pressure vessel. Ammonites with flat or complexly folded sides inhabited shallow waters and those with smooth surfaces and rounded whorl cross sections were capable of diving to greater depths like *Nautilus*.

THE METABOLISM OF DINOSAURS

The function of the ammonite shell can be reconstructed with some degree of assurance on the basis of its living relative *Nautilus*. The way of life of extinct organisms without living counterparts is more difficult to reconstruct. For example, how can we discover the biological factors that explain how the dinosaurs achieved and maintained dominance in most major terrestrial environment for a period of more than 100 million years?

When dinosaurs were first recognized in the early nineteenth century, they were compared with modern reptiles such as lizards and crocodiles. They do share a common ancestry with crocodiles, but does the crocodile provide an accurate basis for establishing the nature of this extremely diverse assemblage of Mesozoic reptiles?

Anatomists have long recognized that all dinosaurs clearly differed from modern reptiles in having a relatively erect posture of the limbs. Whether they were bipedal or quadrupedal, the joint structures show that the body was habitually held off the ground. In contrast, nearly all modern reptiles have a sprawling posture and are active for only short periods of time. Crocodiles and some lizards can draw their limbs under the body and move them in a fore and aft direction, but most of the time the body rests on the ground. Such a posture would be impossible for dinosaurs. The joints are oriented so that the limbs must be held nearly vertically.

The nearly vertical posture of the limbs can be explained in many dinosaurs by their great bulk. Neither bone nor muscle is strong enough to support and lift the body if their limbs were sprawled to the side. Even the elephant, which is small by comparison with many dinosaurs, must keep its legs nearly stiff when running. If the great weight of the large dinosaurs provide the primary explanation for their upright posture, one might expect the small dinosaurs would have a sprawling stance like crocodiles and large living lizards. In fact, some of the smallest dinosaurs, and some of the earliest members of the group, have a skeletal anatomy that can only be interpreted as indicating an upright posture, and many early genera must have been obligatorily bipedal, resembling large terrestial birds such as the ostrich much more closely than any living lizards.

The skeleton of most dinosaurs suggests a level of locomotor activity approaching more closely that of large modern mammals than that of any modern

reptiles. One of the most fundamental differences between modern reptiles and mammals is in their capacity for sustained activity. No reptile can run actively for more than a few minutes, after which it must rest for a long period of time before becoming active again. Many mammals, in contrast, can remain active for many hours without fatigue. The differences in their capacity for continual activity lies in the metabolism of the muscles. In reptiles, most of the energy for contraction of the muscles results from the fermentative breakdown of glycogen, giving rise to lactic acid. Lactic acid is a toxic material that must be removed from the muscles. The slow breakdown of lactic acid requires long periods of rest between bouts of activity. Among mammals, most of the energy for muscle contraction is achieved by oxidative metabolism in which the only waste products are water and carbon dioxide which can be rapidly removed by the blood. Moderate activity may be maintained for hours without fatigue.

The capacity for continuous muscle activity explains the selective advantage for an upright posture in even the smallest dinosaurs. Most paleontologists now assume that dinosaurs must have relied primarily on oxidative metabolism for muscle contraction, and had achieved a roughly mammalian level of activity.

Other aspects of dinosaur metabolism remain more controversial. Modern mammals have approximately ten times the metabolic rate of reptiles of comparable body size (Fig. 14–10). Did dinosaurs have a nearly mammalian metabolic rate, or was it considerably lower than that of mammals and yet significantly above that of typical reptiles?

Robert Bakker and others (14) have suggested that dinosaurs may have had a truly mammalian metabolic level, but there is some evidence to the contrary. Maintenance of a high metabolic rate requires a great deal more food than is necessary for modern reptiles and a more effective feeding strategy, a well as more effective integration of sensory input and motor coordination. In birds and mammals this is associated with a significantly larger brain size than that of modern reptiles. James Hopson (15) has demonstrated that some dinosaurs had a brain size (as measured relative to body weight) approaching that of mammals, but most did not, and the average brain to body weight ratio of dinosaurs may not have been much different from that of their nearest living relatives, the crocodile. Though the metabolism of dinosaurs was almost certainly different from that of living turtles, lizards, and crocodiles, it should not be considered exactly like that of modern mammals or birds.

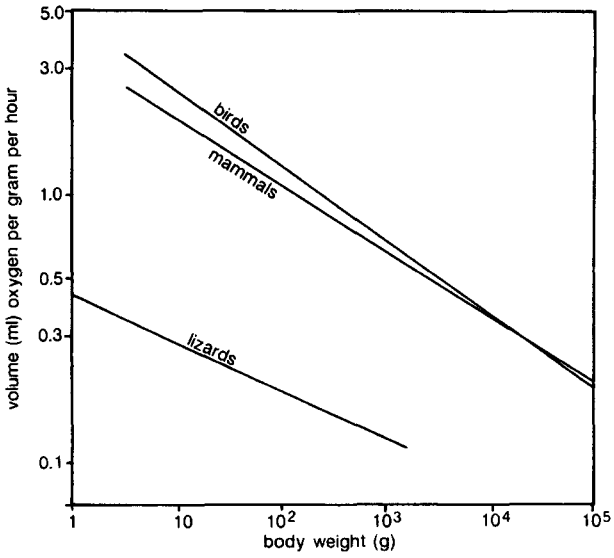

Figure 14-10 Comparison of the metabolic rates (expressed as oxygen consumption) of mammals, birds, and lizards. Note that the scales are logarithmic. For the same body weights, the reptiles have a rate of consumption of oxygen about one tenth of that of birds and mammals. (*Source*: A. F. Bennett & W. R. Dawson, *Metabolism*. Academic Press 1976. Courtesy of A. F. Bennett and W. R. Dawson, *Biology of Reptiles*, v. 5, p. 158, Academic Press.)

A very important fact that should be considered in evaluating the metabolism of dinosaurs is the almost complete absence of small dinosaurs. In small mammals, with weights up to a few kilograms, much of the metabolic energy goes toward maintaining a high, constant body temperature. As was pointed out in Chapter 11, the smallest mammals have an exceedingly high metabolic rate because of the problem of heat loss. Dinosaurs are exceptional compared to all other major groups of vertebrates in the great body size of most species. Only two or three species are known to have had an adult size of less than about 10 kg. In contrast, the vast majority of both birds and mammals are of small size.

Adult dinosaurs would not have had to maintain the extremely high metabolic rate of most birds and small mammals in order to have a high, constant body temperature. In fact, J. R. Spotila (15) has demonstrated that many dinosaurs could have maintained a high, constant temperature without any metabolic expenditure, as long as the ambient

temperature remained as high and constant as it is today over large areas of the tropics.

Modern reptiles are active primarily during the day, rather than at night, and this was presumably the case in the Mesozoic, so that dinosaurs could have taken advantage of the radiant heat of the sun to help maintain a high temperature for most periods when they needed to be active.

Reptiles the size of adult crocodiles have no difficulty maintaining a constant, high body temperature. They may, in fact, be tied to a semiaquatic way of life because the water provides an easy way to lose excess heat to the environment. By their bulk alone, most dinosaurs could have maintained a body temperature comparable to that of mammals. Only the smallest dinosaurs would have required a high metabolic rate for this purpose. Maintenance of a high constant body temperature by being large is, however, highly dependent on the relative constancy of the external environment.

There is much evidence from the distribution of other animals and plants that the climate during the Mesozoic was far different from that in the latter half of the Cenozoic. The temperature was apparently well above freezing for all of the year as far north as the Arctic Circle. The low level of the continents and the vast extent of the inland seas would have provided a maritime climate over much of the globe. The major land masses were close together, making migration easy, if seasonality were sufficiently severe in any one area to interfere with maintenance of a regular body temperature. Under such conditions, lasting scores of millions of years, there would be little selective advantage for evolving a high metabolic rate that would make it possible for a large reptile to warm up rapidly or maintain a high temperature in an occasionally cold environment. As long as the climate remained relatively stable, maintenance of a high, constant body temperature through large size alone would have been adequate for the vast majority of dinosaurs during the Mesozoic. They would, however, have been extremely vulnerable to any long-term and widespread decrease in average temperatures, and especially to rapid temperature increase or decrease. Many reptile groups that were prominent in the Mesozoic did not survive into the Cenozoic, but there appears to have been a relatively gradual extinction of the dinosaurs toward the end of the Mesozoic rather than a sudden catastrophic extinction (see Chapter 16). This accords with the current understanding of dinosaur metabolism, which would have made them more susceptible to climatic change than either mammals or other reptile groups.

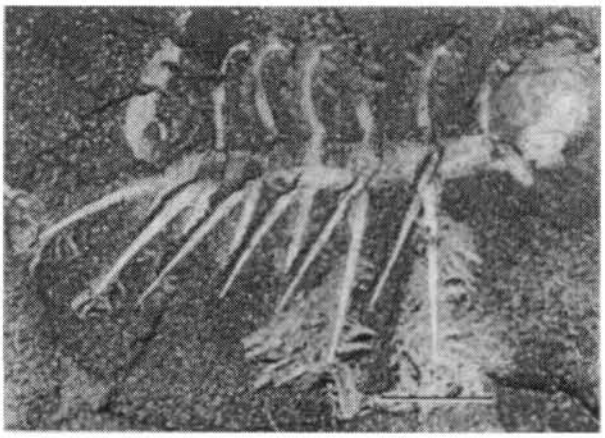

Figure 14-11 The enigmatic fossil *Halucigenia sparsa* from the Burgess Shale. The scale bar is 2 mm. The head is presumed to be the blob on the right and the pairs of spines are thought to have acted as legs. The function of the tentacles along the back is problematic. (Courtesy of S. Conway Morris and Blackwell Scientific Publications, *Geology Today*, p. 91, May–June 1987.)

Enigmatic Extinct Organisms: *Halucigenia*:

Some fossil animals are so unlike any living organism that their interpretation by the principles of functional morphology is difficult. The small fossil *Halucigenia* from the Burgess Shale is such an animal (Fig. 14–11). At one end is a ball-like structure that has been thought to be the head; at the other the pipelike body is turned into a structure like a chimney. The body has seven pairs of spines that are reconstructed in the figure as legs. Along the opposite side of the body are seven tentacles which split into two parts at their tips. Behind them are a set of six smaller appendages. No mouth or anus has been identified, and both the front to back and top to bottom orientation may be incorrectly represented in Figure 14–11. The organism has been reconstructed as a bottom dwelling scavenger that walked on its spines but, in the absence of similar living organisms, or similar structures in living organisms, these reconstructions are as insubstantial as hallucinations.

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Chapter 15

The Mechanisms of Evolution

INTRODUCTION

The term *evolution* is used to refer to the processes by which life has changed through the geological ages. In Chapter 1 it was described as the chain that unites all organisms through the history of life. Implicit in the term evolution is the idea that life has progressed—that, in some way that is difficult to define, life is better adapted and more efficient now than it was at its beginning. That life of the present is more complex than that of the Archean would be difficult to deny, but that modern organisms are better adapted, or more fitted, to their environment than were the bacteria of the Archean would be difficult to demonstrate. Stephen Gould has claimed that substantial progress in establishing new and more complex life forms ended early in the Paleozoic and since then evolution has consisted mostly of fine adjustments in the adaptation of these basic architectures. Viewed from a long perspective, life has become more complex, has colonized a greater variety of environments, has divided the earth's resources more finely, and in exploiting these smaller parcels has evolved more specializations. Whether these trends are considered progressive depends on our understanding of the meaning of that word.

Evolutionary theory today is in a state of rapid flux. Wholesale reexamination of the basis of Darwin's mechanism of evolutionary change is taking place. The conflicts inherent in this reformulation of evolutionary theory have been exploited by conservative religious groups in a new attack on the whole concept of evolution. Such attacks extend from the models that we use to explain the paleontological record to the reality of the record itself. In discussing the validity of evolution, a clear distinction must be made between the record of life preserved in rocks and the models formulated by scientists to explain that record. Scientists disagree on the details of the mechanisms, but the record of life described in the first 12 chapters of this book is verifiable by a diligent observer and documented by nearly 200 years of scientific investigation. That the large-scale continuity of this record is the result of descent of one life-form from another is a conclusion that cannot be avoided except by logical contortions. Yet pressure of religious groups on the educational system has meant that adequate discussion of the history of life and mechanisms of evolution has been excluded from many school biology and natural history textbooks for many years. Disagreement on evolutionary theory should not be interpreted as indicative of doubts within the

biological and paleontological community as to the central truths of evolution: that all life is connected by ancestor–descendant relationships and that sorting of the variations inherent in the reproductive process has resulted in its present diversity. These disagreements are part of any science that is moving rapidly to new knowledge of nature.

DARWINISM AND THE MODERN SYNTHESIS

Although Darwin's book was called *The Origin of Species,* it is not about how species are produced but rather about the origin of adaptations or how species change. Darwin apparently believed that the two were so closely linked that explanations of adaptation were sufficient to explain the origin of species. From the evidence that organisms produce more offspring than survive, and individuals carry different heritable variations, he deduced that in the inevitable conflict for resources, living space, and mates, those with the variations that fit best with the environment would preferentially survive. The individual that survived would reproduce in its descendants the variation that made it better adapted. The process of selection is measured by differential reproductive success. Darwin distinguished two types of selection: natural and sexual. Natural selection depended on the fitness of the organism to its environment; sexual selection on its attractiveness to mates. He recognized that the latter, as in the case of brightly colored birds mentioned in the last chapter, could work against the former.

Darwin postulated that the variations favorable to an organism would accumulate by small increments, generation by generation, until an organism had evolved that was sufficiently different from its ancestors to justify its recognition as a new species. He hoped that the paleontological record, then just being brought to light, would substantiate the continuity of species in time through transitional series of forms. What was then known about the record did not support this hypothesis, and he attributed the failure to the imperfection of the fossil record. The paleontologist Thomas Huxley, Darwin's most vocal supporter, was active in the search of the record for the corroborating evidence of transitional sequences and in particular fixed on *Archaeopteryx* as an example of the transitional forms that paleontologists should expect to find. During the late nineteenth and early twentieth centuries the discovery of transitional series in the fossil record to demonstrate Darwin's concept of evolution was a major goal of paleontologists, but few were documented and some of these, as discussed below, have subsequently failed to survive closer examination.

By the 1940s, geneticists had discovered how variations are inherited, and population biologists had modelled the spread of variations through populations. Julian Huxley integrated this new knowledge in a landmark book, *Evolution, The Modern Synthesis.* The model of evolution assembled in this book became known as the modern synthesis, or neodarwinism, and guided evolutionary thought for the next 30 years. The modern synthesis incorporated the following ideas:

1. Variation arises from random changes in the genes and chromosomes.
2. Selection favors the survival and perpetration of particular variants at the expense of others.
3. Changes within evolving lineages result from the gradual accumulation of favorable heritable variations.
4. Interbreeding of individuals within a species maintains a gene pool that gives homogeneity and stability to the population. The morphological and genetic discontinuities that separate contemporaneous species originate by interruption of this gene flow through isolation of small subpopulations and their adaptation to local conditions.

The modern synthesis included the species concept clearly formulated by Ernst Mayr and discussed in Chapter 3—that species are groups of interbreeding populations occupying a territory and genetically isolated from neighboring groups. New species are thought to originate when the gene flow is interrupted by physical or other barriers to interbreeding and local populations diverge genetically and morphologically from the parental group to adapt to local conditions. Most supporters of the modern synthesis perceived evolution as progressing gradually and continuously as favorable mutations spread through large populations at rates depending on their selective advantage. Such change has been called microevolution.

THE SEARCH FOR MICROEVOLUTION IN THE FOSSIL RECORD

Paleontologists in the late nineteenth and early twentieth centuries assumed that the imperfections of the fossil record that had prevented Darwin and his contemporaries from proving the reality of microevolution by means of paleontology would be eliminated by more careful study and the discovery of successions of sedimentary beds that represent continuous deposition. Various successions have been intensively studied and restudied because they appear to show such gradual change.

The Coiling of *Gryphaea*:

A. E. Trueman believed that he could demonstrate slow, progressive, adaptive changes through several species in a lineage of the oyster *Gryphaea* in the Early Jurassic rocks of England (Fig. 10–15B). The major changes involved the coiling of the large left valve until it had reached one and a half turns, the reduction of the area of attachment of the larger valve, the thickening of this valve, its increase in size, the development of a groove in the large valve, and the restriction of the coiling of the valve to its apical portion.

Detailed studies (1) of four species of *Gryphaea* from the Lower Jurassic show that size has increased irregularly (Fig. 15–1). Counts of the growth lines on these bivalves indicate that the increase in size is related to the greater age of the younger species—that is, the specimens higher in the succession are larger because they lived longer. They are more coiled than their ancestors because coiling is correlated by an allometric function with growth. Trueman's conclusion that increased coiling of the valves was an adaptive trend driven by selection can be shown to be incorrect because no change in the basic geometry of the shell took place; they only lived longer. In younger Jurassic rocks decrease in coiling took place (see following discussion). Although a general increase in size is apparent through four species, within individual species the trend is not gradual but episodic as shown in Figure 15–1.

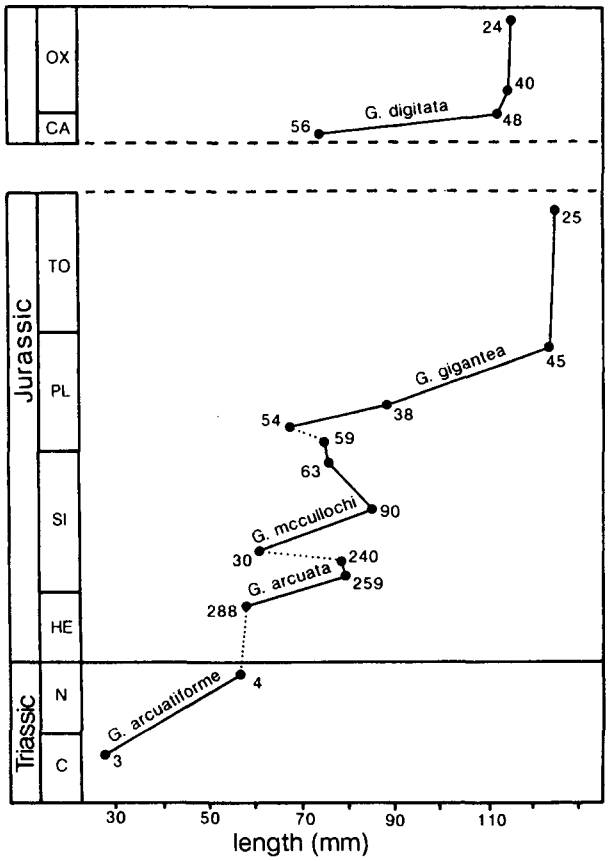

Figure 15-1 Maximum size of the left valve in European species of *Gryphaea* in the Late Triassic and Jurassic. The points represent the means of the length for the number of specimens indicated at each point. Note the general but not regular increase in size with time through the five species. The stages that divide the systems are abbreviated as follows: Carnian (C), Norian (N), Hettangian (HE), Sinemurian (SI), Pleinsbachian (PL), Toarcian (TO), Callovian (CA), Oxfordian (OX). (*Source:* Modified from Anthony Hallam.)

Evolution of the Ammonite *Kosmoceras*:

Ronald Brinckmann collected about 3000 specimens of compressed ammonites from a section of Upper Jurassic Oxford clay in England. Through extensive measurements of seven characters he attempted to establish gradual trends. The 14-meter thick section is thought to represent about 1 million years of evolution. Brinckmann divided his ammonites into four genera each containing several species, but later paleontologists have suggested that only two genera are present and each is dimorphic or that only one genus is represented. The dimorphism explains Brinckmann's observation that parallel adaptive trends occur in the evolution of what he took to be four different genera (Fig. 15–2). He inferred that the parallelism in the trends in different genera was evidence that those trends were adaptations to a changing environment. Although changes occur in the section, these changes

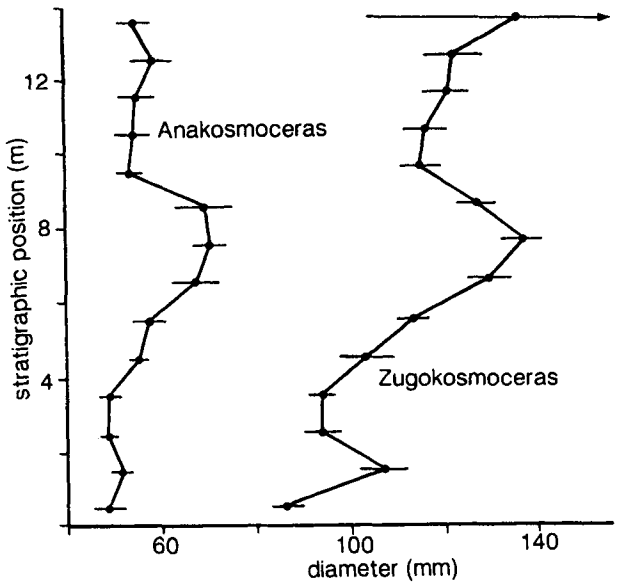

Figure 15-2 Changes in shell diameter of two ammonite genera from the Oxford Clay studied by Brinckmann. The points represent the means for specimens found in 1 m of section and the bars are four standard errors long. The parallelism of the trends suggests that the genera are dimorphic forms of a single taxon. (*Source:* Modified from D. M. Raup and R. Crick, *Paleobiology*, v. 7, pp. 90–100.)

are not obviously directional. As an example (Fig. 15–2), the changes in diameter in two lineages appear to be almost at random. Statistical tests by David Raup and Rex Crick (2) do not eliminate the possibility that the changes in characters in time measured by Brinckmann are random. However, certain segments of the tends can be interpreted as being governed by directional selection, but the direction of this selection must have changed frequently in the course of the evolution of the lineage.

Brinckmann recognized 24 breaks in the succession by sharp boundaries between sets of beds and by the concentration of ammonites on bedding planes (Fig. 15–3). He assumed that these were pauses in deposition and attempted to determine, assuming a constant rate of evolution and deposition, how many centimeters of beds were missing at these breaks (Fig. 15–3). Raup and Crick, by treating his data statistically, could identify 40 horizons in the section at which rapid changes in morphology take place, but only six of these occur at horizons identified by Brinckmann as stratigraphic breaks. They concluded that the rates of evolutionary change vary in the section but the times when the change was rapid do not necessarily correspond to the presumed stratigraphic breaks and that the magnitude of the breaks cannot be estimated from morphologic trends. These later studies have suggested, but not proved without doubt, that Brinckmann's ammonites do show some microevolutionary trends.

Permian Foraminiferans:

Lepidolina is a fusuline foraminiferan from the Pacific Region. Tomowo Ozawa studied nine characters in the evolution of the species *L. multiseptata.* Some of these characters show little evidence of gradualism but four do show evidence, and the most impressive changes are in the size of the initial chamber (Fig. 15–4). In an interval estimated to be about 20 million years the mean diameter of the chamber changes from 200 to 550 micrometers. This study is based on a large group of samples collected over a wide geographic area. The increase in size of the chamber is believed to be a response to a change of habitat from shallow carbonate to deeper clastic-rich environments.

Ordovician Bivalve *Nuculites*:

Sara and Peter Bretsky (3) studied variation in the bivalve *Nuculites* in Ordovician rocks through a section about 800 m thick in Quebec. The range of variation in their specimens is sufficient for the recognition of four different species of this genus, but they found that the characteristics were gradational through the section and referred them all to one species. Their plot (Fig. 15–5) of the proportion of these shells expressed as the length–height ratio, shows (with an initial reversal) the general, slow change to shells of greater elongation.

Microfossils in Deep-sea Cores:

Sedimentary successions deposited on the borders of continents are often interrupted by gaps produced by erosional episodes when the sea retreated and the site of deposition emerged. The deep parts of the ocean basins are not affected by instability of the margins, and continuous sections that could preserve the record of gradual evolution are more likely to be found there. Only recently have such sections become available as cores from wells drilled in the Deep Sea Drilling Project. Unfortunately, complex life forms are not abundant in the deep

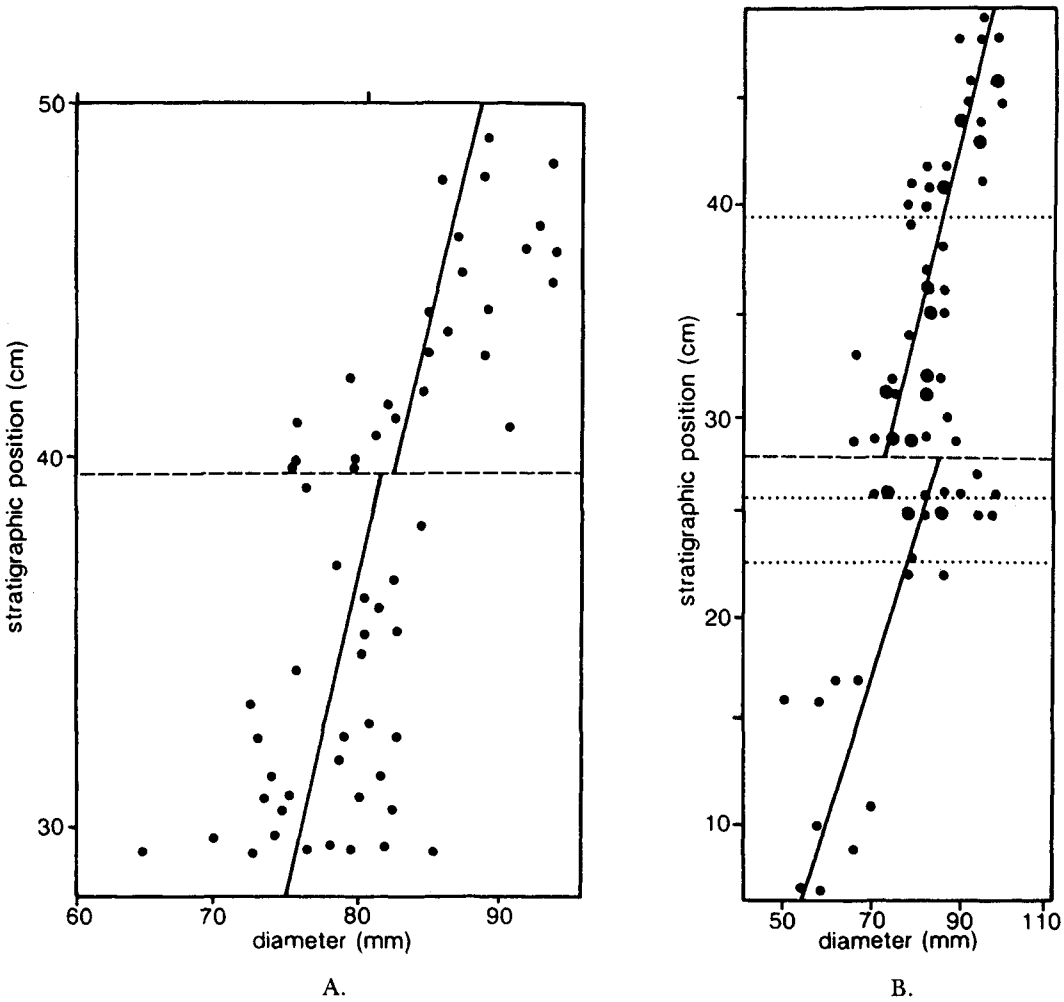

Figure 15-3 A. Brinckmann's analysis of the diameter of *Zugokosmoceras* shells across a horizon on which ammonites are concentrated at 39.5 cm in his section. Each point represents a specimen. The trend lines calculated from the data points on each side of the presumed break show a slight displacement of the trend that Brinckmann used to assess the thickness of sediment apparently missing. B. Raup and Crick's replotting of Brinckmann's data for a longer stratigraphic interval. The plot shows a statistically significant displacement of the trend to increase in size at about 28 cm, but no displacement of the trend at 39.5 cm or at other horizons (shown by dashed lines) where Brinckmann noted stratigraphic breaks. The larger dot is used where two or more specimens have the same coordinates. (*Source:* Modified from D. M. Raup and R. Crick, *Paleobiology*, v. 7, pp. 90–100.)

sea and the major fossils of these cores are of simple planktonic organisms raining down from overlying waters.

Davida Kellogg (4) studied the variation in the radiolarian *Pseudocubus vema* in a deep-sea core representing approximately 2 million years of deposition. Figure 15–6 shows the increase by 50 percent of the width of the thorax through this interval. Although the rate of change of the character is not constant, but stepped, the data can be interpreted as a record of progressive and slow change within a species as it evolves. These radiolarians illustrate some of the problems of recognizing gradualism in the fossil record. Stephen Gould and Niles Eldredge (5) have objected that the stepped pattern of the trend shows that evolution was episodic rather than gradual. They also pointed out that the changes could have been caused by migration into the area of radiolarians with wider thoraxes rather than by evolution in place. The possibility of migration might be eliminated or established by regional studies of the distribution of the species. However, even the

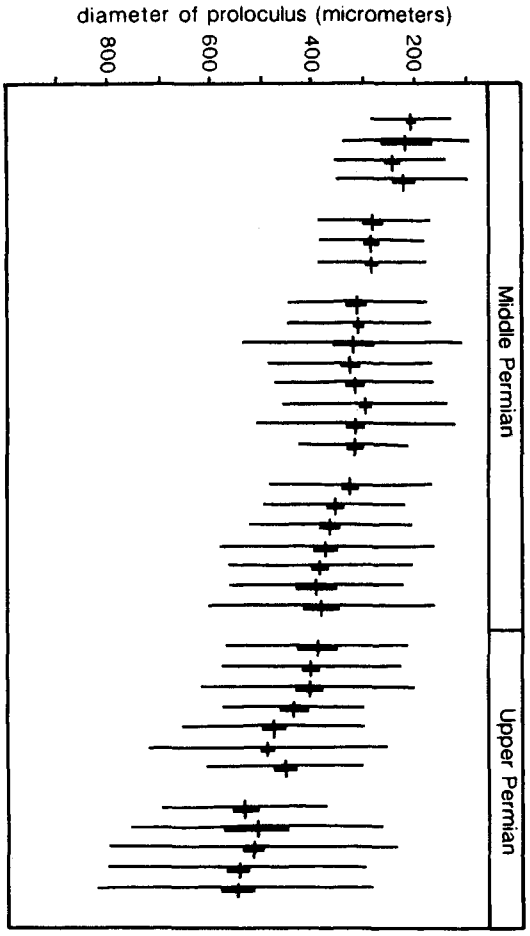

Figure 15-4 Increase in size through the Middle Permian and Upper Permian of the diameter of the initial chamber (proloculus) of the foraminiferan *Lepidolina* in East Asia. Mean values are indicated by vertical lines, black bars are 95 percent confidence limits, finer horizontal lines span two standard deviations. (*Source:* Modified from T. Ozawa, *Memoir*, Faculty Science, Kyushu University, v. D253, pp. 117–164.)

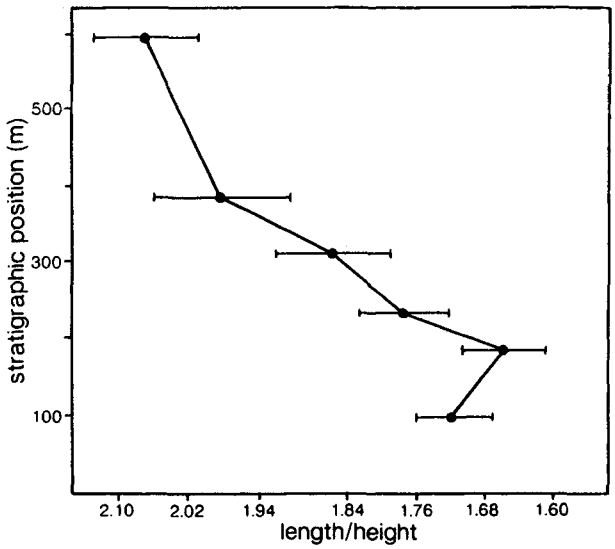

Figure 15-5 Increase in the length-height ratio of the Ordovician bivalve *Nuculites planulatus*. The means and 95 percent confidence intervals are plotted for six collections. (*Source:* Modified from P. & S. Bretsky, *Journal of Paleontology*, v. 51, p. 266.)

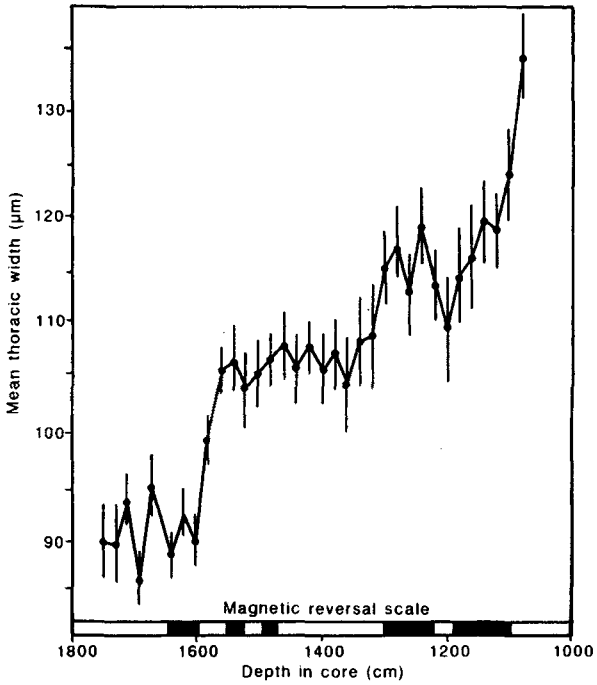

Figure 15-6 Change in the thoracic width of the radiolarian *Pseudocubus vema* from a core through Pleistocene and Pliocene beds. The magnetic reversal scale indicates that this deepsea core represents deposition between about 5 and 2.5 million years ago (dark is reversed). The dots are the means of many measurements and the vertical bars are 95 percent confidence levels of the means. A general increase in size is marked by several steps whose significance has been controversial. (*Source:* Modified from D. Kellogg, *Paleobiology*, v. 1, pp. 359–370.)

most thorough study could not eliminate the possibility that change seen in one stratigraphic section was the result of successive migrations rather than gradual evolution in place.

Early Cenozoic Mammals from Wyoming:

Through studies of collections from the Bighorn Basin, Phillip Gingerich (6) has postulated that gradual change characterizes the history of several genera of mammals. His simplest example, the primitive primate *Pelycodus,* is illustrated in Figure 15–7. The proportions of the first molar, expressed as the logarithm of the product of its length and width, changes almost imperceptibly through the species *P. ralstoni, P. trigonodus, and P. jarrovii.* At the top of the succession, *P. jarrovii* appears to give rise to two new species.

Similar studies of the Eocene condylarth *Hyop-*

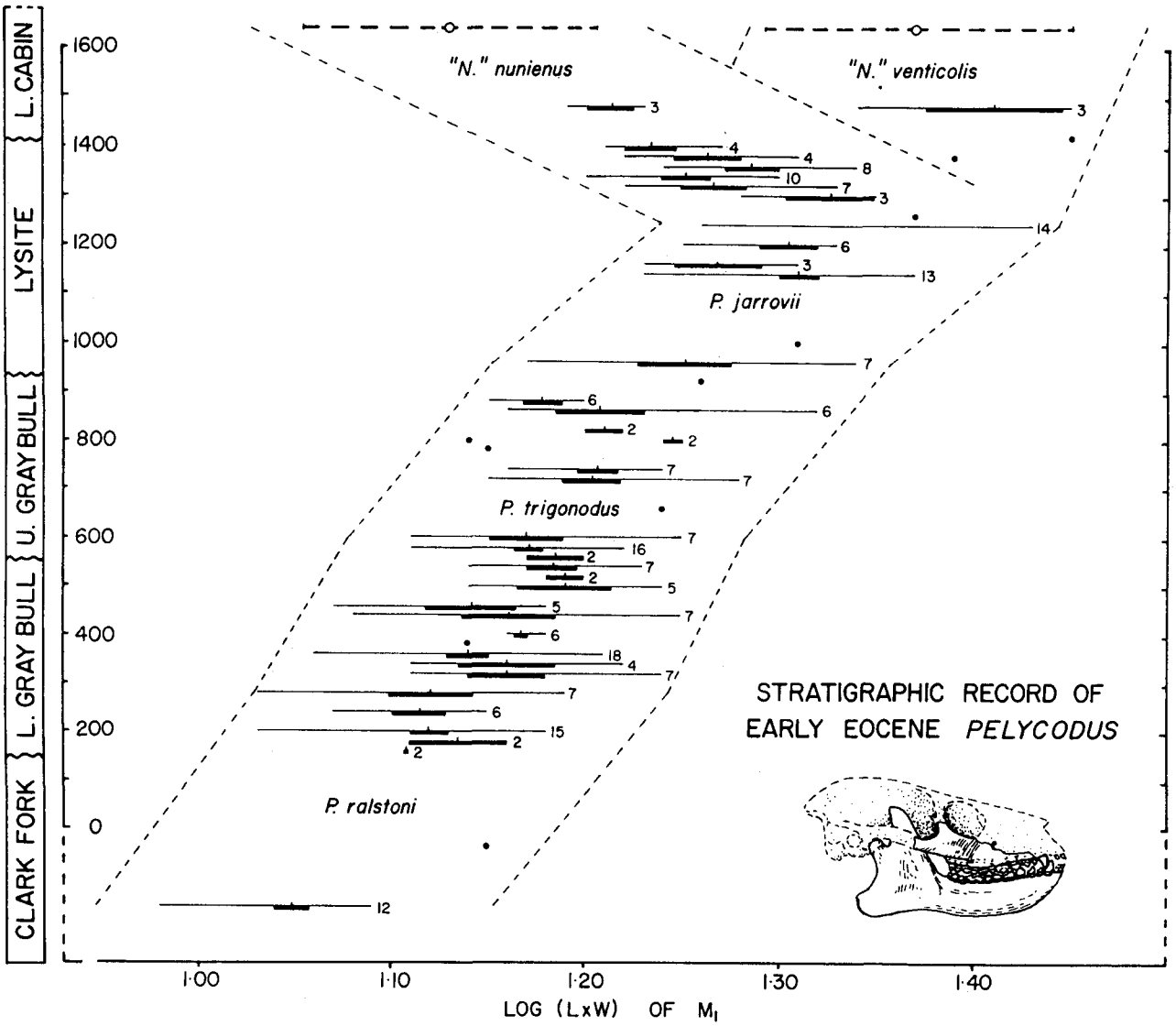

Figure 15-7 Evolution of the early Eocene primate *Pelycodus.* The horizontal scale is a measure of the proportions of the first molar tooth, and the vertical scale is in feet of the stratigraphic section in Wyoming, which is divided into stages. Each horizontal line expresses the variation in the number of specimens noted beside it. The shorter vertical line is the mean, the heavy bar is the standard error, and the light line is the range. The course of the phyletic evolution through this lineage is emphasized by the dotted lines. Several events of anagenesis and one of cladogenesis are suggested. (Courtesy of P. D. Gingerich, *American Journal of Science,* v. 276, p. 16. Reprinted by permission.)

sodus show a more complex pattern (Fig. 15–8) that Gingerich ascribed to gradual change combined with four speciation events.

Phyletic Gradualism:

We can see from these examples that not all cases of gradualism used to support the Darwinian concept of evolution have been shown to be valid by later work. However, enough well-documented examples have now been found to confirm that the type of evolutionary change postulated by the modern synthesis was widespread. Some of these gradual changes were within the range of variation included in a single species and no new species were generated. Changes in other lineages were great enough that taxonomists have divided the specimens that define the evolutionary trend into several different species. Evolution by continuous, progressive changes has been called phyletic gradualism.

The appearance of new species may be the result of two kinds of evolutionary change. Anagenesis takes place when one species becomes extinct by gradually evolving into another. The term *speciation* is applied to the process in which one species divides into two reproductively isolated lineages (Fig. 15–9). A division of one lineage into two may also be referred to as cladogenesis. The term clade (the root of the word cladogenesis) refers to all organisms descended from a progenitor species. Only speciation (or cladogensis) accounts for increasing diversity in an evolving lineage; if only anagenesis occurred, the number of species in a lineage would remain constant.

No evidence is found in these examples of initial isolation of small populations at the periphery of species ranges as required by the biogeographic–genetic model of speciation, but in most cases the data is insufficient to eliminate this possibility. Species formation by peripheral isolates has been called peripatric speciation. Supporters of the modern synthesis contend that these processes (anagenesis, cladogenesis, and peripatric speciation) all take place by the continuous accumulation of genetic modifications as organisms adapt to changes in their biological and physical environments.

EPISODIC SPECIATION

Although Darwin was committed to a gradualistic philosophy of the origin of species, he did not insist that evolution took place at a constant slow rate and implied in some of his later writings that species may originate in small populations evolving at faster than normal rates. George Simpson in his seminal book *Tempo and Mode in Evolution* (7) proposed that evolutionary changes giving rise to major groups (such as the initial stage in the radiation of ungulates in South America) took place in small populations evolving rapidly. As one of the architects of the modern synthesis, he held that most change took place in slowly evolving lineages. In the 1930s and 1940s hypotheses that evolution occurred in large steps were proposed by the geneticist Richard Goldschmidt and the paleontologist Otto Schindewolf. Goldschmidt claimed that major changes in the genetic material (chromosomal mutations) could change an individual so drastically that they would lead to a new major taxonomic group, such as a family or order, in one generation. The existence and effectiveness of such massive genetic changes has been doubted by most later workers. Schindewolf pointed out that major changes in the paleontological record of the ammonites took place in large steps rather than slow transitions. These were early proponents of the idea that microevolution alone will not explain the history of life.

Rate of Microevolution:

The rate of production of new species in the examples cited in the last section is slow. Critics of the modern synthesis claim that it is too slow to account for the diversification of life in the 800 million or so years since the origin of the metazoans.

A measure of the rate of evolution of a group is the average time range, or survivorship, of its species. In rapidly evolving lineages species exist for relatively short intervals before giving rise to new species. The average survivorship of all marine invertebrates has been estimated to be several million years. Survivorships of species ranging from .5 to 15 million years have been estimated by specialists of various invertebrate groups. Anthony Hallam (8) has made the following estimates of the average longevity (in millions of years) of invertebrates in Early Jurassic time: bivalves, 5.6; ostracodes, 3; ammonites, 1.5. Thomas Schopf (9) has argued that various biasing factors combine to lengthen these estimates and that a more reasonable figure for average species survivorship is 200,000 years.

Survivorships calculated from examples of phyletic gradualism in the fossil record are also several

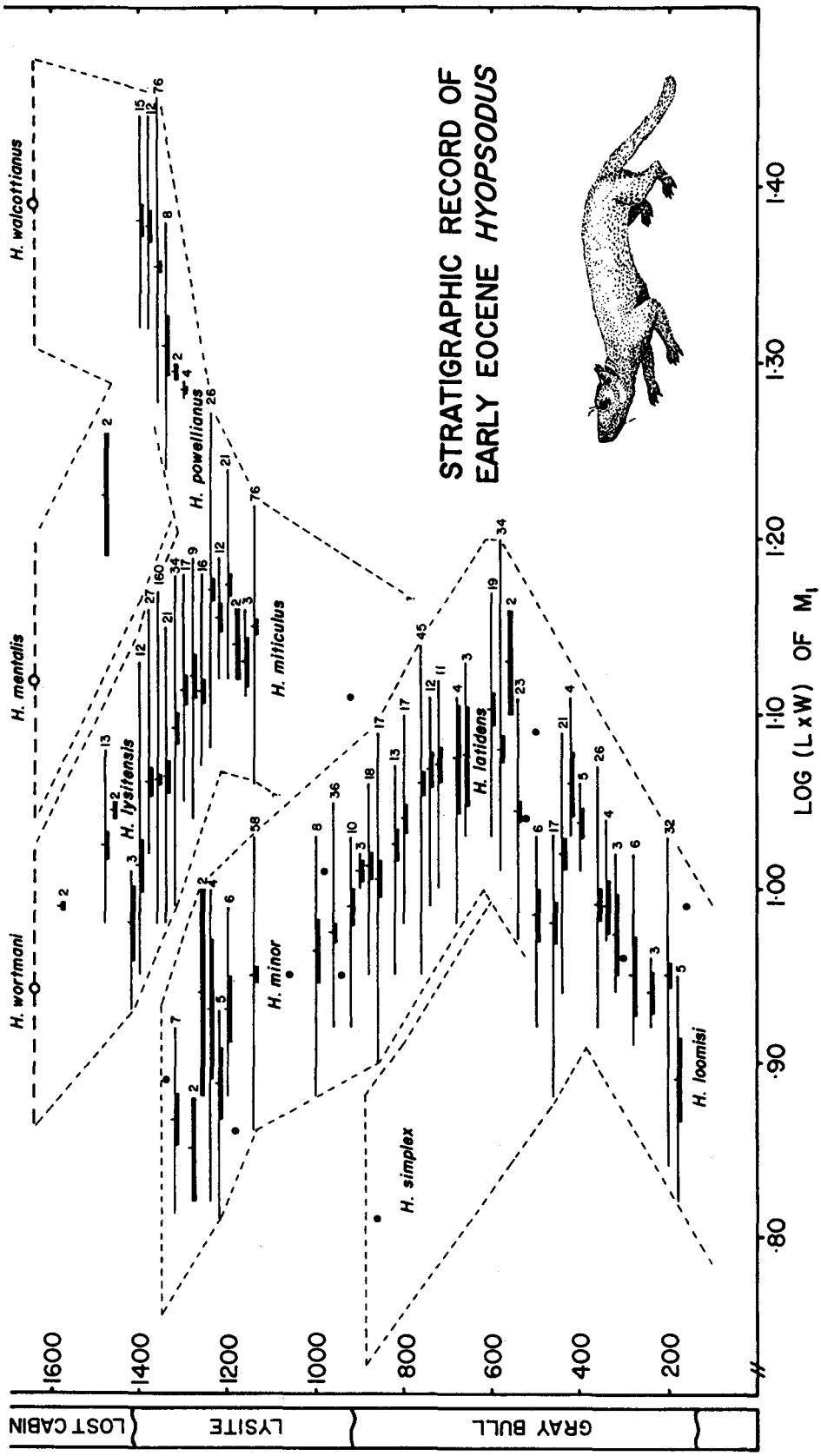

Figure 15-8 Evolution of the early Eocene condylarth *Hyopsodus*. The symbols are the same as in Figure 15-7. The pattern of anagenesis and cladogenesis in this lineage is interpreted to be more complex. (Courtesy of P. D. Gingerich, *American Journal of Science*, v. 276, p. 13. Reprinted by permission.)

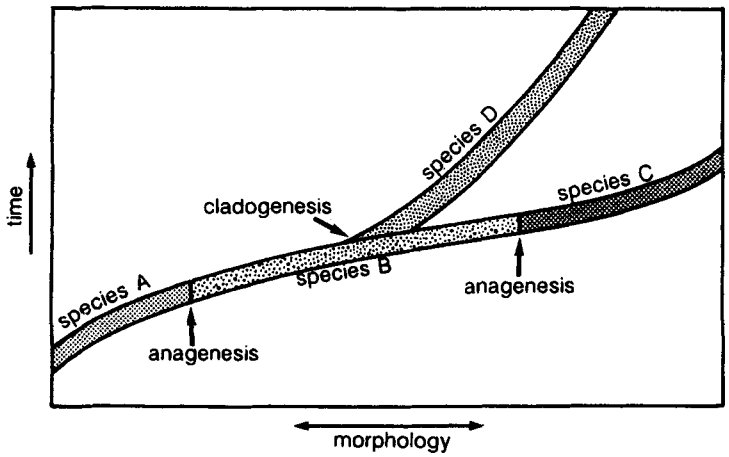

Figure 15-9 Diagrammatic representation of the origin of new species by anagenesis and cladogenesis. The horizontal axis is change in morphology.

million years per species (*Gryphaea*, mammals). Those who believe this rate is too slow to account for the bursts of adaptive radiation documented in the fossil record—for instance, at the start of the Paleozoic when about 135 families of marine invertebrates originated in 25 million years (Fig. 5–15) or at the start of the Cenozoic when 100 new families of mammals appeared in 25 million years—postulate that a faster process is at work and that most evolutionary change takes place during cladogenesis.

Punctuated Equilibrium:

Niles Eldredge and Stephen Gould (10) pointed out that the lack of all but a few examples of phyletic gradualism in the fossil record is what is to be expected if new species arise rapidly as small, peripherally isolated populations. Because emerging species are thought to constitute small populations separated from their ancestral population, we should rarely see the transition from one to the other in a single stratigraphic section. Because the transition takes place rapidly, intermediate forms are unlikely to be preserved anywhere in the fossil record. What we do see is what Eldredge and Gould said we should see: long intervals of no change punctuated by the sudden appearance of a new species as a peripheral isolate differentiated elsewhere spreads into the area of its ancestor. They believed that nearly all evolutionary change takes place at these speciation episodes, and that gradual evolution by anagenesis is an insignificant process in the history of life. The two models can be contrasted in a diagram (Fig. 15–10). Because the period of stability or stasis has

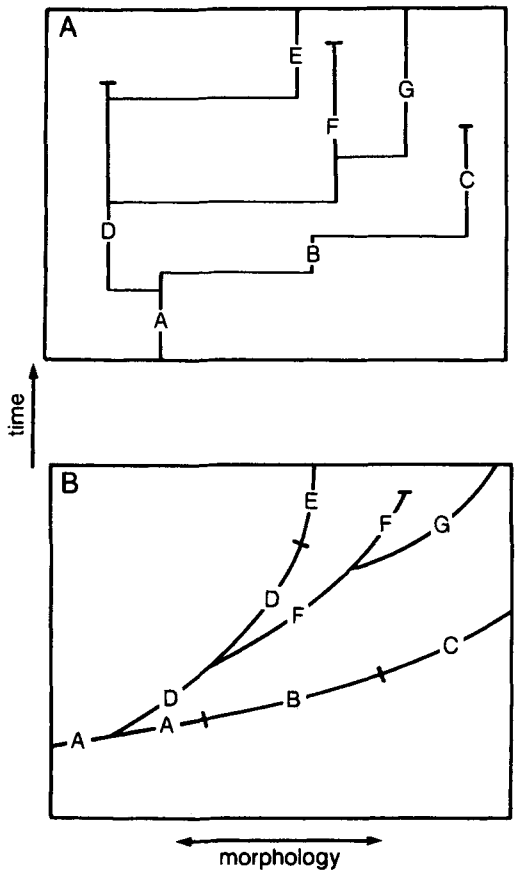

Figure 15-10 Punctuated equilibrium (A) and phyletic gradualism (B) contrasted. A. Species are static in morphology and evolutionary changes are cladogenetic and rapid. B. The origin of some species is anagenetic and some are cladogenetic. Species change gradually along morphologic gradients.

been pictured as a state of equilibrium broken by speciation events, the model has been called punctuated equilibrium. Only detailed sampling of stratigraphic sections of continuous deposition can prove the rapidity of the speciation process and the absence of subsequent change.

Evidence of Punctuated Equilibrium:

During Pliocene time a population of bivalves related to the common cockle, *Cerastoderma,* diversified into 30 genera and many species within a period of 3 million years in the Caspian Sea. During the same time interval the parent population of *Cerastoderma* changed little in the open ocean. Such rapid diversification has been thought to require the concentration of changes at speciation events as an organism adapts to a new environment. The rapid increase in diversity only requires closely spaced cladogenic events; the changes are not required to be episodic.

Niles Eldredge described the changes in the lineage of the trilobite *Phacops rana* in the Devonian of New York (10) using the punctuated equilibrium model. The subspecies and species are distinguished on the basis of the number of vertical rows of lenses in the schizochroal eyes (Fig. 7–26). The oldest species have 18 rows of lenses and the more advanced taxa have 17 or 15 rows. Eldredge believed he could show that the new forms with fewer lens rows first appeared suddenly in the record as peripheral isolates in the eastern part of their geographic range and then spread to the western part. Some doubt has been expressed about this interpretation.

Peter Williamson (11, 12) studied the succession of gastropods and bivalves in the Pliocene and Pleistocene beds of Lake Turkana in northern Kenya. In 19 species lineages he believed he could identify evidence of punctuated equilibrium. At some levels, such as a volcanic ash bed, morphologically distinct subpopulations suddenly appeared without intermediate forms and coexisted with the ancestral population before dying out. Many of the lineages followed the same pattern at the same horizon. Williamson interpreted this sudden appearance as the spread of peripheral isolates into the larger ancestral population. He calculated that the origin and spread could not have taken more than a few thousand years (an instant in geological time). Others have replied that the changes are superficial responses in the growth of the molluscs to changing conditions and not an expression of changes in the genetic makeup of the animals by selection.

The major support for the punctuational equilibrium model according to Gould and Eldredge (10) is the paucity of gradual successions of species despite the search through the record by paleontologists for about 150 years. The most convincing examples of gradualism come from the protozoans whose reliance on asexual reproduction may result in a mode of evolution different from sexually reproducing higher invertebrates and from vertebrates. Although countless paleontologists have approached the paleontological record with hope of finding an evolutionary series, they have found that species generally appear in their sections without obvious ancestors and disappear without obvious descendants.

Conclusion:

Evidence for phyletic gradualism in the fossil record is certainly scarce but it is available. The scarcity of gradualism may be because (1) most stratigraphic successions where paleontologists have searched for evidence of gradualism were deposited on continental borders and are interrupted by many gaps in deposition and on land where even the best-known sequences are too incomplete to show consistent change over less than 5,000 to 10,000 years, or (2), most evolutionary change is concentrated in short periods of speciation (punctuated equilibrium). Several paleontologists have noted that the paleontological record will never be able to demonstrate the nonexistence of either phyletic gradualism or punctuated equilibrium. Times of rapid diversification (adaptive radiation) cannot be accounted for by a background rate of evolution producing species at a rate of about one every few million years. The disagreement among paleontologists is whether this rapid splitting of species and increase of evolutionary pace is just a quickening of the processes of natural selection between individuals that Darwin proposed or whether it is an entirely different process concentrated in speciation.

NATURAL SELECTION

Natural selection is a process that occurs in all populations. It acts upon inheritable variations that result in differences in fitness among individuals—differences that are related either to reproduction of the next generation or to survival of the indi-

vidual. The distribution of variations within the population will reflect these differences in fitness and will change from the parent population to the offspring population. Evolution can be defined as changes in the relative frequency of alternative characteristics that take place progressively from generation to generation.

The model of evolution proposed by Darwin and incorporated in the modern synthesis was based on competition between individual organisms for resources, mates, safety from predators, and living room. Only recently have extensive studies in the field shown the importance of competition between species and within species (13). One school of ecologists maintains that competitive interactions cannot be demonstrated to be the major driving force of evolution. Some of this school have been implied that Darwin's postulate of the "survival of the fittest" was not based on observation but was an outgrowth of the "laissez faire" economic theories of Victorian England (15). John Endler lists over 125 specific demonstrations of natural selection in natural situations (14). Field studies of competition usually involve the removal or transplantation of one of the competitors and the observation of the reactions of the others. While this may show interspecific or intraspecific competition within or between certain species, the general demonstrations of competition are the adaptive features of organisms (their good fit to the environment, see Chapter 14), convergent evolution, mimicry, and protective coloration.

Convergent evolution was discussed briefly in the last chapter and in Chapter 3. The similarity of organisms of different ancestry living in the same environment suggests that processes of selection for the attributes they share have determined their form.

Mimicry:

Although mimicry exists throughout the plant and animal kingdom, the most striking examples are found in the insects. Insect species that are not poisonous to birds have evolved remarkable similarities to poisonous species. The obvious conclusion is that the nonpoisonous species have achieved relief from predators by the progressive selection of those variants that most resemble poisonous species. Those that were least like poisonous species were preferentially eaten by birds and eliminated from the breeding population.

Protective Coloration:

Many animals have a covering of fur, feathers, scales, or skin that resembles the environment in which they live and makes them difficult to detect by predators. The pepper moth, *Biston betularia,* has been repeatedly cited as an example of selection for protective coloration. A dark phase of this moth differs from a light phase by a single gene. Until the 1840s only the light phase was recorded in the English Midlands. Since this time the dark phase has increased in abundance until it now constitutes about 80 percent of the population in heavily industrialized areas. In these areas the trees on which the moth alights have been blackened by industrial soot in the last 150 years. Against this dark background the light moths are conspicuous and have been selectively eaten by birds. The selective advantage of the dark (or melanic) form has been proved by direct observation of the individual fates of light forms bred in captivity and released into the environment, and by release and recapture experiments with both varieties. In competition with the light phase, the dark phase has selective advantage where trees are darkened. Recent restrictions on the release of industrial pollutants have reduced the darkening of trees and led to a slight comeback of the light phase. This is an example of intraspecific selection—a new species has not been formed by this adaptation but the frequency of occurrence of certain genetically controlled features has been changed by selection over a period of a few tens of years. If numerous genetic changes of this type occurred throughout the range of a species, they could lead eventually to its recognition as a distinct species.

The "Arms Race":

All organisms in a community except the primary producers that derive their energy from inorganic nutrients are, in a sense, predators since they rely on organisms below them in the food chain for sustenance. The evolutionary action-and-response relation between predator and prey has been compared to the arms race between superpowers. An advance in the ability to attack by the predator must be balanced by an advance in the ability to escape by the prey, and vice versa, or one of them will become extinct. The reality of this form of interaction can be illustrated by the change in size of the brains in herbivores (prey) and carnivores (predators) during the Cenozoic Era. Carnivores

generally have proportionally larger brains than herbivores because greater intelligence is required to catch prey than to escape from predators (16). Both herbivores and carnivores increase in brain size throughout the Cenozoic but carnivores are always ahead of contemporary herbivores. As the herbivores got smarter, the carnivores got smarter still in order to catch them. This evolutionary trend is difficult to explain unless competition between members of both the predator species (to find more prey) and prey species (to escape more efficiently) is a reality.

These examples leave little doubt that competition within species can be found in nature. Competition between species is more difficult to demonstrate because species generally exclude from their habitat species competing for the same resources.

SPECIES SELECTION

The term *species selection* has been applied to those processes that cause the differential survival of species as opposed to those that affect individual organisms. At present there is controversy over whether these selective processes are distinct.

If phyletic gradualism is rejected as a mechanism of significant evolutionary change and the production of new species is ascribed to major genetic changes that occur at cladogenesis, then selection directed at the individual level loses its importance. The argument has been made by the supporters of punctuated equilibrium that processes which operate only in the production of new species facilitate the rapid evolutionary change necessary to account for periods of rapid diversification in the fossil record. Since gradualistic changes are too slow, the raw material for selection must be produced at these rapid speciation events and the path of evolution must be shaped by selection between the species so produced.

Natural and species selection can be compared in a table which is a modification of one presented by Steven Stanley in his book *Macroevolution*. Stanley, however, identifies the natural selection in this table with microevolution, and species selection with macroevolution.

Although selection among species must take place, disagreement is focused on its importance and whether it is different from, or decoupled from, natural selection. Gould (17) argued that evolutionary processes take place at various levels, or tiers, and that evolution is a hierarchy of processes. Natural selection operates at the level of the first tier and species selection, at the level of the second tier. Biologists have so far discovered few, if any, evolutionary trends that cannot be explained as well by natural selection at the level of the individual as by species selection (18).

MACROEVOLUTION

The term *macroevolution* has been used in many senses. Generally it has been used to refer to evolutionary processes that result in changes giving rise to higher taxonomic categories such as families, orders, and classes. It is in this sense that the term is used here.

The concept of macroevolution comes from the perception that the paleontological record lacks fossils that show the transition between major taxonomic groups. These fossils would be expected if the transition has been bridged by microevolutionary steps. The lack of transitional forms could be due to gaps in the record, to the smallness of the evolving population (and therefore the unlikelihood of preservation), or to the fact that major evolutionary novelties arise by major genetic reorganization or major changes in developmental processes that are too rapid to leave many intermediate individuals. Most of the large evolutionary steps by which the invertebrate phyla differentiated from ancestral metazoans took place before the evolution of skeletons and are therefore not preserved in the fossil record. Whether features of the soft anatomy and physiology that are critical to the origin of many higher taxa of vertebrates appeared abruptly or gradually cannot be determined because these features are not reflected in the bones that are preserved. Examples of such unpreservable features are the amniotic egg that separates all higher vertebrates from fish and amphibians and the mammary glands that characterize mammals.

	Natural Selection	Species Selection
Level of action	Individual	Species
Source of variability	Random individual genetic changes	Major genetic or developmental changes generated randomly associated with speciation
Rewards of success	Survival and reproduction	Speciation
Cost of failure	Death or failure to reproduce competitively	Extinction

Examples of the transitions between major groups that *have* been thought to require macroevolutionary processes include the origin of the invertebrate phyla, the origin of land plants from algae, the origin of the vertebrate body plan from invertebrate ancestors, the transition from fish to amphibians, and that from amphibians to reptiles.

Origin of Higher Taxa:

Ideally, major taxa include all descendants of a single progenitor species. Classes, orders, families, and genera are aggregates of species united by common descent from an ancestor in which the characteristics of the group are first evident.

Methods of classifying organisms make differences between major taxa seem greater than they originally were. Between the end of the Cretaceous Period and the early Paleocene, 16 new orders of early ungulates arose from primitive condylarths in 2 to 3 million years. Many species and genera identifiable in the early part of this period went on to be founders of new families, but had biologists been present to make a classification of the group in Paleocene time, they would have recognized them only as slightly different genera of one family of mammals. The significant characters of founder taxa can be recognized as major steps in evolution only after the successful spread of these characters and after the diversification of the organisms bearing them has taken place.

In well documented transitions that have been described as macroevolutionary events, the initial step that was eventually of great evolutionary importance was not a major reorganization of the organism, as the term macroevolution implies.

Emergence of New Structures:

Three examples from the evolution of the vertebrates will illustrate the nature of some major transitions. Many of the evolutionary changes between major taxa have been associated with changes in habitat, or way of life. The significance of the first small steps in these transitions is that they allowed penetration of a new ecologic zone and led to subsequent diversification into many species that we recognize as constituting a major taxon.

Amphibians evolved from rhipidistian fish in Late Devonian time. The advanced rhipidistians are similar to early amphibians in most anatomical features. The similarities include the capacity to breath air, body shape, and bone structure of the body, upper limbs, and skull. The only major changes from fish to amphibian were the evolution of feet at the ends of the fins, and the elaboration of ribs to support the lungs and viscera. Forms with limbs intermediate between fins and feet have not been found in the fossil record presumably because there was not a broad adaptive zone to be occupied by animals that were only partially adapted to terrestrial locomotion. However, in a shrinking aquatic environment where fish were being stranded, any limb improvement that would allow the animal to move over the drying surface would have given it a competitive advantage and would have rapidly resulted in the refinement of this method of locomotion. This anatomical change corresponded in time and place with the availability of a new environment. The land had recently been clothed with plants and populated by terrestrial arthropods. Subsequent diversification of vertebrates with limbs capable of walking led to the group we now recognize as tetrapods.

Even the one feature that distinguishes *Archaeopteryx* (the oldest known bird), its feathers, are not new structures. The similarity of their embryological development shows that reptilian scales and avian feathers are homologous. Feathers evolved from scales through size increase and an elaboration of their shape. It is difficult to understand how selection could have acted to favor this modification in the ancestors of birds since an enlarged reptilian scale would have little value as a flight surface. However, feathers also serve for insulation, and even a relatively small increase in size of the reptilian scale may have made it efficient in providing insulation for the small endothermic dinosaurs that gave rise to birds. Once the scales were of larger size, selection may have acted to change their shape to assist in flight. Such a change in function is frequently an important factor in the emergence of major new taxa and their adaptation to different ways of life.

Except for the long forelimb and the presence of feathers, the skeleton of *Archaeopteryx* remains almost totally dinosaurian. The distinctive skeletal features that are typical of modern birds evolved long after the first birds had become committed to flight.

The steps by which the mammals evolved from mammal-like reptiles required over 100 million years through Permian and Triassic time (see Chapter 11). Through countless intermediate forms the anatomical and physiological features that we associate with modern mammals evolved in relation to

increased metabolic rate, changes in patterns of feeding, locomotion, and more acute sensory perception. No particular event within this sequence can be recognized as a major macroevolutionary change that in itself produced the higher taxon and yet the final results are as different as those between any of the vertebrate classes.

Conclusion:

Despite more than a hundred years of speculation that mechanisms other than natural selection act on individuals to produce major steps in evolution, no examples from the paleontological record or from studies of living organisms have demonstrated the nature of such processes or proved their existence.

As stated at the beginning of this chapter, this is a time of ferment in paleontology when the record is being searched intensively for examples to corroborate the various models of evolution that have been discussed here. At present a consensus has not emerged from the discussion but when it does, it will probably incorporate parts of both sides of these areas of conflict. The lack of simple answers to many of these questions reflects the complexity and diversity of evolutionary processes. This lack has also stimulated new ways of looking at the paleontological record.

TRENDS AND ONTOGENY

Trends:

Some long-term trends in the fossil record have been discussed in this chapter as examples of phyletic gradualism. By far the most widespread of such trends is increase in size. Size increase among warm-blooded animals has been termed Cope's Law, named after Edward Cope, a vertebrate paleontologist. In the histories of practically all mammalian groups early members are smaller than later ones. Other things being equal, a large animal is more heat efficient than a small one because the rate at which it loses heat is proportional to the area-to-volume ratio. Although size increase has some advantages for invertebrates, such as avoidance of small predators, the trend to size increase in invertebrates is not as widespread. Changes in the coiling of the shell of *Gryphaea* through Early Jurassic time were attributed to allometry and increase in its size. As shells grew bigger, they coiled more strongly. In later Jurassic beds, although the shells continue to be large, their convexity diminishes; the shells have the size of an adult but coiling of a juvenile *Gryphaea*. The mechanism by which such changes take place can be explained by the study of the development of the individual organism from the fertilized egg to reproducing adult, its ontogeny.

ONTOGENY AND THE FOSSIL RECORD

Embryos and Ancestors:

Since ancient times people have been fascinated by the development of embryos of animals and in particular by the human embryo. The studies in ontogeny made by the ancient Greeks were based for the most part on human fetuses available through spontaneous abortions, and from these they learned that ontogeny is not solely a matter of growth and that embryos are not just miniature adults. But in the nineteenth century the Prussian zoologist Karl Ernst von Baer (1792–1876) established that embryos develop from general characters towards more specific ones, and that the similarity between the embryos of different groups of animals is greatest in their early stages of development.

Comparison of the early stages of embryos led some zoologists of the late eighteenth and early nineteenth centuries to postulate that organisms in ontogeny pass through stages of evolution comparable to those of their ancestors. An example will clarify the type of evidence on which this concept was based. At about four weeks the human embryo develops four internal pouches (pharyngeal pouches) in the throat region that are positioned opposite external folds in the neck region. Between these pouches and folds six blood vessels called aortic arches pass from a ventral artery to a dorsal one. This arrangement is remarkably similar to the same region in the embryos of fish. In fish development the internal pouches and external grooves break through and join each other to form the gill slits. The aortic arches are the vessels by which the blood circulates past the gills to be aerated. In the human embryo only one of the pouches and grooves join to produce a canal. This passage becomes the eustachian tube that joins the ear and throat. Some of the other pouches atrophy; others become glands such as the thyroid and parathyroid. Most of the aortic arches in mammals are lost as the embryo develops. One pair (the sixth) goes to the lungs,

and the left half of the fourth becomes the major artery to the head and body.

Ernst Haeckel (1834–1919) formalized and popularized the observation that the anatomy of primitive groups was reflected in the ontogeny of more advanced relatives. He proposed what he called the biogenetic law, usually summarized as: ontogeny recapitulates phylogeny. What he meant was that in its development from embryo to adult the individual passes through (recapitulates) the evolutionary stages of its ancestors. Thus the human embryo progresses from a single cell (protozoan) through a blastula (cnidarian) (Fig. 5–3), through higher invertebrate stages to resemblance to a fish, a reptile, and finally to a primate. This is recapitulation. Evolution consisted of adding on to the end of the ontogenetic sequence new adaptations as they were acquired. Of course, the organism could not repeat the whole of its ancestry, and skipping of stages and acceleration of the sequence was essential if the embryological development were to take a reasonable amount of time. The influence of the concept of recapitulation on paleontological thought of the late nineteenth and early twentieth centuries is hard to overestimate for it seemed to offer zoologists and paleontologists a key to reconstructing the ancestries of all organisms—these ancestries were still preserved in miniature in their ontogenies.

Many kinds of shell-bearing invertebrate animals carry through their lives the record of the development of their skeletons during the embryonic stages. The shells of foraminiferans, most molluscs, and brachiopods are of this type. The horn-shaped skeletons of the rugose corals carry the history of septal insertion in their tips. In other organisms, for example, sponges, arthropods, echinoderms, and vertebrates, the skeleton is either modified during growth or discarded at each growth stage. The early molts of arthropods may be difficult to associate with the adult species into which they eventually grew but this problem has been solved for many trilobites. In the early part of this century much paleontological research was devoted to the search for ancestors in the ontogenetic stages of fossils. Paleontologists ground at the tips of rugose corals to reveal the early septal patterns, pulled ammonites apart to see the patterns made by the sutures in the first-formed chambers, and made thin sections of foraminiferans to study their embryonic chambers.

Yet Von Baer had pointed out in the early 1800s that embryos never resemble the adults of their ancestors, as Haeckel proposed, but only the embryos of related animals. Haeckel admitted that much condensation of ontogenies took place and not infrequently disturbances in the order of embryonic stages led to misleading results in reconstructing phylogenies. In many animals recapitulation did not seem to explain the sequence of developmental changes. In fact, just the opposite took place—early stages of the ontogeny of ancestors became the adult stage in descendants. This process is called paedomorphosis. The process that Haeckel called recapitulation is now referred to as peramorphosis (20) because Haeckel's term had become associated with his evolutionary theories that are now discredited. The basic difference between peramorphosis and paedomorphosis can be illustrated in the following tables.

Peramorphosis

T	A	B	C	D	E	F*
I	A	B	C	D	E*	
M	A	B	C	D*		
E	A	B	C*			
	ONTOGENY →					

Paedomorphosis

T	A	B	C*			
I	A	B	C	D*		
M	A	B	C	D	E*	
E	A	B	C	D	E	F*
	ONTOGENY →					

*adult stage

A to F are ontogenetic stages of individuals. Ancestors are at the base of the table; descendants are at the top.

When the ontogeny of an ancestor is compared to that of its descendant, peramorphosis has occurred, either if the rate of development of nonreproductive features is accelerated so that new adaptations are added before maturity is reached or if onset of sexual maturity is delayed. Paedomorphosis has occurred if the maturation is accelerated so that the organism can reproduce at a stage when its body resembles that of a juvenile, or if the rate of development of nonreproductive features is retarded. The axolotl, a Central American amphibian, is a classical example of paedomorphosis. Most amphibians pass through a stage in which they breathe in water using gills before they reach ma-

turity, then shed their gills, grow legs, and live as adults on land. The axolotl, however, grows to adult size and matures in the water without ever reaching the adult (land) stage of its ancestors and retains ancestral juvenile features, such as gills, which allow it to remain in the water. The human face is another example of paedomorphosis. Our ancestors, the apes, have sloping foreheads and forward thrust mouths but their young have a facial profile much like that of *Homo sapiens*. The face of the human (the descendant) at maturity is much like that of the ape (the ancestor) at a juvenile stage. Paedomorphosis also describes the decrease in curvature of the *Gryphaea* lineage in Late Jurassic time. Their evolution was marked by the appearance of large, mature individuals with the juvenile proportions (in coiling) of their ancestors, a typical example of this phenomenon.

Although the study of peramorphosis does not solve problems of phylogenetic reconstruction, as it was once hoped it would, it helps the paleontologist to distinguish the more general characteristics of an organism from the more specialized ones and therefore is invaluable in classification and useful in establishing descent and ancestry. Embryos are never like adults; they are always adapted to the embryonic environment and recapitulation, in the sense of Haeckel, does not occur. Major changes in the form of an adult can result from minor changes in the genes that control rates of maturation and growth of the individual.

The relation between the ontogenies of ancestors and descendants is more complex than this discussion has indicated (19). Changes in the rates of (1) growth in size, (2) maturation, and (3) morphological change, between the ontogeny of ancestors and descendants define six different relationships, each of which has a name (Fig. 15–11). Space does not allow a discussion of these relationships, and their recognition in the paleontological record is difficult.

Peramorphosis in Fossils:

Studies of fossil lineages have revealed examples of peramorphosis and paedomorphosis but some structures found in the early stages of ontogenies may be larval adaptations and not directly influenced by the ancestry of the organism.

Peramorphosis is shown by many mammalian lineages in which the size of anatomical features, such as horns or antlers, is allometrically coupled to an

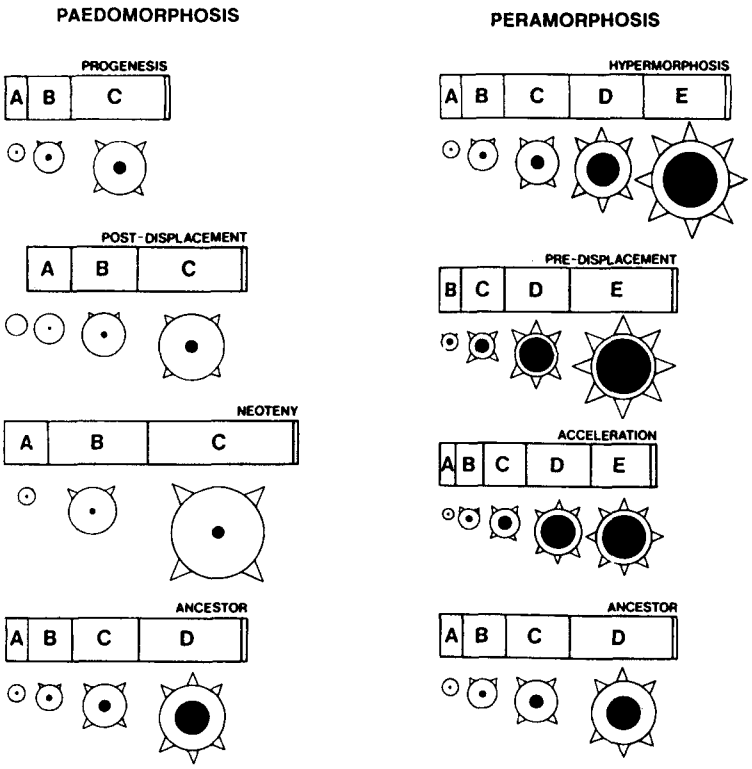

Figure 15-11 Relations of the three paedomorphic processes on the left and three peramorphic processes on the right to the ontogeny of an ancestral form. Stages in the development of a hypothetical organism with a central pore and spines are labeled A, B, C, D, and E. The ontogeny of the ancestor is shown in the lower rows. In neoteny, the rate of development is reduced and in this example, the onset of maturity is retarded, resulting in the descendant adult being larger but having an immature morphology. In postdisplacement, the growth of spines and the pore is delayed; therefore, juvenile characteristics appear in the adult. In progenesis, precocious sexual development results in an adult smaller than the ancestor. In acceleration, increased development rate results in adult characteristics of the ancestor appearing in the descendant juvenile. In predisplacement, the growth of the pore and spines starts at an earlier stage than in the ancestor. In hypermorphosis, the onset of sexual maturity is delayed so that the adult is larger and more developed morphologically than the ancestor. (Courtesy of K. J. McNamara, The Paleontological Society, *Journal of Paleontology*, v. 60, pp. 4–13.)

evolutionary trend for increase in size. For example, the last members of the brontothere family have massive horns which grow from smaller, simpler horns in the ontogeny of the individual (Chapter 12). Early members of the family are smaller in size and have smaller horns. The descendants have gone farther along an evolutionary trend than the ancestors, and the descendant's juveniles resemble the adults of its ancestors. Peramorphosis seems to be a pattern of evolution followed where selective advantage is given (1) to prolonging ontogeny to achieve greater size, and (2) to the advancement into early stages of ontogeny of complex structures that are produced late in growth.

A classic example of a fossil succession ascribed to peramorphosis was described early in this century by R. K. Caruthers from species of the Carboniferous rugose coral *Amplexizaphrentis*. In what he thought were successive layers, four species of the genus replace each other, but their stratigraphic ranges overlap. The ontogeny of the septal pattern is revealed by cutting through the apical regions of their conical skeletons. The adult pattern of the ancestral form, *Amplexizaphrentis delanoui*, occurs in the early ontogenic stages of its descendant, *A. parallela*. The septal patterns of both adult *A. delanoui* and *A. parallela* appear in successive juvenile stage of the descendant of *A. parallela, A. constricta,* and so on (Fig. 15–12). Euan Clarkson (20) has suggested that the pattern of evolution of this coral is

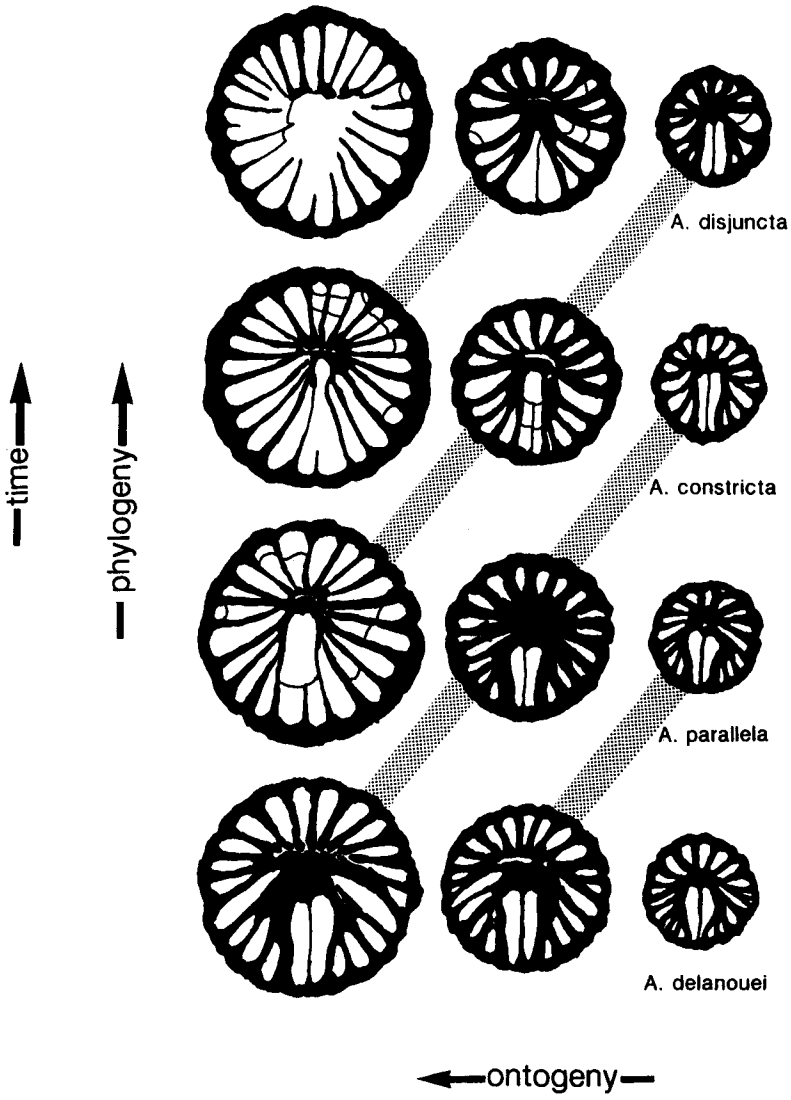

Figure 15-12 Peramorphosis in the Carboniferous rugosan coral *Amplexizaphrentis*. Ontogeny is represented by successive sections across the corallum showing the septal arrangement. The similarity of adult stages of early species to juvenile stages of their successors is emphasized by diagonal bars. (*Source:* Modified from J. A. Caruthers, *Journal of the Geological Society*, v. 66, 1910.)

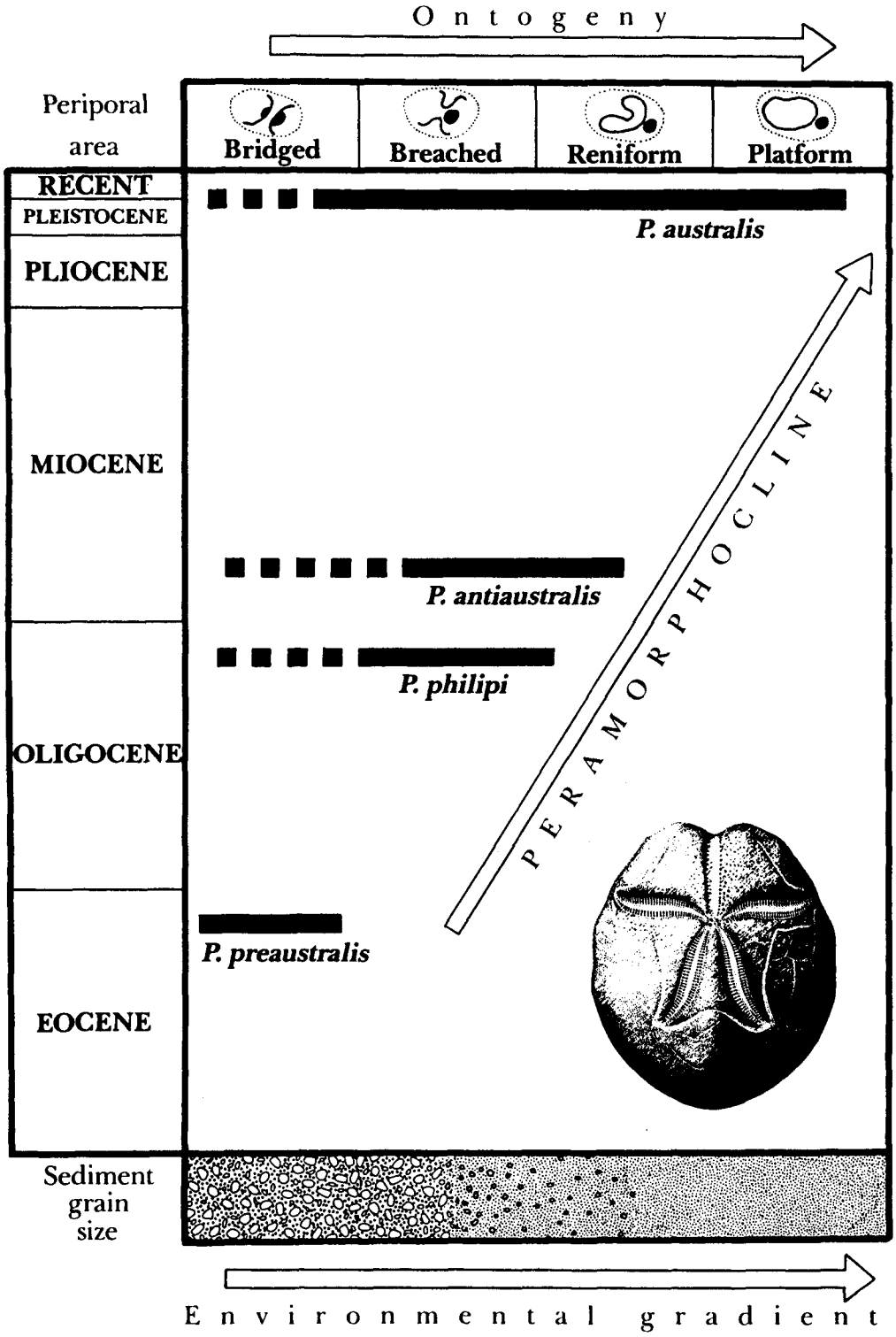

Figure 15-13 Peramorphosis in the evolution of the Cenozoic irregular echinoid *Protenaster* in Australia, shown by changes in the area around the pores illustrated along the top of the diagram. Later species undergo a progressively increased rate of development of this characteristic by acceleration. This change follows the environmental gradient illustrated along the bottom of the figure. The species illustrated in *P. preaustralis*. (Courtesy of K. J. McNamara and *Palaeontology*, v. 28, pp. 311–330.)

complex and not simply explained by Caruther's concept of recapitulation.

Kenneth McNamara (21) has interpreted the evolution of the pores in the plates around the mouth of the burrowing echinoid *Protenaster* as an example of peramorphosis. In the earliest species of the genus of Eocene age, *P. preaustralis,* the pores are all in the bridged condition (Fig. 15–13). In the successively younger species, *P. philipi, P. antiaustralis,* and *P. australis,* the pores in ontogeny pass through stages in which they are like the adult pores of their ancestors and progress from a bridged, to a breached, to a reniform condition In the adult stages of the living species the trend is continued to the platform condition. The trend is interpreted as an adaptation to life in finer-grained sediments.

Paedomorphosis in Fossils:

The evolution of the Cenozoic brachiopod *Tegulorhynchia* through several species to the genus *Notosaria* is an example of paedomorphosis (Fig. 15–14). In adults of the first species of the lineage, *T. boongeroodaensis,* the pedical hole is small and the apical angle of the pedicle valve is large, but in its juvenile stages the hole is proportionally larger and the angle smaller. As the lineage evolves, adult stages of successively younger species have features that are typical of the juvenile stages of their ancestors. The modifications are probably adaptations to life in more turbulent water where a thicker pedicle was an advantage.

The bivalve species *Cardium plicatum* and its descendant, *C. fittoni,* have been cited as examples of paedomorphosis (Fig. 15–15). The adult of the ancestor has many ribs marked by overlapping growth lamellae. Its juvenile form has fewer, more widely separated ribs with spines on them. The adult of the descendant, although larger than the ancestor, has ribs like its juvenile, few and widely spaced.

Some paleontologists have postulated that major groups arose and major steps in evolution were

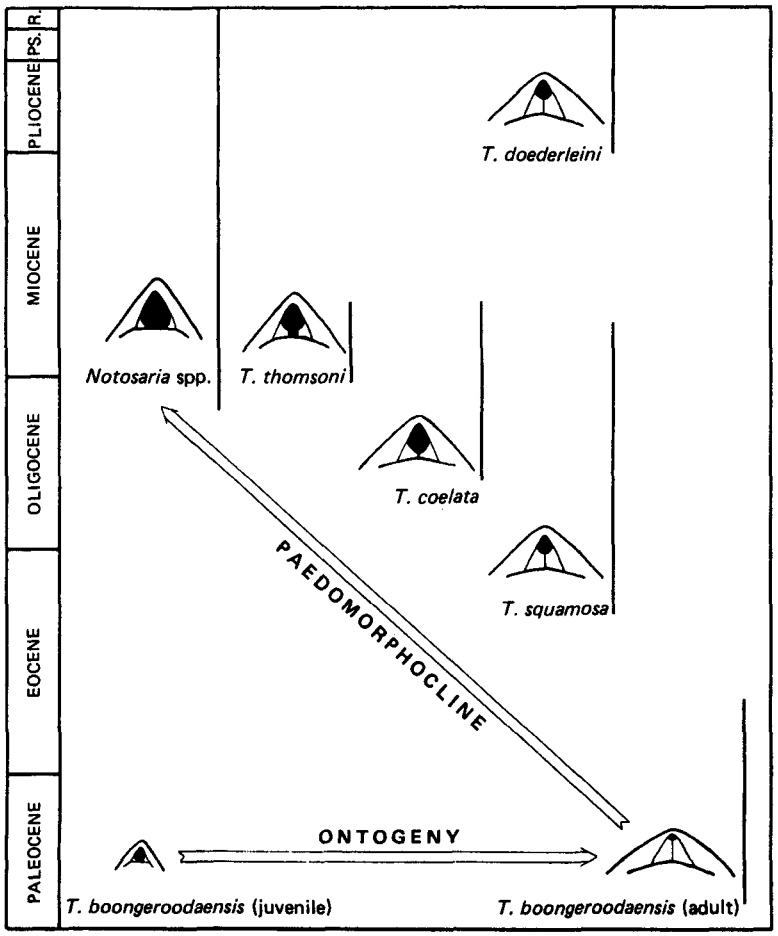

Figure 15-14 Paedomorphosis in four species of the rhynchonellid brachiopod *Tegulorhynchia* and one species of *Notosaria*, all from the Cenozoic of Australia and New Zealand. The ranges in time of the species are shown by vertical lines. The changes occur in the beak region and affect the size of the pedicle opening and the plates closing it, which are illustrated for each species. In the ancestral species *T. boongeroodaensis*, the opening is restricted as the brachiopod develops from a juvenile (ontogenetically). Descendant species progressively retain more juvenile characteristics into adulthood. (Courtesy of K. J. McNamara, The Paleontological Society, and *Journal of Paleontology*, v. 57, p. 465.)

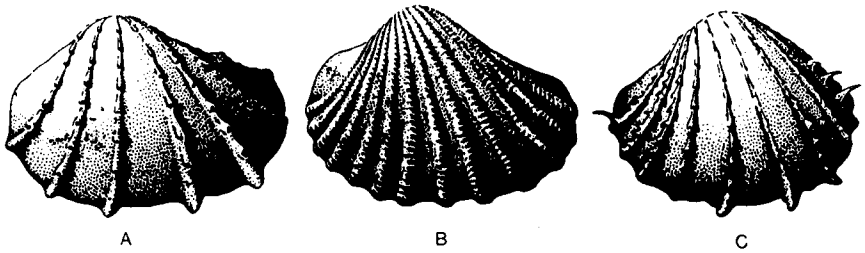

Figure 15-15 Paedomorphosis in two species of late Miocene bivalves of the genus *Cardium*. A. A younger specimen of *C. plicatum* (5 mm). B. Adult of the same species (17 mm). C. The descendant species *C. fittoni* (35 mm) is larger than the adult of the ancestor but has the ribbing of the juvenile ancestor. (*Source:* L. A. Nevasskaya, *Paleontological Journal*, v. 1(4), pp. 1–17.)

taken through paedomorphosis. By small changes in the regulatory genes that control rate of maturation and growth, a paedomorphic adult organism is produced that may be remarkably different from the adult of its ancestor. A highly speculative theory for the origin of scleractinian from rugose corals suggests that the first scleractinians were larval rugosans. The adult sixfold septal symmetry of scleractinians contrasts with the fourfold symmetry of rugosans but the latter pass through a stage early in ontogeny when only six septa are present. Changes in the genes that control rates of development that brought this stage of sixfold symmetry to adulthood might explain the sudden appearance of scleractinians and the lack of intermediates between them and rugosans.

Larval Adaptations:

Larval trilobites have eyes at the front margins in the protaspis stage (Chapter 7). In ontogeny, the eyes move backwards through successive molt stages to their adult position on the upper surface. If this ontogenetic change is interpreted as a result of peramorphosis, then the ancestors of the trilobites must have had forward-looking eyes. An alternative explanation is that the position of the eyes is an adaptation to the free-swimming life-style of the larva to whom forward and downward vision were more important than to the adult living on the bottom.

Ontogenetic changes to greater complexity in the sutures of ammonoids were used by paleontologists of the early part of this century to trace ancestry on the basis of recapitulation theory. Their arguments have now generally been rejected and attention has been focused on the form and ornamentation of the shell. The simpler sutures of larval ammonoids may indicate only that the young lived in a different habitat from the adults and did not need the shell strength given by complex folding of the septa. Embryos, like adults, are adapted to their environment. If that environment is much different from that of the adult, the paleontologist is faced with the choice of interpreting early ontogenetic stages in terms of larval adaptation or ancestry.

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Chapter 16

Evolution in Earth History

Paleontological studies may resolve many of the evolutionary problems discussed in the last chapter and only through the study of the history of life can the long-term effects of evolutionary mechanisms be assessed. In this chapter three facets of evolution are examined: rates of evolution, extinctions, and the effects of chance or stochastic processes.

RATES OF EVOLUTION

Reference has been made in preceeding chapters to the measurement of rates of evolution. Questions that the paleontological record may be able to answer about rates of evolution include (1) Can a common pattern of evolutionary rate changes be detected in the history of groups? (2) Have faster evolutionary rates been more widespread at certain times in earth history than at others? (3) Are slowly evolving organisms, so-called living fossils, characterized by a different style of evolutionary change? (4) Are particular environmental conditions responsible for fast and slow evolutionary rates?

Evolutionary rates can be expressed as (1) survivorships (see Chapter 15); (2) the number of taxa that evolved in an interval of time; or (3) the amount of change in a part or a proportion of an organism in a period of time. The third type of rate has been expressed in terms of a unit designated as a darwin. A character of an organism is said to evolve at a rate of 1 darwin when it changes by a factor of "*e*", the base of natural logarithms (2.718 . . .) in 1 million years. For example, the average rate of evolution of bivalve lineages in the late Cenozoic has been estimated to be less than 10 millidarwins.

Because evolutionary studies in paleontology have been focused on the origin of species or higher taxa, the rates usually considered are taxonomic rates, those that refer to the number of species, genera, or orders, originating or becoming extinct in a certain interval of time. Taxonomic rates express two components of evolutionary change: anagenesis, when one species becomes extinct by gradually evolving into another, and cladogenesis, when one species produces a new species and continues to exist with it. Because the passage from one brachiopod species to another does not include morphological changes comparable to the passage from one mammalian species to another, comparison of taxonomic rates between distant groups is of doubtful validity.

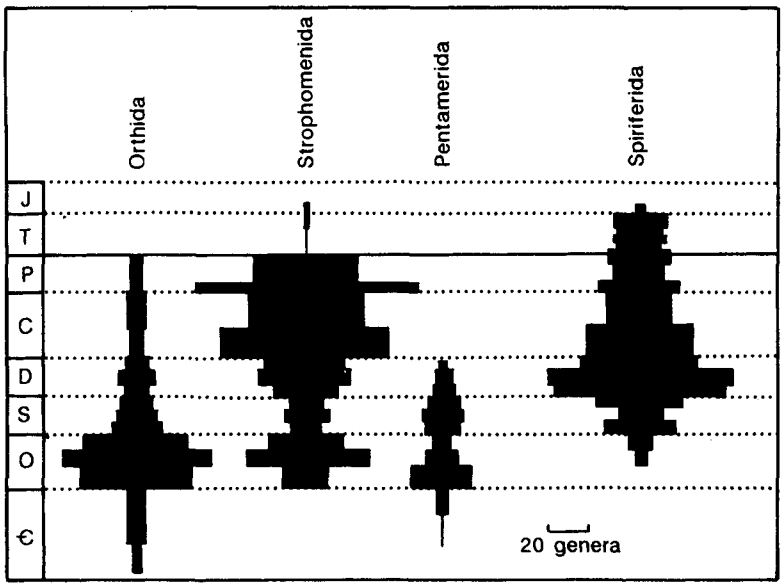

Figure 16-1 Shapes of clades of four major Paleozoic brachiopod orders. Time scale of periods on the left. Note the wide variety of shapes and tendency for a rapid early expansion of diversity. (*Source:* Modified from S. J. Gould and others, *Paleobiology*, v. 3, pp. 23–40.)

Adaptive Radiation:

The history of a clade is usually represented by a diagram in which the varying width of a vertical line represents the variation in the number of taxa through time (Fig. 16–1). Norman Gilinsky and Richard Bambach (1) have shown that on the average the greatest diversity in clades occurs in the early part of their range. Many clades have an initial phase of rapid expansion in diversity followed by a slow decline towards extinction. The shape of the clade in a diagram such as Figure 16–1 is typically a pear or teardrop but a wide variety of clade shapes have been documented. The phase of rapid expansion is the result of a phenomenon known as adaptive radiation—the diversity explosion as the organisms exploit new adaptations or newly available environments.

The potential rate of increase in adaptive radiation may, like the increase in a population by reproduction, be governed by an exponential function:

$$\text{Number of species generated by time } t = e^{Rt},$$

where e is the base of natural logarithms and R is the fractional increase per unit of time. The equation assumes that the clade starts from a single species. The actual number of species present at any time also depends on the rate at which they become extinct. Steven Stanley has calculated the average value of R for families of bivalves is 0.06 per million years and for mammals 0.22 per million years (2). The proportion between these values of R is similar to that between the average time range of species of invertebrates (5 or 6 million years) and mammals (about 1 million years).

In Late Triassic time some scleractinian corals took on symbiotic algae that allowed them to respire and calcify more efficiently (Chapter 10). This adaptation led to a rapid diversification so that from a few Triassic species, 5 orders and 12 families arose in a few million years (Fig. 16–2). The physiological step was not a big one, but the results were far-reaching for the success of the group. Such rapid diversity could not be attained by anagenetic appearance of new species at intervals of several million years that are typical of invertebrates. Rapid cladogenesis, at much shorter intervals than this average figure suggests, is called for. Steven Stanley (2) has used similar examples to justify the concept of macroevolution. If the average time range of invertebrate species is several million years, each step in the adaptive radiation must be a large one in order to bring about the large increase in diversity in the short time available. The diversity could be produced by rapid cladogenesis and progressive, morphological change. The potential of rapid cladogenesis to produce great diversity in a short time can be illustrated by a hypothetical example. If a cladogenetic event occurred every 200,000 years in an adaptive radiation, then from a single species

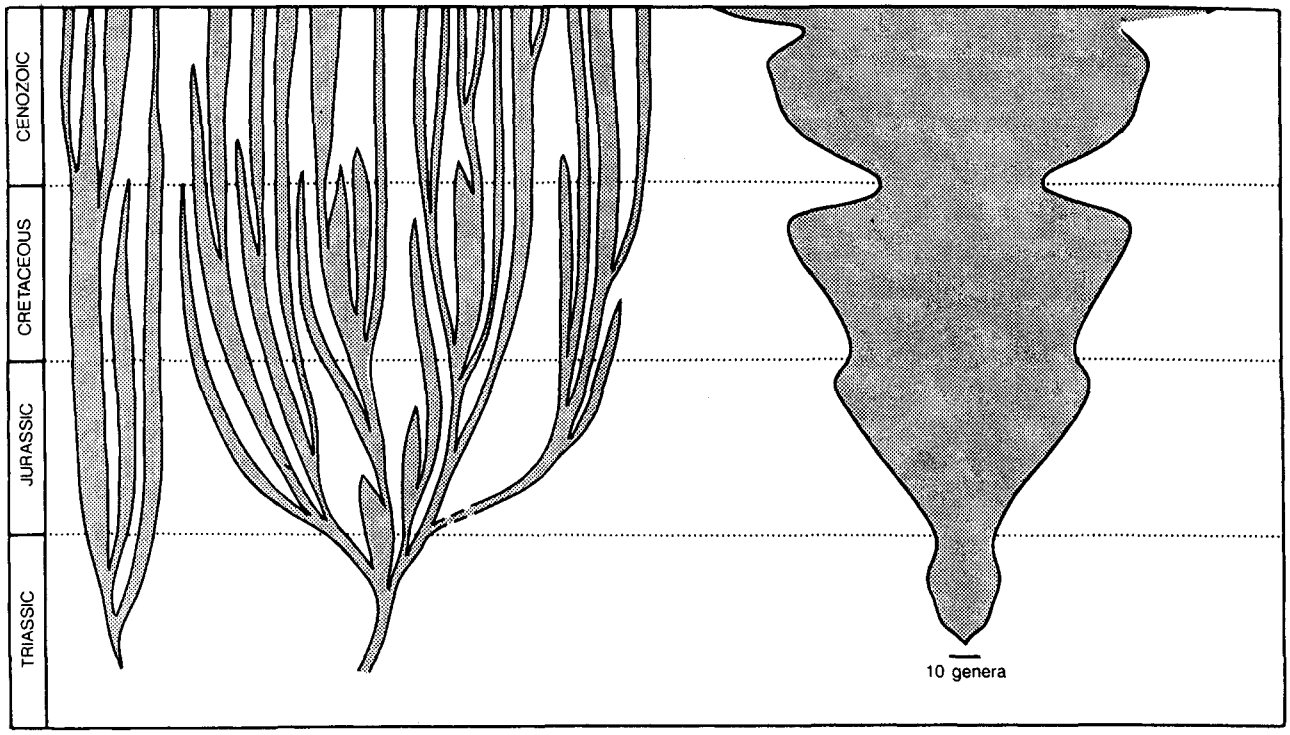

Figure 16-2 Adaptive radiation of the scleractinian corals in Mesozoic and Cenozoic time. At left, the diversification into families is shown after the work of J. W. Wells; at right, the shape of the clade, based on the number of genera as compiled by S. Stanley from information in Wells. (*Source:* J. W. Wells, *Treatise on Invertebrate Paleontology*, v. F, 1956; S. Stanley, *Macroevolution*, 1981.)

1024 species could be generated in 2 million years (2^{10}), and more than 1 million species in 4 million years (2^{20}). This calculation assumes that none become extinct in this time. These figures, though not unrealistic (*R* must be about 3.5), have no basis in the record but they do illustrate the immense potential of exponential increase. Biologists estimate that only about 10 million species are living. Other examples of adaptive radiation in the history of many groups have been reviewed in preceding chapters. Examples of large-scale radiations are (1) the invertebrate phyla in Late Proterozoic and Cambrian time; (2) the invertebrates with calcareous skeletons in Middle Ordovician time; (3) the land plants in Devonian time; (4) the angiosperms in Cretaceous time; (5) the placental mammals in Late Cretaceous and Paleocene time. Examples of adaptive radiation of intermediate scale include (1) the ammonoids at three times in their history; (2) the dinosaurs in Triassic time; (3) the ungulates of Paleocene time. Adaptive radiations at the grandest scale appear to have resulted from the coincidence of an empty ecologic zone and the evolution of a species with the ability to take advantage of this newly available environment. Such major breakthroughs occur only infrequently in life history.

The availability of ecologic zones may be due to biological or physical events. The accessibility of many land environments to mammals was the result of the extinction of the dinosaurs, but the rapid spread of shelled invertebrates appears to have been made possible by a change in the oxygen content of the atmosphere and oceans.

Cycles in Earth History:

Both directional and cyclical trends have been discovered in the history of the earth. Since Archean time the oxygen content of the atmosphere has increased while the carbon dioxide content has fallen. The luminosity of the sun appears to have increased at about 1 percent per 80 million years since Archean time but the effect on the temperature of the earth of its lower radiance in the Archean was probably compensated for by the greater effectiveness than of the greenhouse effect because carbon

dioxide was abundant in the atmosphere until about 500 million years ago. Superimposed on these unidirectional trends in world environments, whose effects on life were discussed in Chapters 5 and 6, are cycles of larger and shorter periodicity that also control evolution. The longest of these cycles is believed to be caused by convective overturn in the mantle of the earth, the layer that lies between the thin crust and the liquid core. The overturn, cycling in a period variously estimated to be 300 to 500 million years, is responsible for the movement of the continents, the expansion and contraction of the ocean basins, and many secondary effects.

Geologists can document only the last two grand cycles in any detail. Late in the Proterozoic Eon the continents were a single mass called Pangaea I. The initial phase of the next to last cycle was the splitting of Pangaea I into continents by rifting, and the widening of the oceans between the continents by the spreading of oceanic crust. During this phase volcanoes were active, carbon dioxide was released by them into the atmosphere (degassing) enhancing the greenhouse effect and warming world climates, the sea level rose expanding the shallow epicontinental seas across the continental platforms, and coastlines were lengthened as the supercontinent split into fragments. Alfred Fischer (3) has called this the greenhouse phase of the cycle. The second phase of the cycle was marked by closure of oceans as the continents again aggregated into Pangaea II, falling sea level, shrinking epicontinental seas and coastlines, decreasing carbon dioxide levels, cooler temperatures, and the icehouse state. In the Paleozoic cycle this phase was marked by extensive glaciation in the southern hemisphere.

These cycles and trends have exerted a strong influence on the history of life. The diversification of the invertebrate phyla and their expansion in numbers occurred in the greenhouse phase of the early Paleozoic when warm epicontinental seas expanded across continental platforms and oxygen content had risen to a level that calcareous shells could readily be secreted. The late Proterozoic icehouse glaciation had passed and the oceans were expanding as Pangaea I broke into continents. The turnover point from the first to second phase occurred in Late Devonian time when oceans began to close and cool and the next icehouse phase came in (Fig. 16–3). This time of extinction was documented in Chapter 7. The most intense biotic crisis in the history of life marks the formation of Pangaea II and the spread of late Paleozoic glaciers across a large part of it. By later Triassic time this supercontinent was breaking up and greenhouse conditions led to the expansion of marine life in what was called in Chapter 10 the second wave of invertebrate diversification. To the present day oceans are expanding but Fischer believes that late Cenozoic glaciations indicate a return to the icehouse condition.

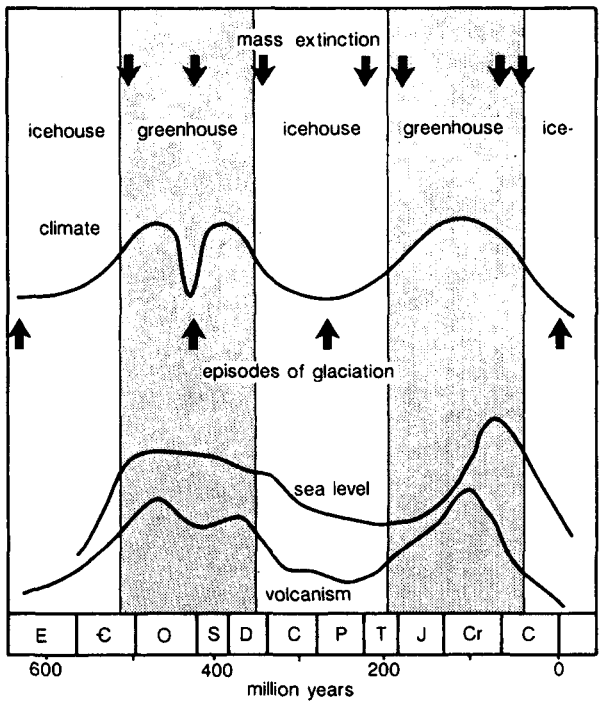

Figure 16-3 Supercycles in the Phanerozoic as outlined by A. Fischer. The letters along the base are initials of the geological periods. (*Source:* Modified from A. Fischer, *Catastrophes in Earth History*, 1984.)

On a broad scale the pace of marine invertebrate evolution can be modelled in terms of this cycle, but did it affect life on the land? Comparison of the effects of the cycles on terrestrial vertebrates and marine invertebrates is possible only for the last 350 million years since vertebrates occupied the land. While restriction and expansion of shallow seas clearly affected marine invertebrates, their effect on land vertebrates is not obvious. The marine biotic crisis of the end of the Paleozoic is not evident in vertebrate communities, or those of marine fish.

Damion Nance and co-workers (4) have traced these supercycles back as far as the Archean Eon and suggested that six rifting episodes took place

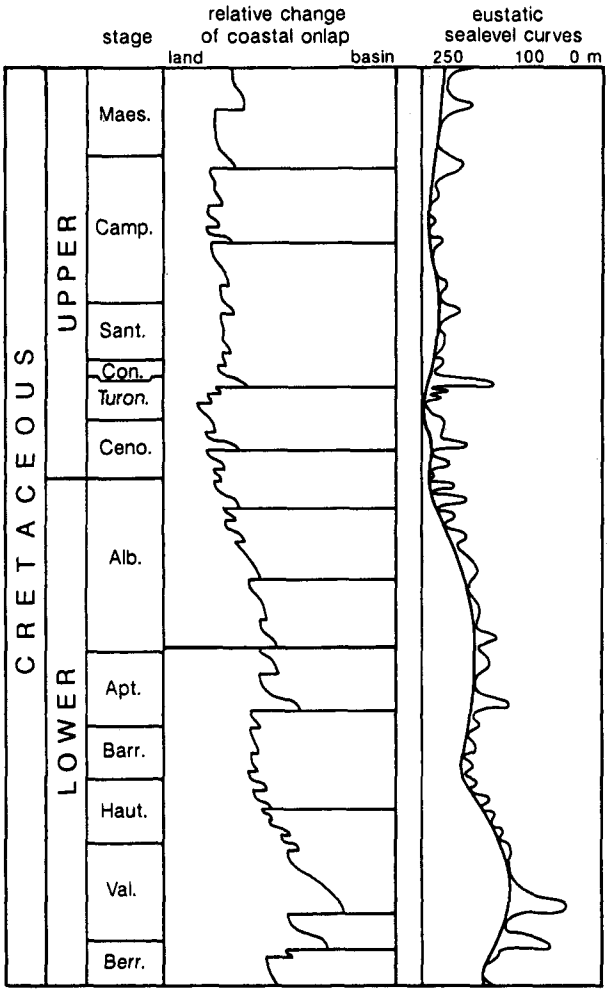

Figure 16-4 Cretaceous cycles of sea level fluctuation. Short-term changes are represented by thin lines; long-term changes by thick lines. Major cycle boundaries are indicated by horizontal lines. The complete Cretaceous stage names can be found in Figure 13-1. (*Source:* Modified from B. V. Haq, J. Hardenbol, and P. R. Vail, *Science*, v. 235, pp. 1156–1167.)

at 2500, 2000, 1500, 1060, and 200 million years ago. They suggest that pre-Paleozoic cycles controlled the appearance of the eukaryotes and siliceous plankton and the collapse of the stromatolite communities.

Much shorter cycles of transgression and regression of the continental margins also affected the pace of evolution of marine life. Peter Vail (5, 6) and his co-workers have compiled curves that document changes in sea level that caused epicontinental seas to flood and ebb in cycles of various orders from a few tens of thousands of years (6th order) to tens of millions of years (2nd order) (Fig. 16–4).

Evolution, Transgression, and Regression:

Erle Kauffman (7) studied the effect of transgression and regression on Cretaceous marine faunas in the western interior states. Transgressions provide increasing space for adaptive radiation of fast-breeding organisms that can take advantage of a variety of habitats, but regression places stress on shallow-water organisms, usually as they compete for shrinking space on continental margins. The response in changes of rates of evolution is not simple and varies from organism to organism. Marine invertebrates that can live in a wide variety of environments (those with general ecological requirements) first speciate rapidly as new environments expand during transgression, and secondly when they are forced to compete as their habitats shrink in regression. Species that are specialists, requiring narrowly defined environmental conditions, reach their highest evolutionary rate just past the time of greatest transgression and decrease in rate of speciation during regression.

Anthony Hallam (8) has suggested that the rate of speciation and extinction should increase at times of maximum regression and competition for space. Remnants of the regression crisis would then expand across the shelves with the ensuing transgression.

Some evidence has been found that offshore species inhabiting stable environments have shorter ranges and more specialized requirements, and inshore species responsive to rapid changes in the environment have longer ranges in time. However, no simple relation between rates of evolution and the transgression–regression cycle has yet been formulated.

Although rates of speciation are higher in offshore stable communities, David Jablonski and his co-workers (9) have shown that innovative faunas originate in nearshore waters and force older communities into offshore slope positions (Fig. 16–5). The Cambrian fauna of Sepkoski (see Chapter 7) originally occupied the inner shelf environment but was successively replaced during Late Cambrian to Late Ordovician time by the Paleozoic fauna of articulate brachiopods, gastropods, bryozoans, sponges, and corals, and then by the beginnings of the modern fauna identified by the prominence of bivalves.

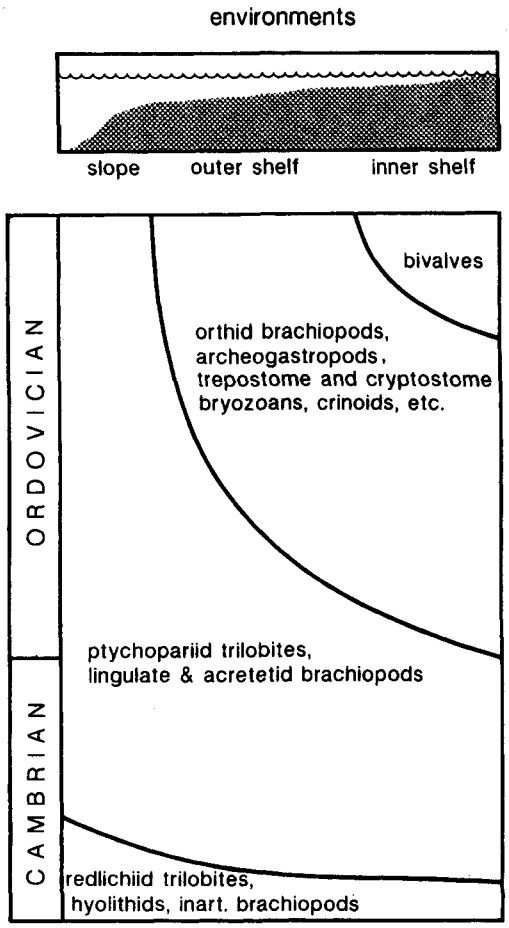

Figure 16-5 Distribution of four Cambrian–Ordovician fossil communities in time and environment. New communities are introduced nearshore and are forced outward by the appearance of another community inshore. (*Source:* Modified from D. Jablonski and others.)

Living Fossils:

Darwin used this term to apply to living animals and plants that slowly evolved but persisted for long periods of time. Since Darwin's time, the term has been used in a variety of ways. Commonly it refers to living representatives with primitive features in clades that reached their greatest abundance and diversity many millions of years ago. Most so-called living fossil species do not have a paleontological record that allows the history of the particular species to be traced back into the past. *Neopilina galatheae*, a monoplacophoran found in 1957 on a Pacific seamount, is a good example. This genus has no fossil record but it is considered to be a living fossil because it is a representative of a Cambrian group that is ancestral to the rest of the molluscs (Chapter 7). The living species with the longest record is believed to be the brachiopod *Triops cancriniformis* whose fossil representatives are known from Triassic rocks. The living lingulate brachiopod, *Lingula*, is commonly cited as the oldest living genus because this name has been used for specimens from Ordovician rocks. The ostracode *Bairdia* has a similar long span. *Equisetum*, the horsetail rush, is a good example of a living fossil of the plant kingdom. It is a primitive representative of the sphenophytes that thrived in Carboniferous coal swamps but have since come close to extinction.

The persistence of primitive members of a clade long after more advanced members have become extinct is a common phenomenon in the paleontological record. The dendroid graptolite *Rhabdinopora* is one of the first of its order to appear and the last to become extinct, long after the more specialized graptoloids had died out. The first and most primitive group of the stromatoporoids are the labechiids. This group was also the last to die out at the end of Devonian time after its more advanced relatives had become extinct in the mid-Late Devonian crisis. The genus *Didelphis*, the opossum, is a living remnant of the original radiation of the marsupials in Cretaceous time. The phenomenon may be explained by the tolerance to a range of conditions of early and late members of clades. Early members are generalists capable of living in a wide range of conditions and as they evolve, members divide into smaller parcels the resources in the clade's ecologic zone. Species become specialists with narrow requirements for food and space and therefore are more likely to become extinct when conditions change. When the environment becomes inhospitable, members of the clade that have retained a tolerance for a range of conditions persist the longest.

Paleontologists are not in agreement about what other features living fossils have in common that could account for their longevity. Peter Bretsky and D. M. Lorenz (10) suggested that organisms adapted to highly variable environments develop the ability to survive environmental shifts that eliminate their contemporaries that have adapted to more stable conditions. For the lungfish, adapted to periodically drying lake beds, this hypothesis appears to apply; but for the living fossils of the deep sea, such as the monoplacophoran *Neopilina*, and the coelocanth *Latimeria*, it is inappropriate.

EXTINCTION

Background Extinction:

Living fossils are interesting because they are exceptional; most species that have ever lived are extinct. Extinction is the complement of speciation and, if the diversity of life has remained constant, the rate of speciation and of extinction must balance. However, owing to biases of the record, we cannot be certain whether total species diversity has risen, dropped, or remained essentially constant through geological time. The diversity curves for skeletal marine invertebrates (Fig. 7–60) show an overall Phanerozoic increase but also show periods of static diversity of hundreds of millions of years. Such curves do not reflect the whole range of even marine life (see discussion at end of Chapter 7).

Intuitively, we would expect diversity to have risen as increasingly specialized organisms displaced early generalists carving out more narrowly defined habitats for themselves, dividing the world's resources more finely. Supporters of this concept suggest that the world's resources are like a barrel that can be first filled with melons but space still remains that could be filled will apples, then with walnuts, then blueberries, etc. The fruits of decreasing size represent organisms with increasingly specialized environmental requirements.

Why, or how, do organisms become extinct? The same factors that limit the geographic spread of a species in space are those that limit its continuation in time. Extinction can be considered to be the reduction of the geographic range of a species to zero. These limiting factors can be reduced to three groups:

1. Competition and predation from other organisms.
2. Changes in the physical environment.
3. Chance events.

The response of organisms to factors 1 and 2 is part of the processes included in the concept of natural selection, but processes grouped under factor 3, such as hurricanes, forest fires, and tidal waves, act indiscriminantly on all life whatever its adaptation. Because most such chance events are local in their effects, they will lead to the extinction of small populations only. The effect of the three factors acting together has been thought to produce a constant average rate of extinction in individual clades.

Leigh Van Valen (11) plotted survivorship curves (Fig. 16–6) for many taxa and found that the trend of points in all approached a straight line but that the slope of the lines for taxa that differ in their ecological requirements were different. The plots indicate that the probability of extinction is constant through the life of the group but that rates vary from group to group. In its simplest form, Van Valen's law states that extinction in a given group occurs at a constant rate. The survivorship curve is analogous to the curve representing the decay of a radioactive isotope (Fig. 2–1). The probability of decay is the same for all atoms (or the probability of extinction is the same for all species) and constant in time, but the decay of an individual atom is a matter of chance and cannot be predicted. Van Valen's work suggests that processes operating at random determine the survival or extinction of individual taxa, but this conclusion has not been universally accepted.

The causes of extinction of species within historic

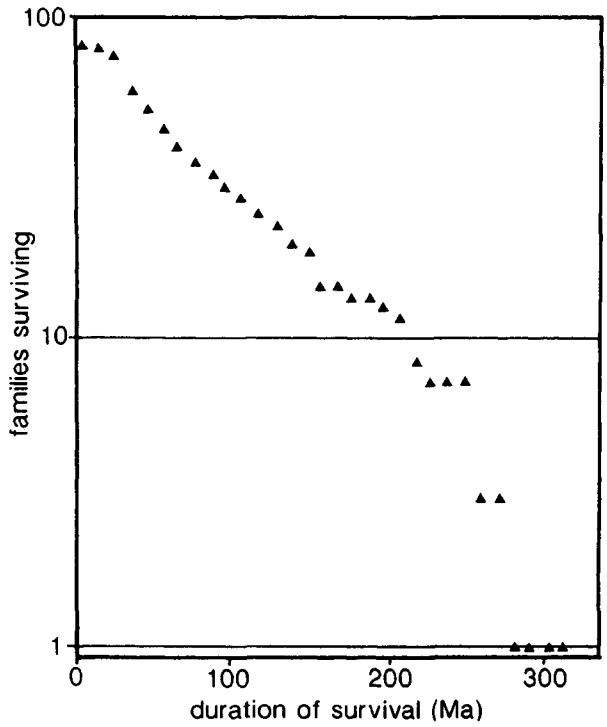

Figure 16-6 Survivorship of families of extinct bivalves. The ordinate plots the number of families having durations at least as long as the value of the abscissa (in millions of years). For example, ten families have survived for 200 million years or more, and only one for more than 300 million years. Note the logarithmic scale of the ordinate. (*Source:* Modified from L. van Valen, *Evolutionary Theory*, v. 1, pp. 1–30.)

times can be assessed accurately. For most of these species, such as the passenger pigeon, the great auk, and the dodo, man has been the immediate cause. He is suspected also of causing the extinction of many species that disappeared at the close of the last ice age. However, for long-extinct species the specific cause of extinction and the nature of their competitors is difficult to determine. Van Valen's law suggests that there is a normal background rate of extinction. However, the rate must have accelerated during certain episodes in earth history when many taxa became extinct at the same time.

Mass Extinctions:

At the end of the Paleozoic and the Mesozoic eras, so many organisms became extinct that the contrasts between life before and after these times were recognized as the basis for the division of the history of life into eras as early as 1821. Since then four additional major episodes of mass extinction and many less important ones have been recognized. The six events in which much of the world biota became extinct occurred at or near the ends of the Eocene Epoch, the Cretaceous, Triassic, Permian, and Ordovician periods, and between the Frasnian and Famennian stages of the Late Devonian Epoch. The extent of these mass extinctions has been summarized by Steven Stanley (12) and has been referred to in previous chapters. On diversity graphs (Fig. 7–60) these extinctions appear as sharp, downward points in the curve. In a relatively short time many clades became extinct. In the crisis just before the end of Ordovician time nearly a third of the brachiopod families disappeared along with major groups of the conodonts, trilobites, bryozoans, graptolites, corals, and stromatoporoids. In the Late Devonian crisis, 30 percent of invertebrate families, and in the Permian crisis 50 percent, became extinct. By far the most research has been focused on the event that closed Cretaceous time when extinctions decimated the dinosaurs, marine reptiles, ammonites, rudist bivalves, and much of the marine plankton. Analyses of curves showing percent extinction of marine families since the Permian (Fig. 16–7) has suggested to David Raup and John Sepkoski that extinctions reach peaks above the background extinction rate in a regular cycle with a period of 26 million years. However, the reality of this cycle has been doubted by other paleontologists (13, 14, 15).

The Impact Hypothesis:

Although paleontologists have speculated about the causes of mass extinctions since the general outlines

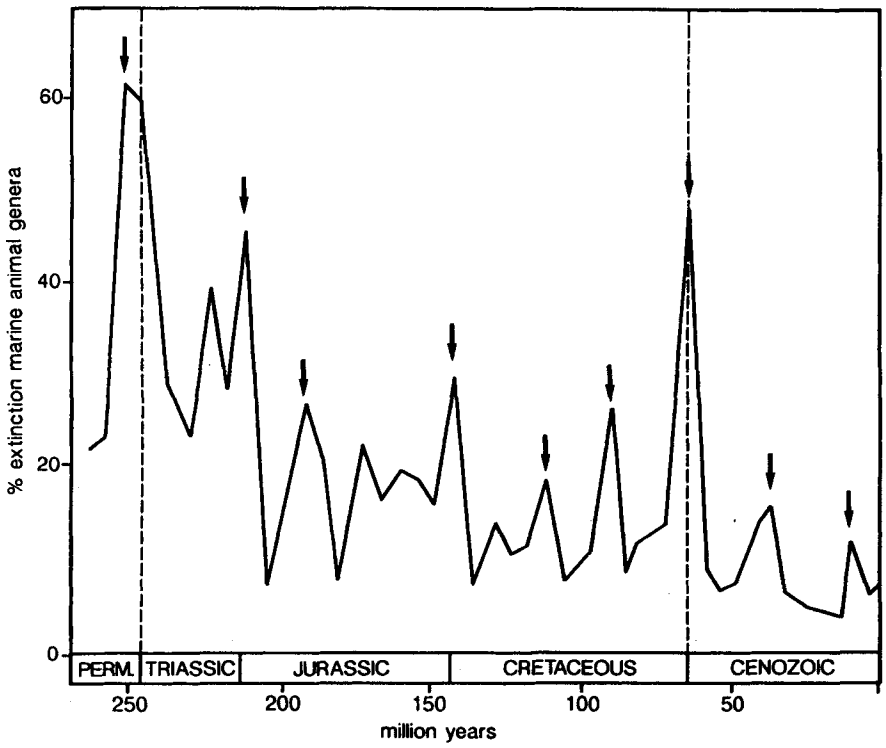

Figure 16-7 Percentage extinction of marine animal genera since Permian time. Arrows indicate times when extinction rate exceeded the background rate, according to Raup and Sepkoski. The line connects means of estimates at each inflection point. Error bars have been omitted to simplify the diagram from the original. Note that the highest points correspond to the Late Permian, Late Triassic, and Late Cretaceous biotic crises. (*Source:* Modified from D. M. Raup and J. J. Sepkoski, *Science*, v. 231, pp. 883–886.)

of the history of life became known, the discussion has intensified during the past decade, stimulated by the hypothesis that the event at the end of the Cretaceous was caused by the impact of a meteorite or asteroid, and that other biotic crises had similar causes. The hypothesis was formulated by Walter and Luis Alvarez and their co-workers (16) to explain the high concentrations of the rare element iridium in the clay layer that marks the boundary between the Mesozoic and Cenozoic sedimentary rocks at Gubbio, Italy. The concentration of this element, and several others of the platinum group found in this layer, is 10,000 times greater in meteorites than in the earth's crust. Subsequently, the so-called iridium spike was found to be widely distributed at the boundary both in cores of deep-sea drill holes and in stratigraphic sections on land. The Alvarezes proposed that a meteorite about 10 km in diameter struck the earth and the impact raised enough debris into the atmosphere to plunge the world into darkness for several months killing most of the plants, cooling the surface by shutting off the sun's heat, disrupting food chains, and causing the extinction of a large part of the world biota. The search for similar trace element anomalies at the horizons of other extinction events produced some successes and some failures. Anomalies were found at the Late Devonian and Eocene events but (apart from a single doubtful occurrence) not at the Permian–Triassic, nor late Ordovician events. However, stratigraphic sections in which deposition across the Permian–Triassic boundary is continuous are rare. Astronomers who accepted the meteorite hypothesis and the hypothesis of cyclic extinctions have suggested that the earth periodically encounters conditions favorable to impact by meteorites or comets. Statistical analysis of the orbits of asteroids that cross the orbit of the earth have shown that during Phanerozoic time the earth is likely to have been struck by an asteroid of the size required by the Alvarezes on average about once every 30 million years but the ages of meteorite craters does not reflect such frequency. Space in this book is not sufficient to include an extensive discussion of the meteorite hypothesis. It has become one of the most controversial theories of the last decade and has stimulated great debate over the importance of catastrophes in shaping the history of life.

If survival of an organism depends not on its fitness tested in competition with other organisms, but on the chance it will escape from a sudden unpredictable catastrophe, then the role of natural selection over long periods of life history differs significantly from that envisaged by Darwin. The mechanism of long-term adaptation cannot be applied to sudden but extremely rare events. No member of a biota can adapt to the chance of a meteorite impact. Stephen Gould (ref. 16, Chapter 15) termed these catastrophic processes the third tier of selection (the first is natural selection acting at the individual level, the second is species selection). Differential survival of catastrophes as a major control on life history is in sharp contrast to selection by competition between adaptations of different utility. Because acceptance of the impact theory radically changes the interpretation of the history of life, it has come under much scrutiny, and many paleontologists react to it with skepticism.

Alternative Theories of Extinction:

If extinction at these crises was sudden and unrelated to the earth's environment, then it should have overtaken the groups affected in an instant of geological time. Evidence has now been accumulated which shows that mass extinctions in many groups occurred over a considerable period of time, rather than at a single stratigraphic horizon. Figure 16–8 shows that ammonite diversity declined steadily through the Late Cretaceous as if responding to declining environmental conditions, and relatively few genera persisted to the end of the Maastrichtian stage when the last genus became extinct. A similar history is shown by the the stromatoporoids before their near extinction in the Late Devonian crisis. The most diverse fauna of dinosaurs is found at the start of the Maastrichtian stage about 10 million years before the close of the Cretaceous Period, and from this time onward their diversity decreased to extinction. Decline in diversity before the extinction event suggests that extinction was due to accumulating effects of environmental deterioration and not to sudden disaster.

Theories of mass extinction must account for the selectivity of the operative process. Many mechanisms for destroying life indiscriminantly can be imagined, but in the major biotic crises, the organisms that became extinct had relatives that survived. When dinosaurs and marine and flying reptiles became extinct, other reptiles, the turtles, crocodiles, and lizards, survived. When the ammonites died out, the nautiloids lived on to expand

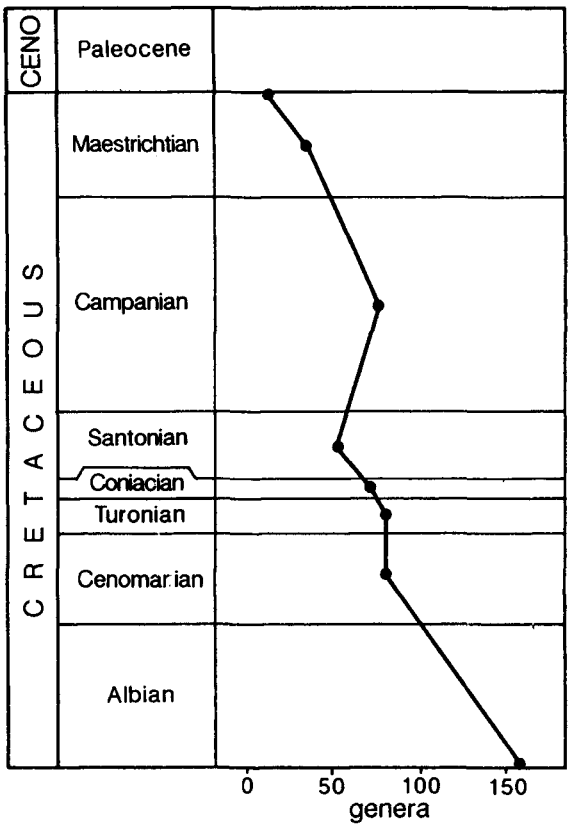

Figure 16-8 Decline in the number of ammonite genera through Late Cretaceous time to extinction at the close of the period. (*Source:* Plotted from information of Jost Wiedmann, *Biological Reviews*, 1969, p. 594.)

into the abandoned habitats in Cenozoic time. Although only 13 percent of planktonic foraminiferans survived the Cretaceous crisis, 75 to 85 percent of benthonic genera survived. A key to understanding mass extinctions must lie in the differences between the victims and the survivors. Catastrophic mechanisms to explain extinction offer an indiscriminant instrument like a bomb when what is needed is a bullet.

Competing hypotheses explain the various iridium anomalies as the result of the eruption of volcanoes, its concentration by dissolution of seafloor sediments, or its accumulation preferentially in organic matter. Evidence for meteorite impact at biotic crises other than that at the Cretaceous–Cenozoic boundary, is meager and, even if the iridium anomaly at that level is accepted as proof of impact, such impacts may have been extremely rare events. The agents of extinction that have been postulated as alternatives to catastrophes by meteorite impact are various worldwide environmental changes. Steven Stanley (12) summarized the evidence that extinctions are climatically controlled. He cited faunal and isotopic evidence that cooling of world temperatures took place at the major extinctions and several of them were accompanied by glaciation in parts of the world. Another cause that has been proposed is worldwide fall of sea level restricting the space available for marine biotas. Both the Cretaceous–Cenozoic and the Permian–Triassic crises correspond to exceptionally low stands of sea level. Other causes proposed include the rise of deep, oxygen-impoverished water onto the continental shelves destroying marine life, violent volcanism that could inject sufficient dust into the atmosphere to produce effects like those of meteorite impact, and spillover of cold Arctic water into the warmer southern oceans, causing mass mortality of microorganisms and the collapse of food chains. None of these mechanisms is as successful as decrease in temperature in explaining either the decline of diversity before extinction or the geographic distribution of extinctions.

The hypothesis of global cooling is supported by the distribution of victims and survivors. If victims are largely equatorial species and survivors are high-latitude species, this would be good evidence of a cooling event. This pattern of change can be detected in the graptolites at the Late Ordovician crisis, and in the stromatoporoids at the Late Devonian one. Through Permian time reef-forming organisms became progressively restricted to equatorial latitudes indicating cooling. Leigh Van Valen and Robert Sloan (17, 18) have concluded from detailed study of the Cretaceous–Cenozoic transition beds in Montana that subtropical forests in which the dinosaurs lived were progressively displaced southward by temperate forests with a fauna of warm-blooded mammals as winters became colder. They also raised the possibility that dinosaurs died out earlier in high latitudes than at low ones as world climate deteriorated. Unfortunately, well-dated, dinosaur-bearing deposits in the tropics have not been found to substantiate this hypothesis.

In summary, mass extinction events can be explained by the occasional intensification and expansion of the processes of normal background extinction. Hypotheses of sudden catastrophe, terrestrial or extraterrestrial, have stimulated reexamination of the evidence at critical stratigraphic sections, but most paleontological work does not support a sudden, indiscriminant event.

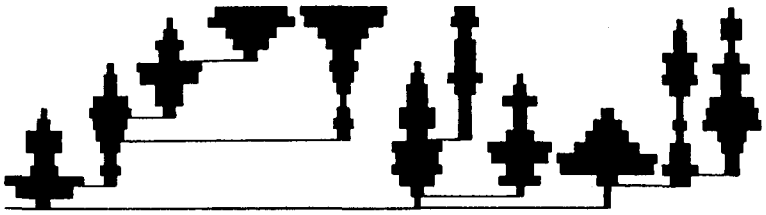

Figure 16-9 Random clade shapes constructed by a computer program. Compare with the real clades of Figure 16-1. (*Source:* Modified from S. J. Gould and others, *Paleobiology*, v. 3, p. 24.)

STOCHASTIC PROCESSES

The impact of a meteorite on earth is a chance event. Although the probability that a 10 km meteorite will strike the earth can be calculated statistically from trajectories and abundance, the year, century, or millenium of its impact cannot be predicted. Events such as this, or the tossing of a coin, are probabilistic in nature and are said to be controlled by stochastic processes. We can predict how many times in a hundred tosses, a coin is likely to yield the result heads but we cannot predict for any one toss what the result will be. Events that predictably follow from a series of causes are said to be deterministic. To say that the results of coin tossing are regulated by stochastic processes is not to imply that the result of a single coin toss is not determined by a series of forces such as the way the coin is propelled, the air resistance, the wind, the surface on which it lands, etc. These interacting forces are so many and so difficult to assess that at present their result can only be treated statistically.

We have already considered hypotheses that mass extinctions are stochastic events whose individual occurrence cannot be determined. The survival of individuals may also be stochastically controlled. The rabbit killed by the fall of a tree is not less well adapted than the rabbit that the tree missed. What are the contributions to the evolution of life of such processes; are they trivial, like the death of the rabbit, or far reaching, like the extinction of the dinosaurs?

The course of evolution is determined by natural selection and by random changes in the gene pool of the population. The second of these alternatives is called genetic drift. It is a stochastic process that may be responsible for the course of evolution taken by small populations where selection pressure is low. Many geneticists take a neutralist view of the importance of natural selection. They note that many genetic differences seem to be neutral from the standpoint of survival, and therefore propose that natural selection is of minor importance in controlling their frequency. Thomas Schopf (19) compares species to atoms in a gas in constant, random motion, whose individual positions cannot be predicted but whose overall effect on the behavior of the gas can be described statistically. From this viewpoint the course of evolution is a statistical summary of the histories of species whose origination and individual fates are determined randomly (compare Van Valen's law) and, if the game of evolution could be replayed, the result would certainly be different. The contrasting deterministic viewpoint is that, given the same physical environmental changes in time, the replay would show life evolving in the same pattern.

David Raup and his co-workers (20, 21) constructed computer programs to draw artificial phylogenies based on arbitrary assumptions about rates of speciation and extinction. At any step in the program, branching, continuation, or extinction of the lineage is determined by a set of random numbers. The shapes of the artificial clades are therefore largely determined randomly but under rules limiting their size and rates of expansion established by the programmers. They found the similarity of the artificial clades to those found in nature to be remarkable (Fig. 16–9).

Nearly all of the factors discussed in this chapter are controversial in terms of their importance in the history of life. The scientific debates between supporters of deterministic and stochastic processes in shaping evolution, between supporters of catastrophic and environmental causes of extinction, and between gradualists and punctuationists, continues in the scientific literature. Meanwhile scientists are driven to unearth more paleontological data to support their viewpoints and our knowledge of nature advances to a point where some of these hypotheses may be rejected, but in most of these controversies, there is some truth on both sides.

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Chapter 17

Paleoecology

INTRODUCTION

Ecology is the study of the relations between modern organisms and the environments in which they live; paleoecology is the study of these relations between species represented in the fossil record and the environments they inhabited. Ecologists can study the relations between organisms in a community by observing their behavior and can measure the characteristics of modern environments precisely, but how can paleontologists reconstruct the complex interrelationships of organisms and their environments when all the organisms are dead and the environments in which they lived have all changed? Paleontologists can only deduce behavior from the functional morphology of fossils and from the effects of the organisms on the sediments. The mineralogy, structures, and textures of these sediments can be used to reconstruct the environment of deposition, and studies of continental movements can add information on geographic position and climate of the habitat. Despite the limitations of dealing with dead and imperfectly preserved organisms, and the lack of direct information on the characteristics of the ancient environments, paleontologists can reconstruct ancient communities in considerable detail.

Paleoecological Inference:

This is largely, but by no means completely, uniformitarian in nature. In living communities ecologists have found that organisms can be grouped according to the roles they play in the flow of energy or food through the unit of interdependent organisms. These roles are called trophic roles (from the Greek *trophe* = nourishment). Plants take nutrients and light from the environment, converting them into organic compounds. They are commonly referred to as primary producers (Fig. 17–1). Plants are eaten by herbivorous animals, which are in turn eaten by carnivores, when alive, and scavengers, when dead. In death, plants and animals are decomposed by bacteria and their organic compounds are broken down into nutrients that are returned to the environment. The organisms united by this flow of energy are referred to as an ecosystem.

Paleoecologists infer that similar relationships existed in the past between organisms and their environment. Obviously many groups in the reconstructed ecosystem will be poorly represented or missing entirely. The primary producers of marine ecosystems are microscopic planktonic plants that are rarely preserved, but are presumed to have existed since the Archean because they are essential

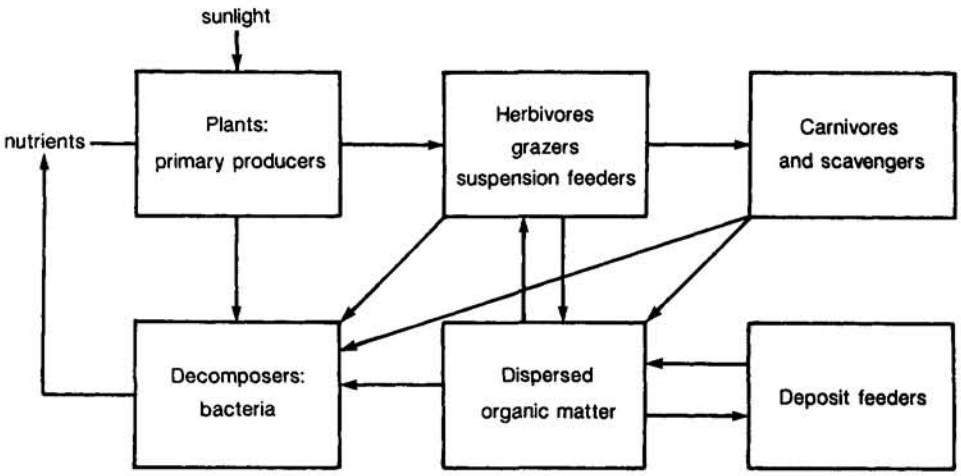

Figure 17-1 Major trophic groups and energy pathways in a community. (*Source:* Modified from J. W. Valentine.)

to life in the marine environment. Within the major trophic groups many subdivisions based on feeding behavior can be defined, and paleoecologists can compare the forms of modern animals of known trophic roles with those of fossils to infer their positions in ancient ecosystems.

This uniformitarian approach does not imply that conditions in the past were exactly the same as those of today—in fact, we know that they were not. It does imply that general laws governing the functioning of organisms have not changed in time, although environments may have. Different kinds of organisms were adapted to the unique atmospheres of the pre-Paleozoic eras, but some must have been primary producers and others decomposers, although herbivores and carnivores were probably absent at first. As life has become more diverse, the complexity of ecosystems must have increased, but the laws governing the flow of energy through them are assumed not to have changed.

Some paleoecological inference is independent of comparisons with modern communities. Some fossils preserve the evidence of interactions between the organisms they represent. Predator–prey relationships are shown by the ammonite shell bearing the tooth marks of the mosasaur that killed it (Fig. 17–2), or the starfish caught in the act of feeding on a bed of bivalves. The presence of scavenger rodents is shown by tooth marks on fossil mammal bones. Parasitism is evidenced by pathologically developed specimens. Interdependence can be deduced from the constant occurrence together of two organisms, such as the gastropod *Platyceras* on the anal openings of Paleozoic crinoids. Fossil lungfish found in burrows give clear evidence of their ability to aestivate. To reconstruct the past environment successfully the paleoecologist must combine comparisons with modern communities with evidence available within the fossil deposit itself.

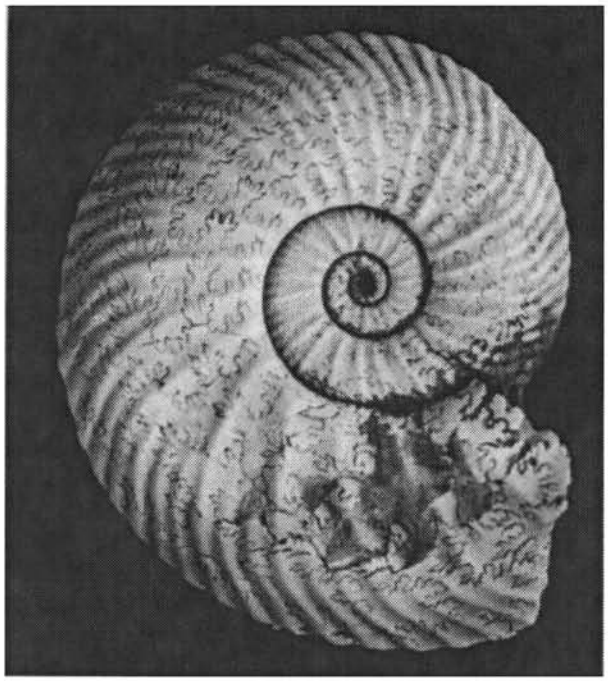

Figure 17-2 Jurassic ammonite *Cardioceras* with the shell broken into by a predator, probably a mosasaur. (C. W. Stearn, Redpath Museum.)

Niches, Communities, and Ecosystems:

Differences in physical and biological features of its environment limit the range of an organism. Physical features include such parameters as temperature, light, oxygen availability, and nutrient supply. Biological features include competition for resources with adjacent species of similar ecological requirements. The "space" bounded by values of these parameters acceptable to the organism constitute its niche. Niches in medieval cathedrals are indentations in the wall made to display the image of a saint. The "fences" to this "space", both physical and biological, restrict the expansion of the species just as the stone walls of the cathedral contain the statue. The word *space* is placed in quotation marks to indicate that the niche of an organism may be bounded by other than geographical changes. Its expansion may be limited as much by internal factors, such as its cycle of reproduction, or the number of offspring produced. A more theoretical definition of a niche is "an abstract hypervolume situated in a space whose axes correspond to the biological and environmental variables affecting the organism in question" (1).

Some organisms are adapted to a narrow range of conditions and are said to be specialized or to have narrow niches. Many parasites are of this nature and can live only in a particular part of their host organism. The narrowness of the niche of many animals is determined by their restriction to a specific food. The koala spends most of its life in eucalyptus trees because it only eats the shoots of this plant. Animals with broad niches include the common rat (*Ratus norvegicus*) and the house fly (*Musca domestica*). Species that live in rapidly changing environments must adapt to a wide range of conditions and have broad niches. These environments are common at middle latitudes and at shorelines. The modern bivalve *Hiatella arctica*, which is found from Greenland to Hawaii, is such a species. Species that live in stable environments, such as tropical seas, tend to have narrow niches and more specialized life-styles.

Ecologists use a hierarchy of terms to refer to groupings of organisms. The members of a species living together are commonly referred to as a population. The different species that live together in a particular environment may be referred to as a community. The deciduous forest community or the intertidal marine community are examples. Communities are commonly named after the dominant or diagnostic species. Ecosystems are larger units consisting of all the organisms that interact in an area. A small ecosystem might be an isolated island; the largest constitutes the whole planet. Paleoecologists have concentrated on the reconstruction of ancient communities as a first step in formulating a history of the world ecosystem.

PALEOECOLOGICAL EVIDENCE

Taphonomy:

In Chapter 1, the variety of pathways by which organisms enter the fossil record was traced. The probability that a pathway will open is much less for some organisms than for others and therefore the fossil record is neither a complete, nor even a random, sample of the life of the past but is biased. The path to preservation is almost always barred to soft-bodied organisms and is rarely open to organisms inhabiting environments where sediment is not being deposited rapidly. Even hard-shelled organisms must run the gauntlet of predation, abrasion, bioerosion, and dissolution in order to reach a permanent place in the fossil record. The branch of paleontology that is concerned with the way organisms enter the fossil record is called taphonomy. The effects of the preservational processes must be taken into account before a paleontologist can start the interpretation of an ancient community from its fossil remnant. Distinctive modes of preservation may aid in reconstructing ancient environments.

The extent of information about an ancient community lost to the paleontologist by the selectivity of the preservational processes can be estimated for specific communities but results are not applicable to other communities. Comparison of living communities with fossil assemblages derived from similar communities has given interesting but discouraging results. Only Cenozoic fossil assemblages contain species whose ecological requirements we can be confident were like those of living species. In one of the first studies, David Lawrence (2) compared the macroscopic organisms of a modern oyster bank community on the southwest coast of the United States with a fossil assemblage from an Oligocene oyster bank in the same area. He found that almost 50 percent of the species of the modern oyster community had no chance of preservation because they did not have hard shells. Represent-

atives of only 25 percent of all the macroscopic organisms of the oyster bank community were found in the equivalent fossil assemblage—a loss of 75 percent of the species.

Taphonomic studies by Anna Behrensmeyer and her co-workers (3) of bones in the Amboseli basin in east Africa showed that only 74 percent of the vertebrate fauna was represented by bones lying on the plain, and these were rapidly falling apart under the influence of scavengers, bacterial decay, and weathering during the ten-year observance period. Most of the species that are not represented in the bone deposits are of animals under 1 kg in weight and are believed to have been eaten by predators and scavengers.

The most valuable communities for paleoecological analysis are those that have been overwhelmed by a catastrophic storm or a flow of sediment that by burial "freezes" the assemblage on the bedding plane. Such assemblages of fossils have been called census assemblages or, less correctly, life assemblages. In a true life assemblage all the species of the living community are present in the same proportions as they were in life. However, no fossil assemblage could be preserved in this way. All bear the impression of preservational processes and are therefore death assemblages, not life assemblages. The effect of these processes must be assessed by the paleoecologist in reconstructing ancient environments.

Comparisons can also be made between the living community and the potential fossils, that are accumulating in the sediment from its skeletal parts. Charles Peterson (4) studied the shelled animals in lagoons along the California coast, sampling the living and dead mollusc shells in the sediment. He found that more species were represented in the deposits than in the living community on its surface. From season to season different species occupy the sample site and leave their shells behind so that what accumulates is a sample, not merely of the group of species that happens to be at the site when the survey was taken, but of a much wider community spread over a larger area. He found that the difference between the species composition of live and dead communities at a site was greatest where the communities are most variable in time.

Time Averaging:

Most marine, fossil-bearing, sedimentary beds contain an accumulation of shells representing the fauna that occupied the site over a period of many years. If sedimentation is slow and conditions at the site change, different communities may get mixed in the fossil deposit, that is, a succession of communities are condensed into the bed. If deposition is rapid, the effects of this time averaging are not as great because the record of the ecologic events is distributed through a greater thickness of sediment (Fig. 17–3).

Most fossil collections consist of specimens collected from a single bed of sedimentary rock. The relative proportion of the various species living in an environment is rarely constant over the years required to deposit a bed and may change as a response to the seasons (Fig. 17–4), catastrophic environmental events such as hurricanes, diseases, or the invasion of a new predator. After a hurricane in Barbados the area covered by the most abundant coral, *Porites porites*, dropped from 11 to 1 percent. Following a disease that decimated the common Caribbean sea urchin *Diadema antillarum* in the early

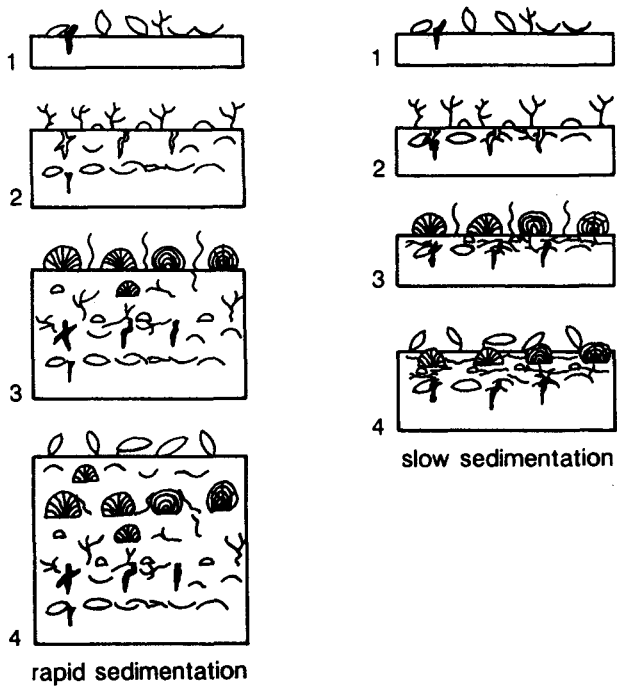

Figure 17-3 The effect of rate of deposition on the condensation of a succession of faunas at a depositional site into a single bed. If sedimentation is rapid, the four faunas (1, 2, 3, 4) are separated in the accumulating sediment; if it is slow, they are difficult to distinguish from one another and the infaunal organisms in one are mixed with epifaunal organisms in earlier communities.

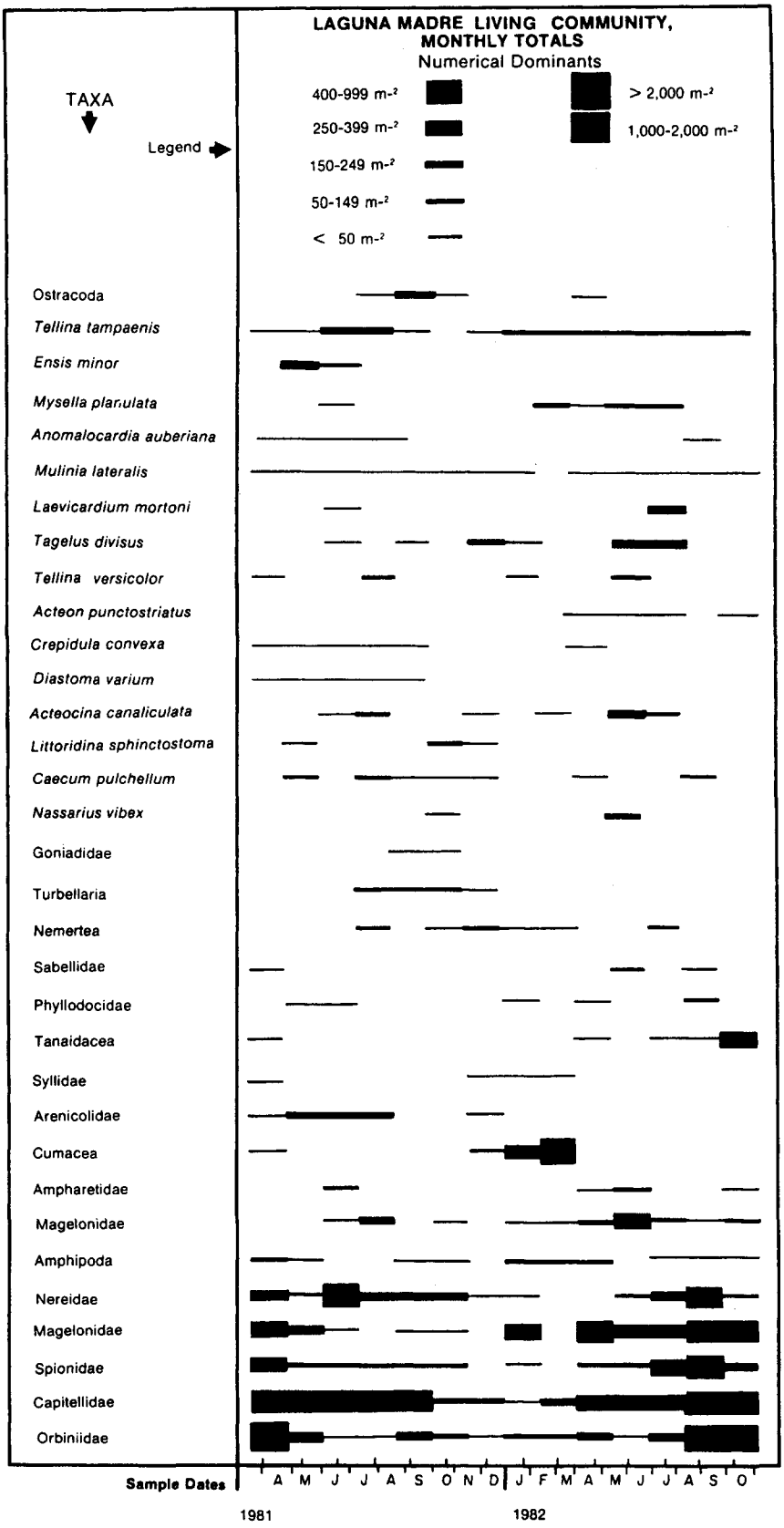

Figure 17-4 Variation in time of the numerical abundance of the dominant taxa in a living community in the Laguna Madre, Texas Gulf coast. The abbreviations along the base of the diagram are the months of 1981 and 1982, when the samples were taken. (Courtesy of George Staff and others, Geological Society of America Bulletin, v. 97, p. 433.)

1980s the density of this species on the same reef dropped within a few months from 23 per m^2 to 0.3 per m^2. The plague of the coral predator starfish, *Acanthaster*, on Indo–Pacific reefs in the 1970s caused sudden radical changes in the coral biotas that will affect the composition of the communities for many tens of years. These biotic changes may not be caused by changes in the physical parameters of the environment and may have little long-term effect on the community. Swings in species composition are evened out by the condensation of successive faunas into a single bed and the paleoecologist may get a better picture of the average community composition from the fossil record than the ecologist who measures the distribution of species over only a few years. However, these short-term variations in communities should make the paleoecologist wary of using proportions of species to conclude that adjacent fossil assemblages came from different environments and of taking census communities as typical of past environments.

George Staff and his co-workers (5) assessed the effects of taphonomy and time averaging on death assemblages in two Texas bays (Fig. 17–4). They concluded that because fossil assemblages are described using time-averaged data, they cannot be accurate representations of the living community. The fossil assemblages will be less similar to the living community the greater the temporal variability of the living community and the longer the time averaged in the fossil assemblage. They found that the order of numerical abundance of species is rarely the same in life and death assemblages.

Most studies of marine taphonomic processes have been made on coastal molluscan communities in areas of soft sediment deposition. These studies suggest that new principles may have to be formulated to interpret fossil assemblages because ecological principles formulated to interpret life assemblages may have limited application. Closer resemblance between fossil and living assemblages may be found in reef communities whose members are largely cemented in place and in deeper water communities in areas of constant sedimentation.

Dissolution of shells:

The destruction of hard parts does not end with their entombment. During millions of years of burial many shells are dissolved by water seeping through the sediment. Peterson (4) estimated the rate of dissolution of shells in the sediment of the Californian lagoons and determined by extrapolating short-term rates that different molluscs had residence times of from 5 to nearly 900 years in the sediment.

Of the two calcium carbonate minerals common in invertebrate shells, aragonite and calcite, aragonite is more soluble and therefore shells composed of it soon dissolve and such shells are rare in older sediments. If the aragonite shell is dissolved after the sediment is cemented, a mold of the shell may be left behind but if the sediment is poorly consolidated and collapses into the cavity, no trace may remain. C. F. Koch and Norman Sohl (6) used the extent of preservation of aragonite in many bulk collections in a particular Cretaceous clayey sandstone of the Gulf Coastal Plain to assess the effects of postdepositional dissolution on species composition. Collections in which aragonite shells are well preserved (and are deduced to have been little affected by dissolution) contained 75 different species; those from which aragonite was dissolved contained only 18 species. The authors concluded that a great many species of the community will not be recognized in the most altered samples, and therefore only those collections in similar states of preservation should be compared in paleoecological analyses to minimize postdepositional modification of species distribution.

Transported Assemblages:

The hard parts of organisms, like pebbles and sand grains, can be carried by streams, currents, and waves from one place to another. If the remains of organisms are transported from the environments in which the organism lived, they will give false information about the environment in which they are eventually deposited. Tidal currents flush the shells of animals living in brackish water of estuaries onto the continental shelves and wash shelf shells into estuaries. Shells of shallow-water invertebrates are carried to abyssal depths down continental slopes by slumping sediment and turbidity currents. Many Paleozoic deep-water successions consist of shales containing fossils of planktonic animals, such as graptolites, and no bottom fauna, interbedded with limestones bearing shallow-water fossils, such as brachiopods and crinoids. These deposits are not a record of two basically different environments alternating as the site of deposition went repeatedly from shallow to abyssal depths; the deposit was formed as muds accumulated in deep water at the

base of the continental slope and shallow-water sediments and organisms were introduced periodically by the slumping of sediments from a shallow shelf into the abyss. Because the wind carries pollen and spores from plants and drops them in all environments of deposition, these tiny fossils are particularly valuable for correlating diverse facies but not necessarily diagnostic of the environment of the sediment in which they are found. The bones of dryland species of animals may be carried by streams in flood into swamp and lake deposits far from where they lived.

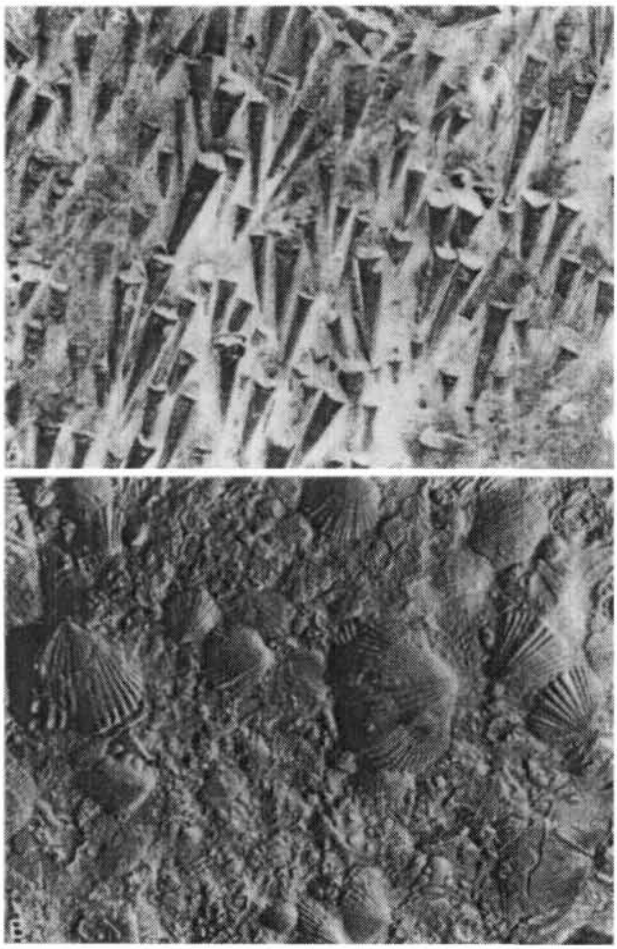

Figure 17-5 Orientation of fossil shells. A. The enigmatic conical Cambrian fossil *Salterella* aligned by currents or waves on a bedding plane. (Courtesy of William Fritz, Geological Survey of Canada (#85898); *Canadian Journal of Earth Sciences*, v. 25, pp. 403–416.) B. Brachiopods *(Hebertella)* and trilobite gabellas *(Ceraurus* and *Flexicalymene)* in the hydrodynamically stable position (convex upward) on the bedding surface of an Ordovician limestone. (C. W. Stearn.)

Evidence that most invertebrate fossil assemblages have been affected by waves and currents is everywhere. On bedding planes most saucer-shaped shells of brachiopods and bivalves are preserved with the convex side upward—the most stable position in moving water (Fig. 17–5B). Shells in a fossil assemblage are usually similar in size because currents have carried away the small, immature shells, sorting the deposit just as a stream sorts sand, clay, and cobbles. Bivalved shells should be represented in an undisturbed deposit in equal numbers, but if the valves have different sizes and shapes and are deposited in moving water, they will be sorted like any other sedimentary particles and deposited in different areas. Log-shaped shells are commonly oriented by waves or currents on a bedding plane (Fig. 17–5A). The paleoecologist must watch for such signs of transported assemblages and take into account that not all the fossils in the collection represent animals that lived in the area where they were collected. However, most studies of recent biotas suggest that extensive transportation of marine shells is uncommon.

Eliminating Collection Biases:

The collection from an outcrop should be representative of the fossils in the rock, yet casual collectors do not make such collections. They are naturally attracted to large specimens, unbroken specimens, and rare specimens. Once they have collected a few of the common species, they will tend to ignore them and seek rarer members of the assemblage. Such collections are not representative of what was preserved in the rock.

These collection biases can be avoided by bulk collecting. A certain volume or weight of rock (e.g., 0.5 m^2 or 2 kg) is collected at each site. Many Cenozoic sediments are poorly consolidated and can easily be broken down into their grains and fossils in the lab. All the fossils in the rock are identified and counted. This method is difficult for well-cemented rocks, such as those of Paleozoic age, and the paleoecologist who uses it must patiently break the rock into small pieces with hammer and chisel to identify all the fossils and their fragments.

An estimate of the proportion of fossil species on a rock surface may be made by quadrats (a square sample area) or line transects. Typically a bedding plane is marked out in a grid pattern whose dimensions depend on the area to be surveyed. All the fossils in each square may be identified and

counted if the area is small, or the squares can be numbered and those in which the fossils are to be counted are identified from a table of random numbers. The line transect method is used by both paleontologists and ecologists. Paleoecologists draw lines or stretch strings across a bedding surface at regular intervals or at random. Each fossil or fragment intersected by the line is identified and counted. The result may be expressed simply as a count of the number of individuals of each species, or the distance along the line occupied by the fossil may be measured to estimate the area of the bedding plane occupied by each type of organism. Point count methods are simpler. The line is marked at regular intervals, for example every 2 cm, and a count is made of the species (or sedimentary rock) at each mark. The counts for each species will be proportional to the area occupied on the surface.

If the proportions of organisms preserved in a deposit are so dependent on temporal changes in the living community, transportation of some of the constituents from the burial site, and loss of many community members during preservation, why should the paleoecologist be concerned with the precise composition of the fossil assemblage? Paleoecologists can hope to make some adjustments for the previously described biases but the first step in any analysis must be the determination of exactly what has been preserved.

LIMITING ENVIRONMENTAL FACTORS

Niches are bounded by an organism's tolerance for environmental change. Important physical parameters of the environment that limit niches are temperature, light, salinity, nature of the soil or bottom sediment, and rainfall. Study of the distribution of living animals controlled by these environmental factors may allow the paleontologist to assess the environmental requirements of fossil assemblages and determine the conditions under which the organisms lived.

Temperature:

Decrease in temperature is correlated with increase in latitude, depth in the sea, and height on the land. These gradients are major controls on the worldwide distribution of organisms at present, and are assumed to have been in the past. Cooling climates result in the migration of organisms toward the equator and towards sea level from mountain heights and ocean depths. For marine invertebrates control by temperature has its greatest effect on larval stages. Unless the temperature of the water is within the range of their tolerance, the larvae will not develop into adults.

The fossils of living species whose temperature tolerance is known are obviously of value for determining temperatures of ancient seas. However, most fossil species are extinct and we do not know their tolerances. Morphologies of living species that can be correlated with environmental temperature may also be shown by fossils. For example, the plants of tropical rain forests have large leaves, large breathing pores (stomates), and tips of leaves shaped for dripping moisture. These features in extinct fossils plants, such as those of the coal forests, are interpreted as indicative of warm, moist climates. Among warm-blooded animals the largest members of many groups live at the highest latitudes and have smaller appendages (such as ears and fingers) than their warm climate relatives. Both are clearly adaptations for greater efficiency in retaining heat. The distribution of fossil mammals would be expected to show the same pattern. At present reef-building organisms thrive only in shallow water in the tropics, although some corals do build substantial mounds in deep, cold water. Geologists reason that most ancient reefs must also have been confined to tropical latitudes and construct paleogeography on this basis. However, the assumption that ancient reef builders (rugosans, tabulates, and stromatoporoids) had ecological requirements comparable to modern ones (scleractinians and coralline algae) is not firmly based.

Because no other major environmental feature varies as regularly with latitude as temperature, latitudinal biotic changes are often ascribed to temperature effects even though the action of temperature on the organisms may be obscure. The diversity of animals and plants is correlated with latitude—a greater variety of organisms inhabit equatorial environments than polar environments. When the number of species of a group is plotted against latitude, a gradient of diversity is defined from equator to pole (Fig. 17–6). Although the general conclusion that fossil biotas of high diversity are likely to have lived in low latitudes and those of low diversity in high latitudes can be used in reconstructing paleogeography, sufficiently detailed information on the diversity of fossil groups on a worldwide basis is not available to allow diversity

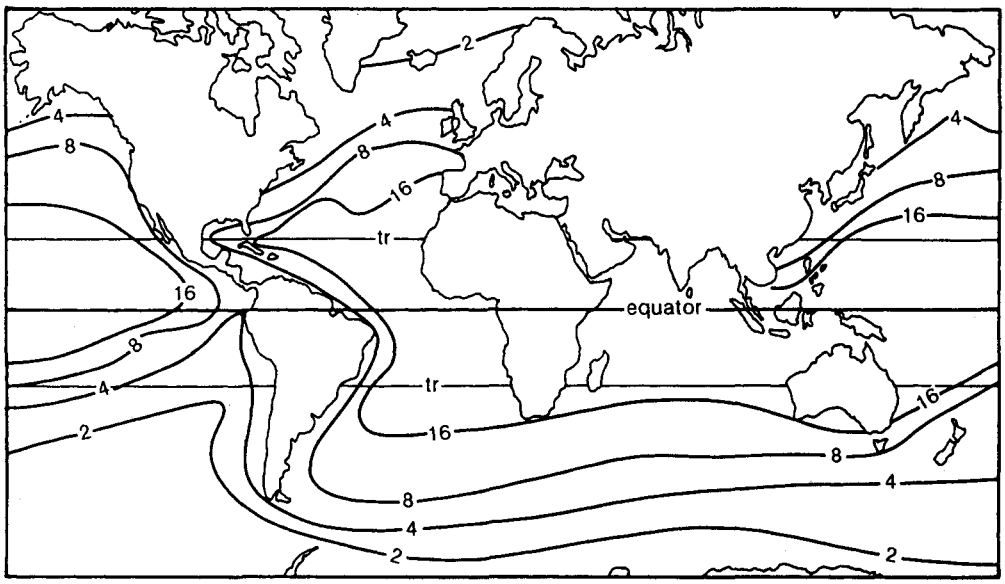

Figure 17-6 Contoured pattern of species diversity in recent planktonic foraminiferans. (*Source:* Modified from F. G. Stehli and C. E. Helsey, *Science*, v. 142, pp. 1057–1059.)

studies to be useful in determining the location of ancient equators and poles.

Decrease in diversity with latitude may be controlled by the greater variability of temperatures in higher latitudes rather than by the latitudinal gradient in average temperature. In low latitudes the temperature changes little from season to season but in temperate and polar latitudes, organisms must be able to withstand wide seasonal and daily variations in temperature. Many ecologists believe that highly diverse biotas can only develop under stable environmental conditions and that environmental instability of any type results in low diversity biotas.

Although the ability of the land to support plants and animals decreases poleward, the productivity of the sea does not and the decrease in diversity of marine biotas is not accompanied by decrease in the total mass of plants and organisms (biomass); that is, the few kinds of organisms that live at high latitudes have large populations. The "cake" representing available marine resources is sliced thinly into many morsels in the tropics and into large portions in subpolar and polar seas.

Determination of temperatures from fossils has been of particular interest to paleontologists examining drill cores of ocean floor sediments. During the recent Ice Age the temperature of the oceans changed cyclically, and continental ice sheets expanded and shrank. The shifting of the climatic zones caused changes in the distribution of planktonic foraminifera whose tests are major constituents of deep-sea sediments. The tests are composed of a series of chambers in a trochoid spiral and may be secreted in a dextral or sinistral pattern (see Chapter 7 for a discussion of these terms for gastropod shells). The proportion of the two types of test secreted by the forams depends on the temperature of the water in which they live (Fig. 17–7). For *Neogloboquadrina pachyderma* the water temperature dividing populations in which most of the tests are dextral from those in which most are sinistral is about 9°C. For *Globigerina bulloides* 80 percent are sinistral in water at 4°C; but only 60 percent at 15°C. Other test features that vary with temperature include shape, number of chambers in the final whorl, porosity of the wall, and overall size. In addition, the specific temperature tolerances of many living foram species are known and, if these species are found in ancient deposits, an estimate of the temperature at which they were laid down can be made.

The proportion of the isotopes of oxygen incorporated in the shells of marine invertebrates varies with the temperature of the ocean water in which they live. The ratio of the isotopes ^{18}O and ^{16}O in fossil shells is used to estimate the temperatures of ancient seas. As invertebrates extract oxygen in the form of carbon dioxide from seawater to form the

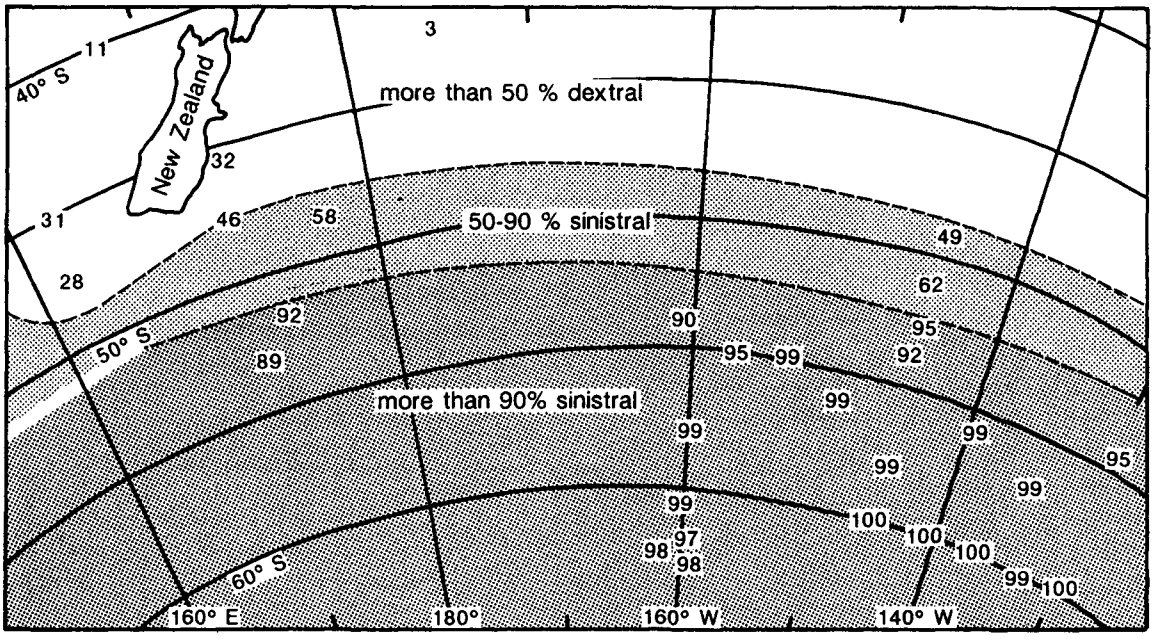

Figure 17-7 Relative proportion of sinistral and dextral specimens of *Neogloboquadrina pachyderma* from recent sediment samples in the South Pacific Ocean. The figures plotted represent the percentage of sinistral specimens. (*Source:* Modified from J. P. Kennett, *Micropaleontology*, v. 14, pp. 305–318.)

calcium carbonate of their shells, fractionation takes place, that is, the proportions of the oxygen isotopes are changed by incorporation in the shell.

$$\frac{{}^{18}O\ /\ {}^{16}O \text{ of shell}}{{}^{18}O\ /\ {}^{16}O \text{ of water}} = 1.021 \text{ at } 25^\circ\text{ C}$$

This relationship indicates that ^{18}O isotope is concentrated slightly in the shell relative to the water. The value of the fractionation factor (1.021 in the equation) is dependent on temperature, and its value at various temperatures is known (Fig. 17–8). If the isotope content of the shell and the water are known, the temperature is easily calculated. The change in ^{18}O in fractionation ($\delta^{18}O$) is usually expressed in parts per thousand with respect to a standard which may be a belemnite guard from the Cretaceous Peedee Formation (PDB) or standard mean ocean water (SMOW). The isotopic ratios in fossil shells can be measured by means of a mass spectrometer but the isotope ratio of the ocean water in which the shells lived must be calculated on the basis of several assumptions. A major control on the sea water ratio is the amount of water removed from continuous circulation in precipitation and evaporation in the weather cycle into continental ice caps, and most paleotemperature measurements involve an assumption as to the extent of glaciation at the time the shell was secreted. The seawater isotope ratio also varies with salinity and for shells from estuaries, or other areas where salinity is abnormal, a correction factor must be applied. Unfortunately, processes of preservation that

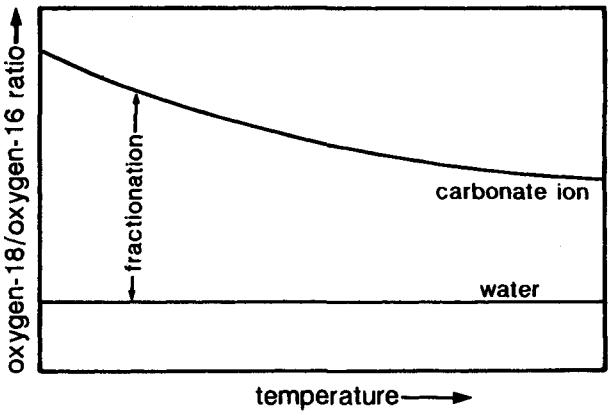

Figure 17-8 Schematic representation of the difference in the $^{18}O/^{16}O$ ratio in water and carbonate precipitated in equilibrium with that of water at different temperatures. The separation of the lines is a function of the temperature-sensitive fractionation. (Courtesy of J. R. Dodd, *Paleoecology, concepts and applications*, Wiley Interscience, 1981.)

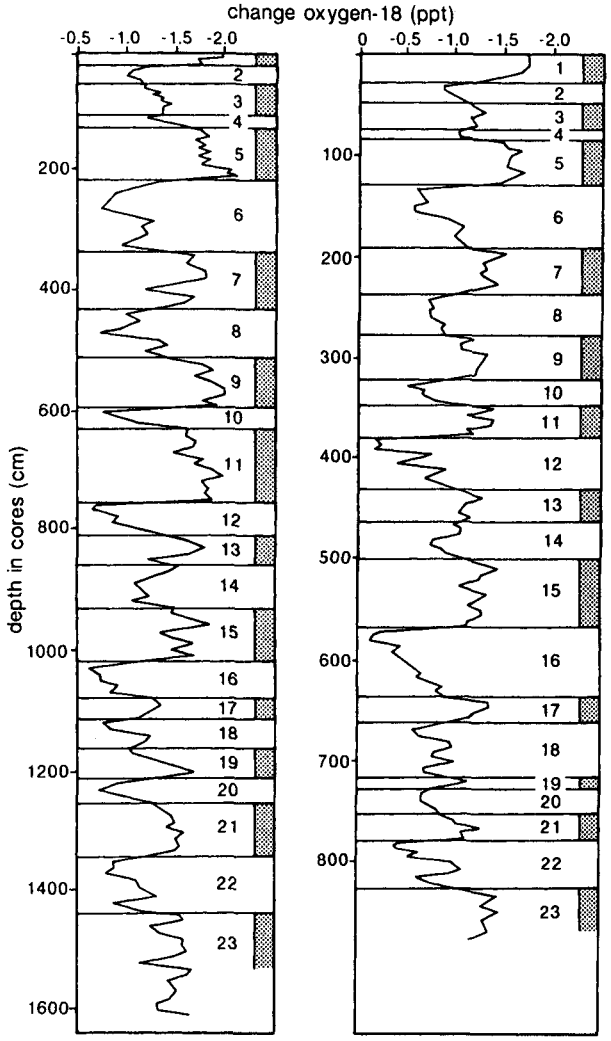

Figure 17-9 Variation in the $^{18}O/^{16}O$ ratio of two cores from the Pacific Ocean, showing the use of the ratio in correlation. The numbers and the shaded bars identify the temperature-based time divisions of this interval, as proposed by C. Emiliani. (*Source:* Modified from N. J. Shackelton and N. D. Opdike, *Geological Society of America Memoir 145*, pp. 449–464.)

alter the shell in any way usually change the isotopic ratios and make accurate paleotemperature determinations impossible. Most shells older than late Mesozoic have been so changed that paleotemperatures cannot be measured from them.

The greatest success of the oxygen isotope method has been in the study of foraminiferal tests of Cenozoic age, particularly those recovered from the Deep Sea Drilling Project. Variations in the isotope ratios have been correlated from hole to hole and interpreted as variations in temperature although they may also reflect changes in the volume of continental ice caps (also temperature dependent) (Fig. 17–9). General temperature curves for Late Cretaceous and Cenozoic time (Fig. 17–10) show high early Cenozoic ocean temperatures and decrease toward the late Cenozoic glacial period in which we now live. Separate measurements from planktonic and benthonic foraminifera in the same sample indicate the temperature difference between surface

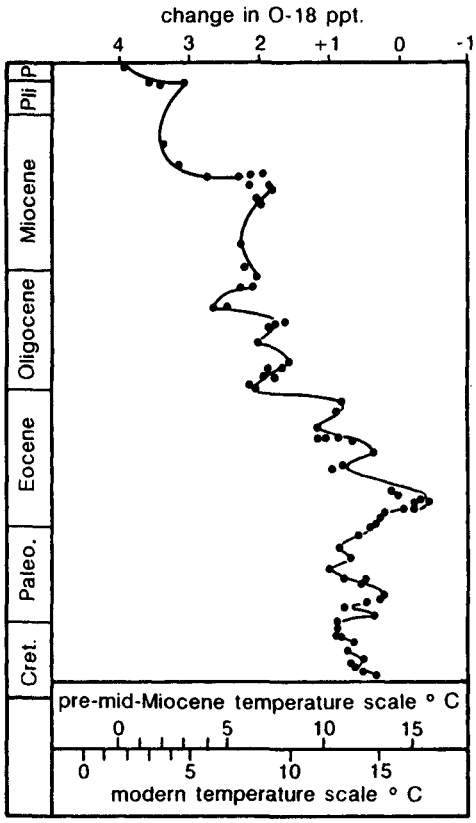

Figure 17-10 Oxygen isotope composition of multispecies assemblages of benthonic foraminiferans from several deepsea cores. The figure shows how they can be used to interpret temperature trends. The pre-Miocene temperature scale is calibrated on the assumption that there were no glaciers at this time. The modern temperature scale is based on the present distribution of glaciers. Temperatures based on oxygen isotopes can only be interpreted on the basis of assumptions about the extent of glaciation. The oxygen isotope scale is in parts per thousand. (*Source:* Modified from S. M. Savin, R. G. Douglas, and F. Stehli, *Geological Society of America Bulletin*, v. 86, pp. 1499–1510.)

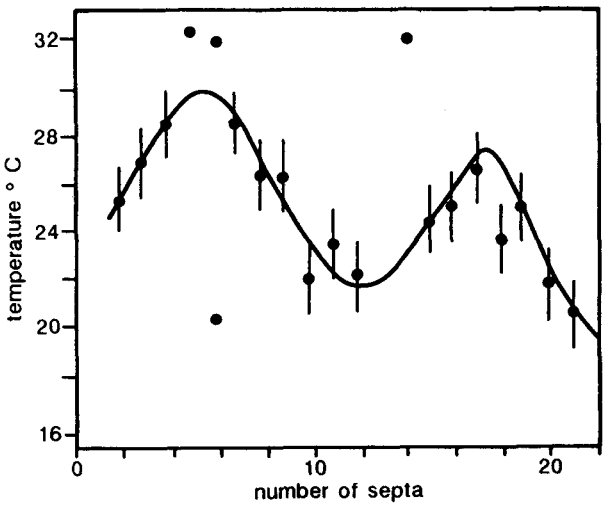

Figure 17-11 Temperature of formation of septa of a Jurassic ammonite, based on oxygen isotope values. If the variation with age is interpreted as seasonal, the ammonite must have been born in the spring and died in the winter of its second year. The values far off the curve are questionable. (*Source:* Modified from W. Stahl and R. Jordan, *Earth & Planetary Sciences Letters*, v. 6, pp. 172–178, Elsevier Scientific Publishing Co.)

and bottom waters for that location. Studies of variation of oxygen ratios within a single shell, such as an ammonite (Fig. 17–11), may reveal not only the temperature of the ocean in which it lived, but also its seasonal range, the age of the animal, and the time of year that it died.

Salinity:

Salinity is an important control on the distribution of aquatic animals and plants. Organisms living in salinities greater than that of their internal fluids tend to lose water through their cell walls and must have mechanisms to retain or replace it. Those in salinities less than that of their fluids must have mechanisms to get rid of the water that enters through their cell walls. The laws of osmosis apply to these relationships. Through such mechanisms organisms are adapted to a particular salinity environment, and only a few can tolerate large changes, or ranges, of salinity. Marine fish that spawn in fresh water are an example of such animals. However, echinoderms, foraminiferans, and brachiopods are now confined to water of close to normal marine salinity (about 35 parts per thousand) and no evidence has been found to suggest that they lived differently in the past. Their fossils therefore indicate marine conditions of deposition. Bivalves and gastropods have adapted to freshwater environments but other molluscan classes are confined to marine water. Most sponges, cnidarians, brachiopods, bryozoans, cephalopods, and hemichordates are exclusively marine. The shells of freshwater invertebrates may be distinguished by the thickness of the organic covering formed to prevent dissolution of the calcium carbonate in the undersaturated water, or by signs of post-mortem dissolution where the covering has broken down.

Biotas in hypersaline environments, such as coastal lagoons in areas of high evaporation, are of low diversity and are rich in ostracodes and stromatolites. Hypersaline environments can also be identified by the association of the sediments with evaporite minerals such as halite.

Estuaries are characterized by salinity gradients that may be identified in the fossil record. As salinity lessens upstream in the estuary, the amount of calcium carbonate available for shell secretion decreases and the shells of animals of wide salinity tolerances become thinner. The living mussel, *Mytilus edulis*, can live in a wide range of salinities from 5 parts per thousand to normal seawater and penetrates far into estuaries, but its shell in lower salinities is thinner and smaller than in normal sea water. Gradients in shell thickness in fossil species may point to gradients in salinity. Since most marine species have limited tolerance for salinity changes, the number of species in estuaries decreases as the water freshens. The Baltic Sea is not a simple estuary but the salinity drops from normal at its North Sea entrance to about 5 parts per thousand at the Gulf of Bothnia (near Finland). Figure 17–12 shows a diversity gradient in molluscs that accompanies this salinity gradient. A similar gradient dependent on salinity can be traced in the fossils of the sediments of the Champlain Sea that flooded into the St. Lawrence estuary at the close of the last glaciations, about 10,000 years ago (Fig. 17–13).

The proportion of carbon isotopes ^{12}C and ^{13}C has been used to estimate the salinity in which fossil shells secreted calcium carbonate. The method is based on the deficiency of the ^{13}C isotope in land plants and humus that supply carbon to estuarine brackish waters. The $^{18}O/^{16}O$ ratio also varies with salinity as fresh water derived from rainfall and

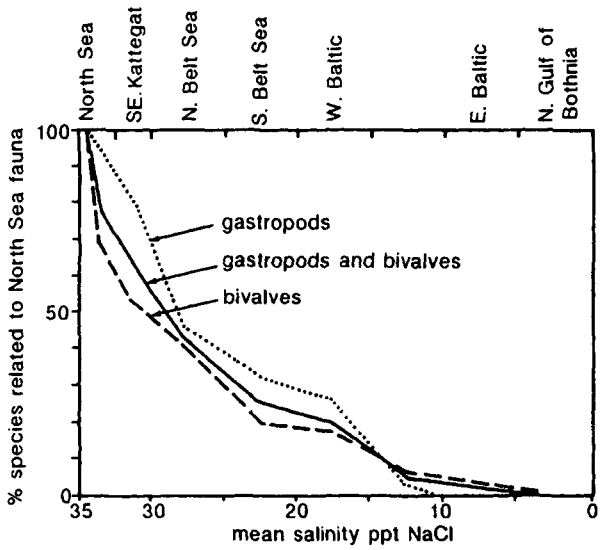

Figure 17-12 Decrease in the number of molluscan species from the normal salinity environment of the North Sea, along the salinity gradient of the Baltic Sea. The mean salinity is expressed in parts per thousand (ppt). (*Source:* Modified from D. V. Ager and T. Sorgenfrei; courtesy of Geological Survey of Denmark, 1958.)

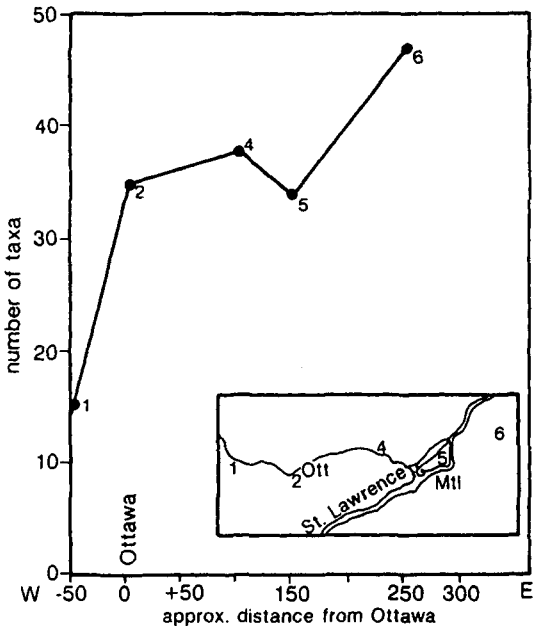

Figure 17-13 Diversity gradient believed to be related to decreasing salinity westward in the late Pleistocene Champlain Sea, in the region of the Ottawa and St. Lawrence valleys. The position of the six collections with relation to Ottawa (Ott) and Montreal (Mtl) is shown on the inset map. (*Source:* Plotted from information of F. Wagner, *Geological Survey of Canada*, 1970.)

ultimately from evaporation of seawater is enriched in the light isotope ^{16}O.

Illumination:

Light is essential to the process of photosynthesis and the life of all green plants. As all animals are dependent on plants, directly or indirectly, most life forms are limited in their range by the availability of light. At the land surface light is generally available everywhere but is locally restricted by a thick overhead canopy of vegetation that limits the type of plant that can grow at ground level. In the sea, sunlight penetrating the surface is absorbed in passing downward through the water. Light of red wavelengths is the first to be absorbed so that to a diver deeper than 10 m most objects appear to be shades of blue. The depth at which all light has been absorbed is about 200 meters but varies with the clarity of the water and the amount of sunlight penetrating the surface. This level is the base of the photic zone and the top of the aphotic zone. The amount of sunlight refracted into the water depends on the angle at which the sun strikes the water, and hence the latitude and season, and also on the turbulence of the water surface. Planktonic plants, the primary food producers of the sea, are confined to the photic zone and are concentrated near the surface. As a result animal life is most abundant in surface waters where food is plentiful because the light is strong. Animals living below the photic zone must rely for food on dead organisms that "rain" down from above. The abundance of fossil algae is direct evidence of a shallow-water environment. Any marine deposit in which invertebrate marine fossils are abundant is likely to have been formed in shallow water in the photic zone.

Several groups of invertebrates rely on algae within their cells to supply their oxygen needs through photosynthesis while the algae use the cell's waste carbon dioxide for their own metabolism. In modern reef corals the symbionts are a form of dinoflagellate called zooxanthellae. In terms of light requirements the corals act as if they were plants because they have become completely dependent on their symbionts. Reef corals only thrive within a few meters of the sea surface and are sparsely distributed and slow growing at depths below 50 meters. The lower limit for survival of corals dependent on zooxanthellae is about 70 meters; below this level the light is not strong enough for the photosynthesis of the zooxanthellae to satisfy the

Next Page

oxygen requirements of the coral. The rapid secretion of calcium carbonate which is characteristic of scleractinians is also believed to depend on the zooxanthellae because corals secrete skeleton faster in sunlight. Several mechanisms have been proposed to explain how they help in secretion but no consensus has been reached. Some paleoecologists have argued that the massive carbonate secretion evidenced by Paleozoic corals points to a symbiotic relationship between the corals and zooxanthellae, but as the microorganisms are not preserved, no direct evidence supports this suggestion. The strong domal form of many Paleozoic corals has suggested to some the opposite conclusion: that they had to grow wave-resistant colonies because their relatively slow growth rate in the absence of zooxanthellae made the repair of broken skeleton difficult. They reason that one difference between the scleractinians and Paleozoic corals is that the former much more commonly grow to branching fragile forms because their relatively rapid growth rate, helped by zooxanthellae, allows them to repair wave damage without difficulty. George Stanley (7) presented evidence that the scleractinians did not become diverse and abundant until latest Triassic time yet they first appeared in the Middle Triassic. He suggested that they did not achieve their present dominant position in reefs until they teamed up with zooxanthellae at the end of the Triassic Period.

The larger foraminiferans of today also have a variety of algal symbionts including zooxanthellae, red and green algae and diatoms, and those of the past, such as the nummulites and fusulines, probably also had them. The giant clam *Tridacna* supports its extravagant deposition of calcium carbonate through zooxanthellae in the mantle and paleontologists have speculated that the rudists of the Cretaceous satisfied their massive skeletal requirements through a similar symbiosis. All these animals, being light dependent, must have been confined to shallow water.

Dissolved Gases:

The distribution of organisms in the sea is also controlled in part by the concentrations of the two gases involved in metabolism, carbon dioxide and oxygen. As these gases dissolve in the sea from the atmosphere, their concentration might be expected to decrease with depth but the situation is more complex. The flow of ocean water along the deep-sea floor from pole to equator brings dissolved gases to great depths and allows animals to live in abyssal environments.

A larger amount of carbon dioxide is dissolved in the oceans than is present in the atmosphere. The availability of the gas does not limit the range of marine plants that use it, but its distribution in the ocean controls the solubility of calcium carbonate and therefore the occurrence of modern and fossil shells. The solubility varies inversely with the concentration of carbon dioxide: the more CO_2 present in the water, the more soluble is $CaCO_3$. Carbon dioxide, like all gases, is more soluble in cold water than hot. The warm surface waters of the ocean are therefore relatively deficient in dissolved CO_2 and are supersaturated in $CaCO_3$. Shells secreted in this environment have no tendency to dissolve and extraction of the carbonate from seawater is easy. The colder water deep in the ocean can dissolve more CO_2 and is undersaturated with $CaCO_3$. In this water $CaCO_3$ dissolves and the shells of planktonic organisms, such as foraminiferans, that fall from warm, saturated surface water begin to disappear like snowflakes melting as they reach warmer air. This dissolution occurs at depths of 4000 to 5000 meters in the sea and the zone is known as the lysocline. Sediment deposited below the lysocline contains no carbonate fossils despite the steady supply from above of calcareous tests. The lack of carbonate fossils in some post-Jurassic sedimentary rocks is therefore an indication of deposition below the lysocline. Planktonic foraminiferans did not evolve until Late Jurassic time and the absence of their tests in older sediments cannot be used as an indication of deposition in deep water.

The oxygen content of the sea is between 5 and 6 milliliters per liter at the surface and decreases to values of less than 1 ml/l at depths of about 800 meters before gradually increasing again into abyssal water. As abyssal sediments amount to only a small part of the stratigraphic record, the paleontologist is most concerned with environments in the upper 800 meters of the ocean in which O_2 content declines. The water in which oxygen content ranges from surface values to about 1 ml/l is the aerobic zone. That in which oxygen content is 1 to 0.1 ml/l is the dysaerobic zone, and that with less oxygen is the anaerobic zone. The last of these cannot support any significant amount of metazoan life. The effect of the oxygen gradient on life has been studied in the Black Sea and off the California coast (8). Faunal changes that take place along the gradient and might be recognized in the paleontological

Chapter 18

Paleobiogeography

INTRODUCTION

Modern Faunal Realms:

The terrestrial faunal realms were first outlined by Alfred Wallace, Darwin's co-author of the first paper on natural selection. Wallace established biogeography, the study of the geographic distribution of animals, as a science and divided the continents into five faunal realms: the Holarctic, comprising North America, Africa north of the Sahara, Europe and northern Asia; the Neotropical, comprising South America; the Ethiopian, comprising most of Africa; the Oriental, comprising India and southeast Asia; and the Australasian, comprising Australia, eastern Indonesia, and New Zealand (Fig. 18–1). The differences between the realms are not basically environmental. Tropical rain forests exist in South America, Africa, and Indonesia but, although environments are duplicated, the fauna and flora differ for reasons that cannot be strictly environmental. The contrast of the larger animals of the Neotropical and Ethopian realms illustrates the order of magnitude of biogeographic differences. The monkeys of Brazilian jungles are a completely different suborder from those of the Congo. There are no proboscidians, giraffes, or hippos in South America and no sloths or armadillos in Africa. These differences are accounted for by the barrier, the South Atlantic Ocean, that separates the realms and prevents mixing, and by the history of the separation of the two continents in mid-Mesozoic time so that their faunas, then similar, have evolved along different paths in the intervening 150 million years. In the previous chapter we considered differences in contemporary biotas caused by environmental differences; in this one we consider differences arising from barriers and history.

Because the oceans flow into each other and are not completely separated by land barriers as the continents are by the sea, modern marine realms are less distinct. Pacific and Atlantic realms are usually distinguished and the Indian Ocean fauna is recognized as a subdivision of the Pacific realm. The barriers separating these realms are the continental masses of the Americas and Africa–Asia. They are effective in restricting the mingling of the warm-water faunas of the two realms because they extend into cold, or polar, waters at each end and warm-water animals cannot migrate through these inhospitable temperatures. The differences be-

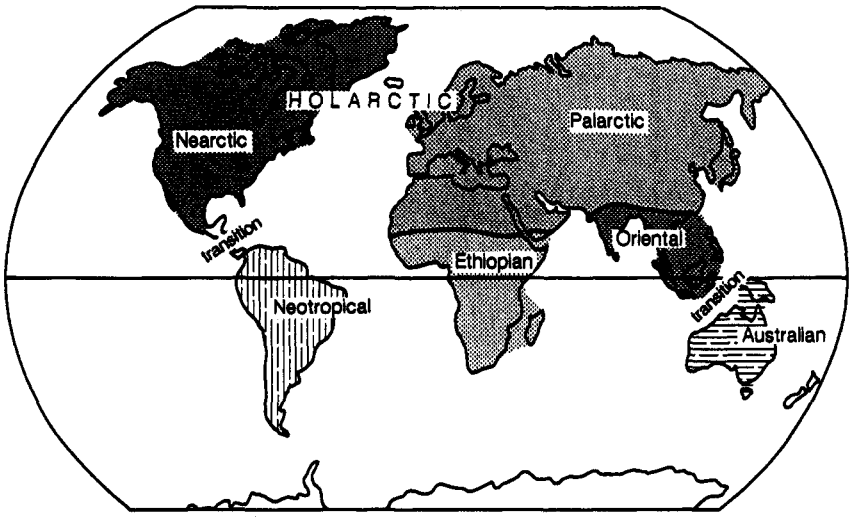

Figure 18-1 Modern terrestrial faunal realms.

tween Pacific and Atlantic faunas are illustrated by the contrast on opposite sides of Panama where they are separated by a narrow land barrier. Similar environments are available, but no species of coral is common to the two faunas although typical reefs on the Caribbean side include 50 species and those on the Pacific side, 15 species. Many years ago William Dall studied the shelled invertebrates on either side of the isthmus of Panama and found that of the 517 species on the Caribbean side and 805 species on the Pacific side, only 24 were common to the two oceans. Although the isthmus is cut by a canal, the canal is filled with fresh water and is as much a barrier to the migration of marine species as land.

Ancient Faunal Provinces:

Comparable faunal differences are found in the fossil record. William Oliver (1) has described the distribution of rugose corals in the Devonian of North America in terms of two faunal realms. The western part of North America was a part of the Old World realm which included much of the rest of the world. It was separated during Early Devonian time from the Eastern Americas realm by a low ridge extending through the central part of the continent (Fig. 18–2). The number of species that occur exclusively in this realm increases in Early Devonian time from 57 to 91 percent. Species that are confined to one biogeographic unit are called endemics. Barriers to mixing with the Old World fauna were effective; otherwise this degree of endemism could not have developed in the Early Devonian sea. During Middle Devonian time the percentage of endemics decreased from 67 percent in the early part of the epoch to 45 percent in the late part. By Late Devonian time none of the species in the eastern part of the continent was endemic. The barrier had begun to leak Old World corals in Middle Devonian time and by Late Devonian time it had become ineffective and probably inundated. The distinction between the two provinces disappeared. The study gives useful information about the placement of land and sea in the Devonian Period.

In mid-Mesozoic time a long equatorial ocean separated the united continents of North America, Europe, and Asia from India, Africa, and South America (Fig. 18–3). From this seaway, called Tethys, arose the Alpine, middle eastern, and Himalayan mountains as Africa and India collided with Europe and Asia in Cenozoic time. The Mediterranean, Black, Caspian, and Aral seas are remnants of the Tethys. A distinctive fauna is found in Jurassic rocks deposited in this seaway. Almost all of the rudist bivalves, brachiopods, corals, and some families of ammonites were confined to the Tethyan faunal realm. New groups evolved in the Tethyan realm and spread northward onto the continental shelf seas of Europe. The uniqueness of the Tethyan faunal realm may have been the result of contrasts between its tropical waters and the cooler water towards the poles or to the greater depth of water in it. It was not isolated from neighboring oceans by physical barriers yet maintained a distinct faunal character for tens of millions of years.

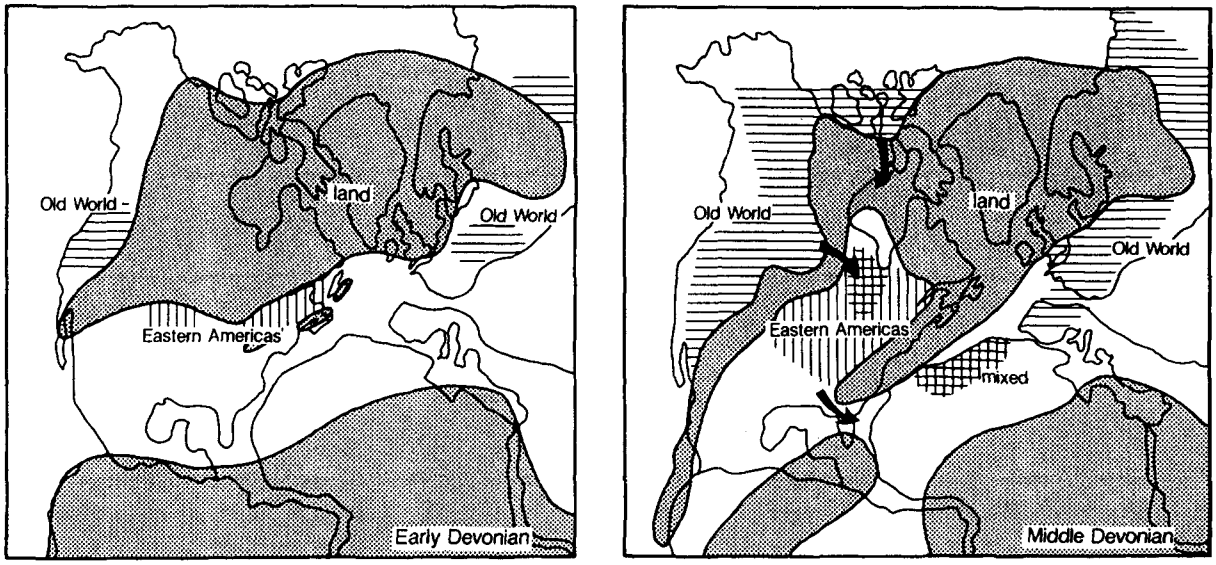

Figure 18-2 Distribution of faunal provinces based on rugosan corals in Early and Middle Devonian time. The areas of the Old World province are indicated by horizontal ruling; those of the Eastern Americas province; by vertical ruling. Where the two patterns intersect, mixed faunas are found. Possible migration routes are shown by arrows. (*Source:* Modified from W. A. Oliver, *Journal of Paleontology*, v. 50, pp. 365–373.)

BOUNDARIES AND DEFINITIONS

Paleoecologists have difficulties distinguishing between dissimilar contemporaneous faunas separated by barriers and those separated by differences in environment. Barriers between some biogeographic units are environmental changes such as latitudinal changes in temperature. The faunal contrasts between modern realms are partly the result of environment, not barriers or history. For instance, the holarctic realm does not include tropical rain forest environments as the other four do, and therefore organisms adapted to this environment are missing from the holarctic realm. If differences between fossil biotas cannot be explained by differences in environment, paleontologists conclude that they were produced by barriers even though such barriers may be difficult to identify in distant geological periods.

Realms are the largest biogeographic units. Some lesser units in order of their decreasing size are: region, province, and subprovince. Quantitative definitions of this hierarchy of units on the proportion of endemic species have been proposed. One proposal requires a province to have between 50 and 25 percent endemic species. If the area has over 75 percent, it is a realm, and under 25 percent is a subprovince. Most paleontological studies do not use such strict definitions and are more qualitative in nature.

Statistical procedures may be used to assess quantitatively the similarity of biotas of various regions. The comparison is made by using one of the similarity coefficients described in the previous chapter and by cluster analysis, which suggests which regions have sufficient similarity to be placed in the same realm, province, or subprovince.

Division of faunas into provinces and subprovinces is rarely based on an analysis of the whole fauna or flora, but usually on a single group. James Valentine (2) divided the continental shelves of the world into many provinces on the basis of molluscs, but a biologist studying corals would distinguish only two or three major provinces. Biogeographic boundaries are different for different groups because the effectiveness of barriers separating provinces depends on the way in which an animal disperses itself.

Obviously, land is a barrier to marine migration and seaways are barriers separating continental biogeographic units, but other barriers may be equally effective. Mountain chains separate the modern holarctic and oriental realms. The Sahara desert forms the boundary between the holarctic and Ethiopian realms. Rainfall and temperature control the distribution of plants as well as the distribution of

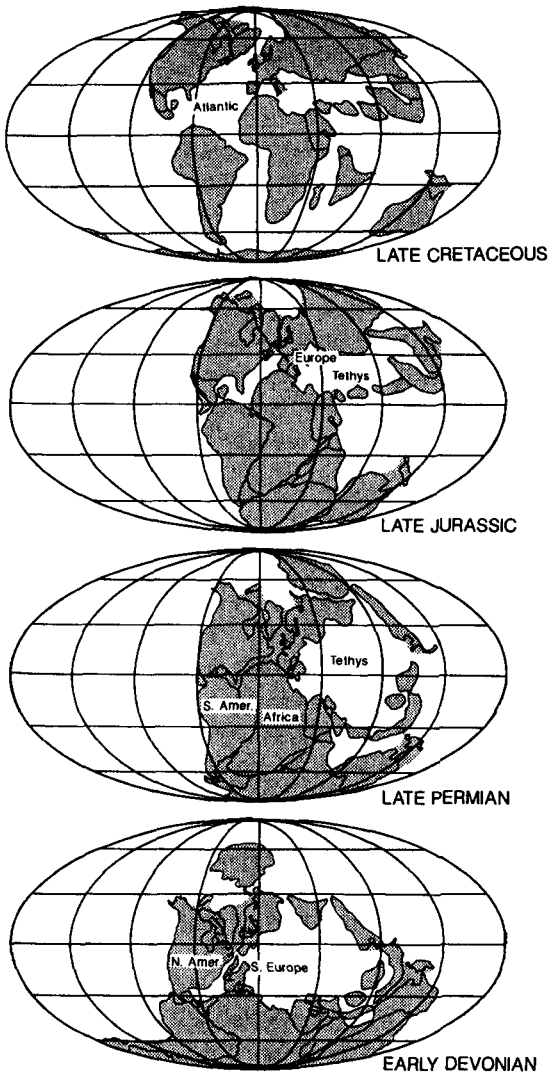

Figure 18-3 Paleogeographic reconstructions of the positions of the continents in Early Devonian, Late Permian, Late Jurassic, and Late Cretaceous time. The shading emphasizes the outlines of the continents and is not a representation of the land and sea distribution. The precise positions of the continents in the Paleozoic is still open to question. (*Source:* Compiled from various sources, particularly the maps of C. R. Scotese.)

the animals that depend on them. For benthonic animals of shallow seas, the deep ocean may be an effective barrier because their free-swimming larvae mature in a relatively short time and must then find a place to settle to the bottom. They will die if they are swept out into water of abyssal depth.

CONTINENTAL MOVEMENT AND FOSSIL DISTRIBUTION

Since the early 1960s geologists have established that the continents move laterally in a 350 million year cycle. Early cycles of Proterozoic time are obscure. The first cycle that can be clearly discerned starts with the continents collected into one supercontinent (Pangaea I) in late Proterozoic time. From that time until the Ordovician Period, they continued to separate as oceans widened. From Ordovician to Carboniferous time they moved together, coalescing to form the supercontinent of late Paleozoic and early Mesozoic time called Pangaea II. Since mid-Mesozoic time the earth's crust has returned to the rifting phase of the cycle that continues to the present day as Pangaea splits apart (Fig. 18–3).

The foundations of biogeography were laid in the nineteenth century when the positions of the continents and oceans were regarded as fixed. Each group of plants and animals was considered to have first appeared in a location where it is now most diverse, and to have extended its range outwards as it was successful in competition with similar species. Where the range of a group of related taxa is now separated into segments by barriers, those barriers were postulated to have been passable when the organism established its range. The shallow-water aquatic reptile *Mesosaurus* is found in late Paleozoic sediments of Africa and South America that are now separated by the barrier of the South Atlantic Ocean. In the last century a hypothetical late Paleozoic land bridge, like the isthmus of Panama, spanning the Atlantic was required to explain how *Mesosaurus* could have extended its range from one continent to the other. Many other animals and plants (such as the seed fern *Glossopteris*) that are common to the southern continents at that time required the bridge. We now know that the two continents were part of Pangaea in late Paleozoic time and that *Mesosaurus* would have had no problem in crossing from one to the other. The geographic range of *Mesosaurus* was split into parts in the Mesozoic Era when South America and Africa separated, long after the animal was extinct. Distributions of terrestrial animals that were puzzling before the acceptance of continental drift, have become much clearer in the last 20 years. However, geologists are not in agreement about the positions of the continents before their union in late Paleozoic time and much has yet to be learned about the

relationship of continental disposition and marine organism distribution in early and middle Paleozoic time.

Closing Oceans:

When the faunas of two regions become increasingly similar in time, the change may indicate the decreasing effectiveness of a barrier separating them as we have seen for the Devonian rugose corals. In the early Paleozoic, North America and Europe were separated by an ocean called Iapetus which was closing as the continents united into Pangaea. The approach of the continents is reflected in the fossil faunas on either side. In the Ordovician only animals that were planktonic, such as graptolites, were able to cross the deep ocean barrier and establish themselves on both sides. In the Silurian benthonic organisms that had swimming larvae, such as brachiopods, stromatoporoids, and corals, were able to spread across the gap. By Middle Devonian time the northern part of Iapetus had closed and species that could not cross a marine barrier, such as freshwater fish, were common to the two continents.

During the late Mesozoic South America separated first from North America and then from Africa and was then surrounded by water. In the early Cenozoic episode of isolation a distinctive mammalian fauna rich in marsupials developed. In mid-Cenozoic time no families of mammals were common to the two Americas; 29 families lived in South America, and 27 families lived in North America. In late Pliocene time, only a few million years ago, the isthmus of Panama was raised between the continents, breaking the ocean barrier between the lands and making a land barrier between the oceans. Mammals migrated in both directions but mostly into South America, and 22 families are now common to the two continents. North America received as immigrants the opossum (a marsupial), the armadillo, and two mammals that became extinct in the Pleistocene Epoch, the glyptodont and ground sloth.

Opening Oceans:

During the past 150 million years the continents around the Atlantic Ocean have drifted apart. Australia has separated from Antarctica and Antarctica from Africa (Fig. 18–3). Only the Tethys Ocean has been closing. Those groups of terrestrial animals that evolved and spread before the breakup of Pangaea have had their ranges fragmented (examples have been discussed in Chapter 12). The marsupials are a good example. During the Late Cretaceous the marsupials arose from primitive mammalian stock in the New World and dispersed across an island chain linking North to South America and thence to Australia by way of Antarctica, which had not yet entirely separated from South America (Fig. 18–3). In the northern continents the marsupials had limited success in competition with the rapidly diversifying placental mammals but in the southern continents, which were becoming increasingly isolated, they thrived. The similarity of the marsupials in South America and Australia is difficult to explain without knowledge that these continents were once connected through Antarctica.

Faunas of Accreted Terranes:

Split geographic ranges may lead to important conclusions about the history of the continents. The Cambrian rocks of the eastern seaboard of North America from Newfoundland to Florida contain trilobite faunas unlike those of the rest of the continent but similar to those of northwestern Europe. For instance, the Middle Cambrian trilobite *Paradoxides* is unknown in North America except in this so-called Avalon terrane but is common in northern Europe. Yet in the early Paleozoic, fossil faunas from other parts of North America indicate that it was separated from Europe by the Iapetus Ocean. The trilobite faunas tell us that during the early Paleozoic the Avalon terrane must have been part of, or close to, Europe and therefore separated from the rest of North America by the Iapetus (Fig. 18–4). When the Iapetus closed in mid-Paleozoic time, the Avalon terrane was attached to North America. In Jurassic time when the continents again separated and the Atlantic Ocean formed, the rift occurred east of the old Iapetus suture, leaving the Avalon terrane, a bit of the opposite shore of Iapetus, attached to North America. Geologists have discovered that many mountain chains are composed of masses containing exotic fossil faunas.

Many out-of-place terranes can now be recognized in the North American Cordillera. They are sections of the crust brought eastward from the Pacific Ocean basin. As the oceanic crust spread and was subducted beneath the Cordillera, these terranes collided with and were attached to the west side of the continent and are, therefore, called accreted terranes. Each contains an exotic fossil fauna brought by the movement of the crustal plates into

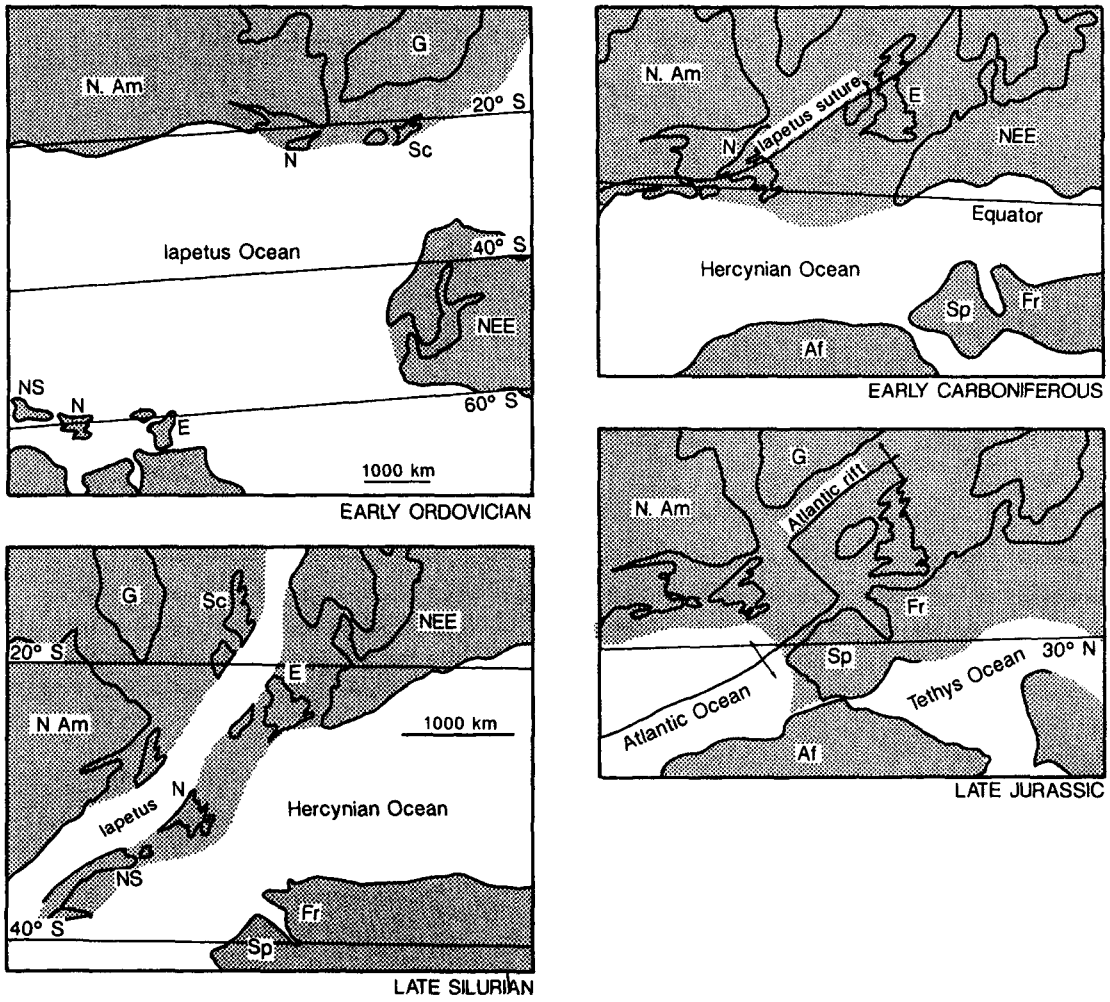

Figure 18-4 Development of the North Atlantic region from early Paleozoic time. Land areas are shaded, and the coastlines of the present land masses identify the movement of the land masses through time. Note that the maps are not all drawn to the same scale. N. Amer. = North America, N = Newfoundland, N.S. = Nova Scotia, Sc = Scotland, G = Greenland, E = England, NEE = northeast Europe, Fr = France, Sp = Spain, Af = Africa. (*Source:* Compiled from maps of L. R. Cocks and R. A. Fortey, A. G. Smith and others, and C. R. Scotese and others.)

contact with contemporary faunas that lived in North America many thousands of kilometers away (3). They are now identified, and their pathways across the Pacific reconstructed, by a combination of paleomagnetic and paleontological studies. Figure 18–5 shows various exotic terranes of the Cordillera spread out across the Pacific as they might have appeared in Carboniferous time.

Biogeographic Theories:

Biogeographers who believe in dispersal from centers of origin require special mechanisms to explain the occurrence of a taxon—order, family, or genus—in two or more areas now separated. For them each newly evolved species spreads from a center as it competes with less well adapted organisms. The ranges of these latter are fragmented as they find refuge in the less desirable corners of the world. Many biogeographers ascribe a major influence to repeated advances and retreats of ice sheets in the recent Ice Age which split formerly continuous ranges into segments and caused latitudinal migration of biotas. In Europe the southward advance of the continental ice sheet from Scandinavia and the northward advance of mountain glaciers from the Alps formed a frigid zone across central Germany, splitting the European fauna into segments that

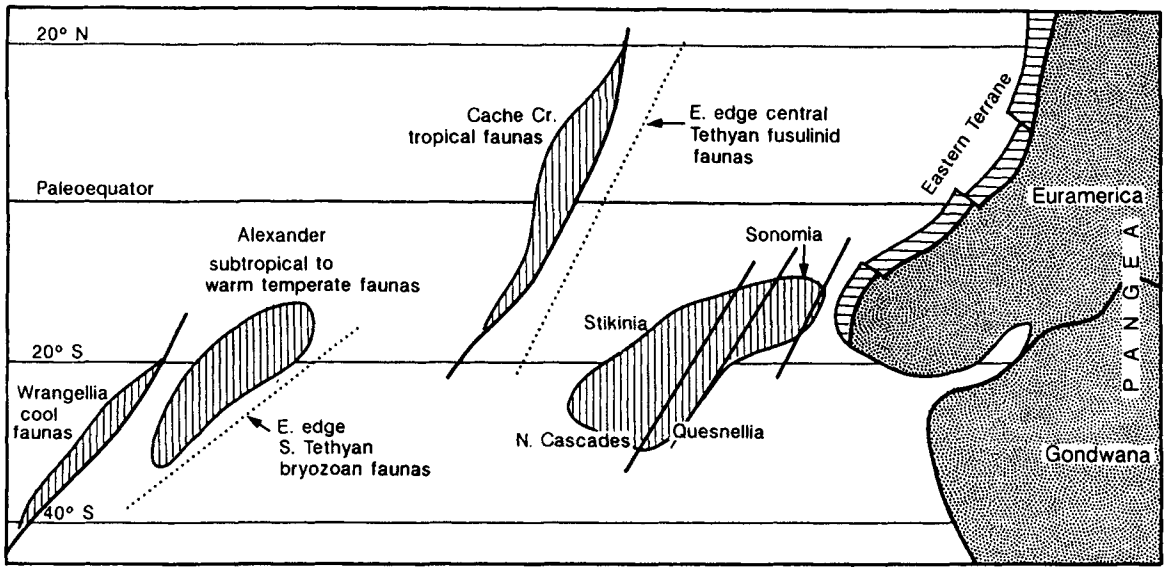

Figure 18-5 Reconstruction of the position of the accreted terranes of the Cordillera in their positions in the Pacific Ocean in Late Carboniferous and Early Permian time. The terranes carry faunas typical of various Tethyan realms and foreign to the Eurasian continent (which was then becoming part of Pangaea). In Mesozoic time, these terranes docked with North America and became part of the Cordillera. (*Source:* Modified from C. A. and J. R. P. Ross, with their assistance, SEPM, Pacific Section, 1983.)

found refuge in the relatively warmer climates of the Balkans and Spain (Fig. 18–6). As a result of the genetic isolation, eastern and western species of many animal groups developed and have remained distinct even though the barrier separating them disappeared with warming climates.

Leon Croizat (4) formulated concepts that have come to be called vicariance biogeography. Vicariance biogeographers explain modern distributions largely on the basis of separation of ranges of organisms as the components of Pangaea drifted apart and ascribe a major role in allopatric speciation to the breakup. Primary dispersal of organisms is postulated to have taken place at times of continental union, and speciation and "vicariating" or fragmenting of the ranges, to have occurred during breakup phases.

The union and separation of continents was an important, but not exclusive, control on the distribution of organisms throughout geological time. Many processes are active in dispersal and fragmentation of organisms that together determine their geographic range at any one time.

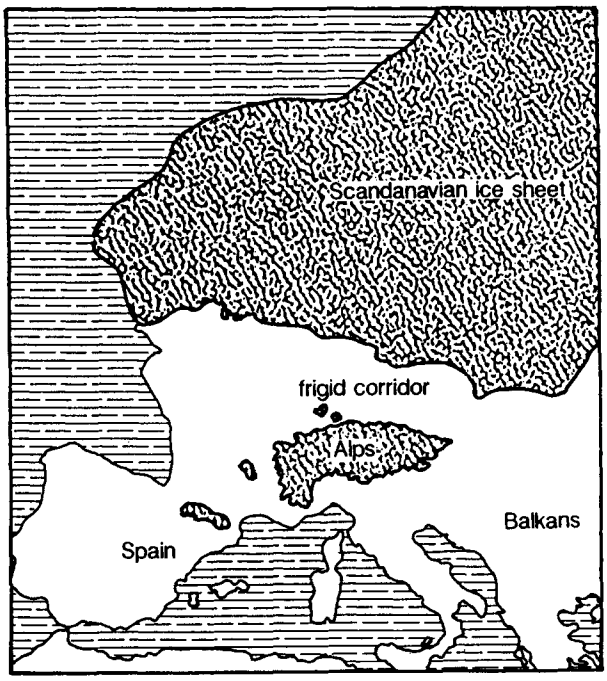

Figure 18-6 Extent of ice sheets in Europe during their maximum advance in Pleistocene time. Although Alpine and Scandinavian glaciers did not meet, central Europe became a frigid corridor that restricted the mixing of animals between Spain and the Balkans. Coastlines are shown as extended by the drawdown of sea level. (*Source:* Modified from the work of R. F. Flint.)

Continents and Evolution:

James Valentine and Eldredge Moores (5) have drawn attention to the relation between episodes

of expansion and extinction of marine life and the rifting and suturing of the continents. The breakup of the continents leads to extension of coast lines, expansion of shallow-water environments of continental shelves, and diversification of marine life. The first rifting episode took place at the end of Proterozoic time and influenced the expansion of the metazoa at the beginning of the Paleozoic Era. The second, in early Mesozoic, was accompanied by the rise of modern invertebrate faunas in Late Triassic and Jurassic time (Fig. 7–60).

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Chapter 19

Fossils as Builders of Sedimentary Rocks

INTRODUCTION

Fossils make significant contributions to the volume of sedimentary rocks that cover most of the earth's surface. Many sedimentary rocks, such as limestone and coal, may be composed almost entirely of the remains of animals and plants. Many sandstones and shales also contain a high proportion of fossil particles. When the organisms that formed them die, shells, bones, or leaves become sedimentary particles carried by streams or ocean currents and deposited in sediments just as are grains of sand or pebbles. The growth of organisms also controls sedimentary environments such as oyster banks, tropical reefs, and coastal and deltaic swamps. In order to understand the role of fossil organisms in forming rocks and controlling depositional environments, we must examine the minerals they use to secrete tests, shells, and skeletons and the microscopic structure of these hard parts. With this information the geologist may be able to identify the organisms that secreted the shell fragments that form sedimentary rocks.

Limestone is by far the most important of the sedimentary rocks formed by fossils. Many invertebrates in the sea and in lakes secrete some form of calcium carbonate by extracting the ions dissolved in water. In the tropics where the shallow seawater is supersaturated with calcium carbonate, the tests and shells of invertebrates do not dissolve in the water when they die but accumulate on the seafloor to form limestone. A high proportion of limestone is composed of fragments of the skeletal tissue secreted by animals and plants. Some constituents are precipitated by physical processes, such as evaporation, from the sea and others are precipitated by modifications of the carbon dioxide content of seawater by the metabolic processes of plants. At present about 7 percent of the sediments on the deep-sea floor are carbonate deposits in the process of becoming limestones. About 5 percent of all the sedimentary rocks in the earth's crust, or 3500×10^{14} metric tons, are limestone. Seventy-five percent of this vast quantity is of Phanerozoic age, for only since the beginning of the Paleozoic has carbonate been extracted in quantity from the sea and stored in the crust (1).

Limestones are uncommon in Archean sedimentary sequences but their rarity is probably related to the absence of shallow-water sediments in general. Remember that limestone does not accumulate below the lysocline (Chapter 17) and most Ar-

chean seas appear to have been deeper. The abundance of carbon dioxide in the Archean atmosphere and ocean would also have raised the level of the lysocline to near the surface. In some Proterozoic shallow-water deposits carbonates are relatively common rocks. Dolomite, the double carbonate of calcium and magnesium, is much more abundant in these older sediments than in post-early Paleozoic sedimentary sequences. Pre-Paleozoic limestones and dolomites could not have been produced by the accumulation of the skeletal carbonates, for calcified skeletons did not appear until the Cambrian Period. They must be precipitates from saturated marine water produced either physically by the evaporation of the water, or biochemically by the extraction of carbon dioxide from the water by algae.

Even Phanerozoic limestones do not consist entirely of fossil fragments but include carbonate particles a few micrometers across that were originally a fine lime mud. Some of this mud is derived from the breakdown of skeletal parts of animals and from carbonates in the tissues of marine plants, but other mud is precipitated physically or biochemically from marine water. After calcium carbonate in crystals a few micrometers across is consolidated into limestone, it is called micrite. Micritic limestones of Phanerozoic age commonly contain or are entirely made up of ellipsoids less than a millimeter in diameter of fine grained carbonate. Many of these particles, technically called peloids, are produced as pellets when deposit-feeding organisms pass the lime mud through their guts; there is some evidence that others may be produced by bacterial or inorganic processes after the deposition of the limestone. Filter-feeding organisms also form waste products into pellets that are ejected in the effluent stream. Aggregation of waste into pellets insures that it will be too heavy to stay in suspension and reenter the organism in the incoming current. Pellet-forming organisms may be soft-bodied and may leave behind only the peloidal limestone as evidence of their former presence on the seafloor.

MINERALOGY OF SHELLS AND TESTS

Carbonate Minerals:

Invertebrates secrete calcium carbonate in three forms: high-magnesium calcite, low-magnesium calcite, and aragonite. The difference between calcite and aragonite is not in the proportion of the calcium, carbon, and oxygen that constitute the minerals but in the way the ions are arranged in the crystal lattice. The packing of the ions in calcite results in crystals of rhombohedral shape and symmetry; packing in aragonite results in needlelike crystals of the class known as orthorhombic. Because the ions are packed differently, the space available for the calcium ion is different in calcite and aragonite. All the sites in the crystal lattice available for the calcium ion are not occupied by it in naturally occurring calcium carbonates; other ions may substitute for calcium if they fit into its space. In calcite magnesium ions fit into the space available with little disturbance of the crystal structure. Organically secreted calcites have been found to contain up to 20 percent magnesium. Calcites with more than 4 percent magnesium are classed as high-magnesium calcites, those with less than 4 percent as low-magnesium calcites. Iron and manganese ions are also of appropriate size to fit into the calcite lattice. Larger ions, particularly strontium, prefer the aragonite lattice but do not occupy more than 3.3 percent of the positions.

At surface temperatures and pressures calcite is the stable form of calcium carbonate, and aragonite is unstable. Despite its theoretical instability, aragonite is secreted by many organisms and converts to calcite only very slowly. It is said to be metastable. The oldest aragonite fossils are of Carboniferous age but in most deposits older than a few million years aragonite shells have been dissolved away or replaced by calcite. Even in replaced fossils the higher strontium content characteristic of aragonite may persist and allow the paleontologist to identify the original shell mineralogy.

Calcite can be distinguished from aragonite most effectively by X-ray diffraction analysis where the spacing of the ions in the crystal is measured. In thin sections a stain called Feigel's solution can be applied to the polished surface, depositing a dark coating on the aragonite, but leaving the calcite clear. The crystallographic differences of the two minerals give them different optical properties, but these can rarely be distinguished under the light microscope because aragonite is secreted by organisms in extremely fine microcrystals whose properties are obscured by their aggregation into compound crystals.

The ratio of marine organisms secreting calcite to those secreting aragonite appears to change in

earth history. Calcite is secreted by more fossil groups in post-Cambrian Paleozoic time but aragonite became more abundant in skeletons early in the Mesozoic and has continued to be favored to the present. Does this change indicate that the geochemistry of Paleozoic seas was different from that of Mesozoic and Cenozoic seas? Philip Sandberg (2) has studied the changing mineralogy of calcium carbonate precipitated inorganically from the ocean and postulated that it was controlled by the carbon dioxide level in the atmosphere and hydrosphere. Times of high concentration of carbon dioxide and high sea levels favor calcite precipitation; times of low carbon dioxide concentration favor aragonite. These intervals correspond with the greenhouse and icehouse phases described in Chapter 16. From late Proterozoic to Cambrian time aragonite was favored. From then until the beginning of the Carboniferous, oceanic conditions favored the precipitation of calcite. The aragonite phase returned from Carboniferous to Cretaceous time, was briefly replaced by the calcite phase in Cretaceous and early Cenozoic time, and resumed in early Cenozoic time until the present. The trend in skeletal carbonates does not show such frequent changes but probably is in some way related to the icehouse–greenhouse cycle.

Opal:

Opal is hydrous silica of amorphous structure, which means it is not crystalline. It is relatively soluble in seawater and waters that circulate in sedimentary rocks. Therefore organisms with shells of this material are usually poorly preserved or have been replaced by less soluble minerals soon after burial. Much of the opal secreted by microorganisms near the surface of the sea is dissolved before it reaches the bottom.

Chitin:

Chitin is a complex polysaccharide, a polymer that forms long chains which unite into fibers. It is secreted in the ectoderm and commonly forms the exoskeleton of invertebrates. It is a material much like collagen, which forms the connective tissue of many advanced animals, but collagen is secreted in the mesoderm. In the exoskeletons of invertebrates chitin is one component of a protein–chitin complex. Chitin may be decomposed by bacteria and digested by enzymes but, if buried, may persist for hundreds of millions of years and is known from rocks as old as Cambrian in age. When its volatile constituents are lost during preservation, it is carbonized to an opaque film on rock surfaces.

Dahlite:

Dahlite is the calcium phosphate mineral in bone. It is basically a variety of the mineral apatite, a calcium hydroxy phosphate [$Ca_5(OH)(PO_4)_3$]. Some carbonate generally enters the structure and its presence is expressed in the following formula for dahlite: $Ca_{10}(PO_4)_6CO_3.H_2O$. Phosphates are secreted largely by the chordates but are present in a few invertebrate groups where the mineral has been identified as a similar variety of apatite called francolite [$Ca_5(PO_4,CO_3OH)_3(F,OH)$].

MINERALOGY AND MICROSTRUCTURE OF MARINE INVERTEBRATES

If each group of organisms secreted a particular mineral in a particular pattern, even fragments of their hard parts would be easy to identify in sediments. Unfortunately for the paleontologist, few groups of animals consistently secreted a single carbonate mineral or secreted it in a single crystalline form. In addition the mineralogy and microstructure originally secreted may have been changed by the time the limestone is examined. The arrangement of the crystals in the skeletal tissue of an animal can be investigated microscopically by means of slices of the material ground to a few micrometers in thickness so that light is transmitted through them, or by means of the scanning electron microscope which forms an image of a broken or etched surface of the object.

The table on p. 413 shows in summary form the distribution of these minerals in animals and plants.

Algae:

The red algae secrete skeletal carbonate of high-magnesium calcite in crystals that are fractions of a micrometer across and difficult to resolve with the light microscope. The magnesium content ranges from about 2 to 18 percent and appears to be greater when the seawater in which the plant lived was warmer. The green algae secrete aragonite needles. Coccoliths are composed of tiny plates that are single crystals of low magnesium calcite.

The cyanobacteria that form stromatolites trap

MINERALOGY OF THE SKELETAL TISSUE OF ANIMALS AND PLANTS
(only the minerals secreted by a major section of each group are shown)

ORGANISM	CALCITE LO-MG	CALCITE HI-MG	ARAGONITE	OPAL	PHOSPHATES
ALGAE coccoliths	x				
diatoms				x	
green			x		
red		x	x		
FORAMS planktonic	x				
benthonic		x	x		
RADIOLARIANS				x	
PORIFERANS Calcarea		x			
hexactinellids				x	
demosponges				x	
sclerosponges	x		x		
stromatoporoids			?		
CNIDARIANS			x		
scleractinians					
BRYOZOANS		x	x		
BRACHIOPODS					
articulates	x				
lingulates					x
MOLLUSCA gastropods			x		
bivalves	x		x		
cephalopods			x		
ECHINODERMS		x			
ARTHROPODS		x			
PROTOCHORDATES			x		
VERTEBRATES					x

(Table modified from Chave and Erben, Encyclopedia of Paleontology)

whatever carbonate grains are suspended in the water and do not have a characteristic mineralogy. There is some evidence that precipitation of carbonates also takes place in the cyanobacterial film at the stromatolite surface.

Foraminifera:

Porcellanous tests of foraminifera are composed of high-magnesium calcite in which the crystals are very small and randomly oriented. Fusulines and endothyrids have similar microstructure but their tests are now low-magnesium calcite. The hyaline or glassy tests, such as those of the Rotalliina, are composed of sheets of calcite that may be of the high or low variety, or mixtures of the two. Only a small group of forams secrete aragonite tests.

Sponges:

The spicular skeleton of demosponges and hexactinellids is composed of opal. When preserved as fragments in sedimentary rocks, the spicules can be distinguished from glassy volcanic fragments, which they resemble optically, by the canal which runs through the center of most of them. Sponges of the class Calcarea secrete spicules of high-magnesium calcite.

The nonspicular skeletons secreted by some demosponges, sphinctozoans, and sclerosponges are of a variety of compositions and microstructures. The microstructure of many is duplicated in corals. Some are composed of spherical aragonite masses in which the needlelike crystals radiate from the center (Fig. 19–1B). This microstructure is said to be spherulitic. In others the aragonite fibers are inclined outward radially from a linear axis in a bundle that is called a trabecula (Fig. 19–1A). The fibrous and spherulitic microstructures are not confined to sclerosponges composed of aragonite but also develop in those with calcite mineralogy. Fibrous carbonates in which the fibers spread outward from the axis of the plates and rods of the skeleton either perpendicularly or obliquely to their surface are also found in Mesozoic stromatoporoids. The Paleozoic stromatoporoids generally do not show this fibrous microstructure. Both types are generally preserved in calcite but rare Mesozoic stromatoporoids are aragonite and the Paleozoic ones may

Figure 19-1 Scanning electron micrographs showing the microstructure of nonspicular carbonate skeletons secreted by sponges. A. Fibrous aragonite crystals of the modern sclerosponge *Ceratoporella* (×2500). B. Spherulitic aragonite of the modern sclerosponge *Astrosclera* (×1200). C. Fibrous calcite of the Devonian stromatoporoid *Hammatostroma*, probably derived from an originally aragonitic skeleton (×220). (C. W. Stearn.)

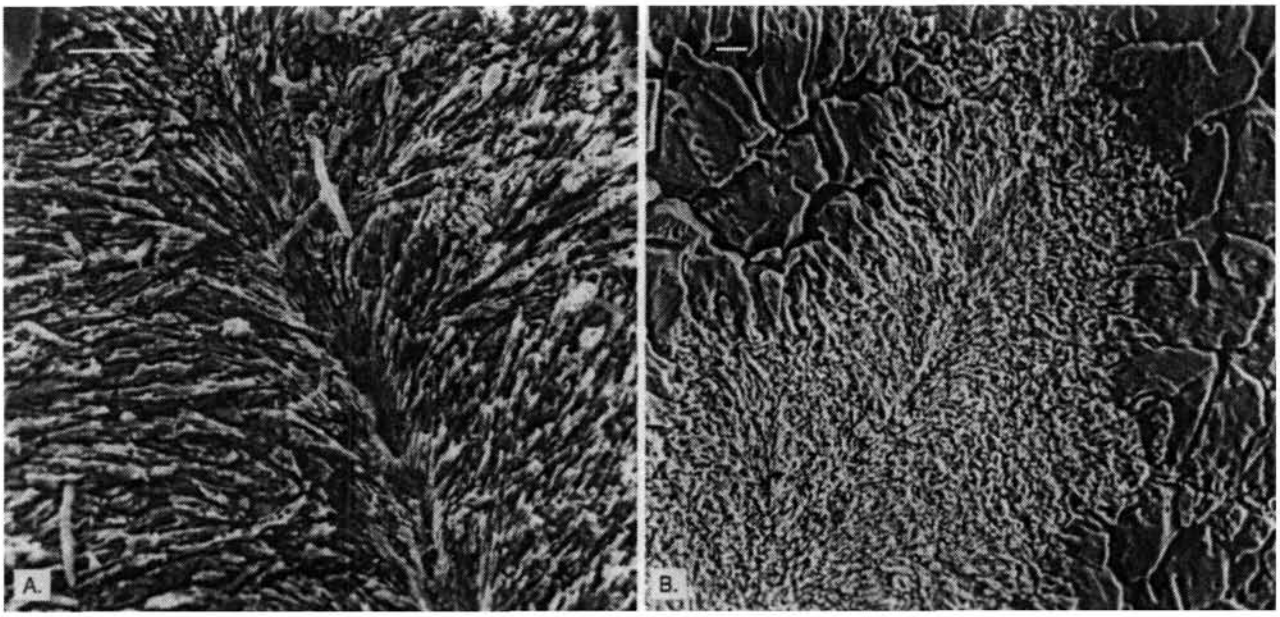

Figure 19-2 Scanning electron micrographs of coral microstructure. The scale bars are 20 micrometers. A. Trabecular microstructure of the aragonite of the septum of the Pleistocene scleractinian *Siderastrea*. B. Fibrous calcite of the Devonian colonial rugosan coral *Pachyphyllum*. (Courtesy of James Sorauf, and The Paleontological Society, *Journal of Paleontology*, v. 45, pp. 23–32.)

have also secreted aragonite and been completely replaced in preservation (Fig. 19–1C).

Corals:

All modern scleractinian corals secrete aragonite. The septa consist of upward and outward-radiating bundles of aragonite microcrystals, called trabeculae, set side by side. In cross section the structure appears to be spherulitic, but in longitudinal section the relationship of the crystal fibers to the axis of the trabeculae is clear (Fig. 19–2A).

Rugose corals are now all composed of calcite but some paleontologists have suggested that this is a replacement of an original aragonite skeleton. However, the faithfulness with which the fine fibrous carbonate microstructure is preserved has convinced most that it could not have survived the replacement of aragonite by calcite, and therefore the rugose corals must have secreted calcite originally (Fig. 19–2B). The same reasoning can be applied to similar microstructures of the tabulate corals. In rugose corals individual trabeculae are uncommon and the fibers grow outward from the axial plane of septa. The lamellar calcite found in some rugose corals is believed by some paleontologists to be primary and by others to be diagenetic.

Brachiopods:

Articulate brachiopods have consistently formed their shells of low-magnesium calcite since their first appearance. The shell is composed of a thin, outer, primary layer of fibers perpendicular to the surface and a thicker, inner, secondary layer of much coarser fibers lying oblique to the surface (Fig. 19–3B,C). Some thick-shelled brachiopods, pentamerids for example, add an inner prismatic layer. Lingulate brachiopod shells combine chitin and francolite.

Bryozoans:

Bryozoan microstructure is also characterized by laminar and fibrous units (Fig. 19–3A). Fossil bryozoa are all calcite, but modern ones use calcite, aragonite, and mixtures of the two.

Molluscs:

Molluscs secrete both aragonite and calcite in a bewildering array of complex microstructures. These can be simplified into four basic patterns. In prismatic microstructures the carbonate prisms are parallel-sided and generally elongated at right angles to the surface. Laminar structures are formed of

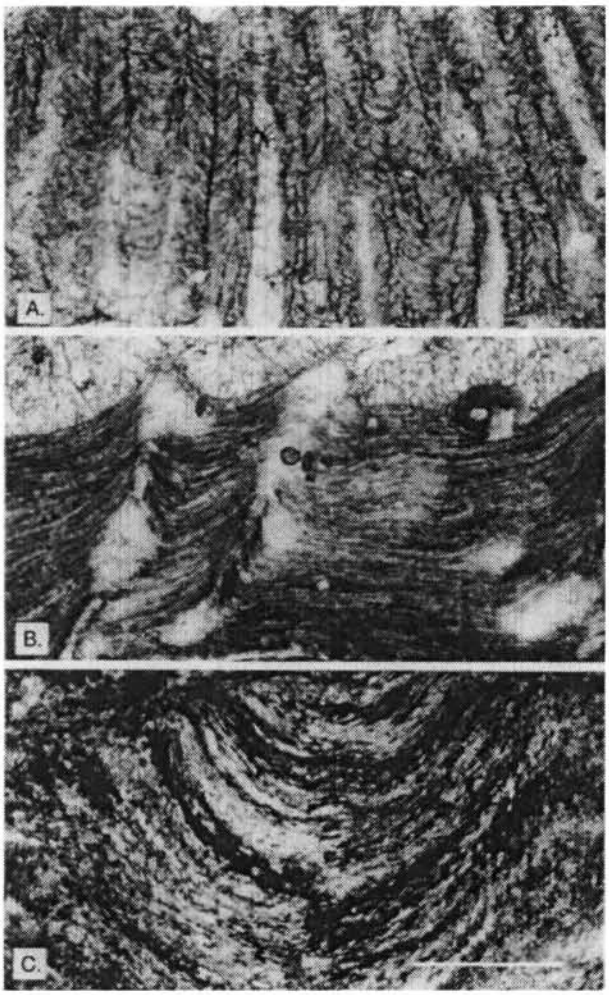

Figure 19-3 Laminar calcite microstructures of bryozoans and brachiopods in thin section. The scale bar is 0.5 mm. A. Ordovician trepostome bryozoan. B. Strophomenid brachiopod, showing the rodlike pseudopunctae characteristic of this order forming spines on the shell surface. C. Rhynchonellid brachiopod. (Photomicrographs C. W. Stearn.)

rods, laths, and blades parallel to the growth surface producing a foliated appearance. A special type of laminar structure composed of stacked polygonal tablets of aragonite forms mother-of-pearl or nacre on the inside of many mollusc shells. Nacreous layers are deposited by certain oysters around irritating sand grains in their shells to produce pearls. Cross lamellar structures consist of three orders of carbonate units called lamels. The first order plates or lenses are elongated parallel to the surface. The second order cross them perpendicularly and are oblique to the surface, and the third order is oblique to the second order (Fig. 19–4). In homogeneous microstructures, the equant crystals are unoriented in a mosaic. Although nacreous and cross lamellar structures are generally aragonite and laminar structures are generally calcite, the microstructures of molluscs are largely independent of shell mineralogy.

Cephalopod shells are mostly aragonitic, and therefore pre–Mesozoic cephalopods tend to be poorly preserved. Belemnite guards are now calcite but some paleontologists believe they were originally aragonite. Gastropods also have shells composed mostly of aragonite but bivalves use both

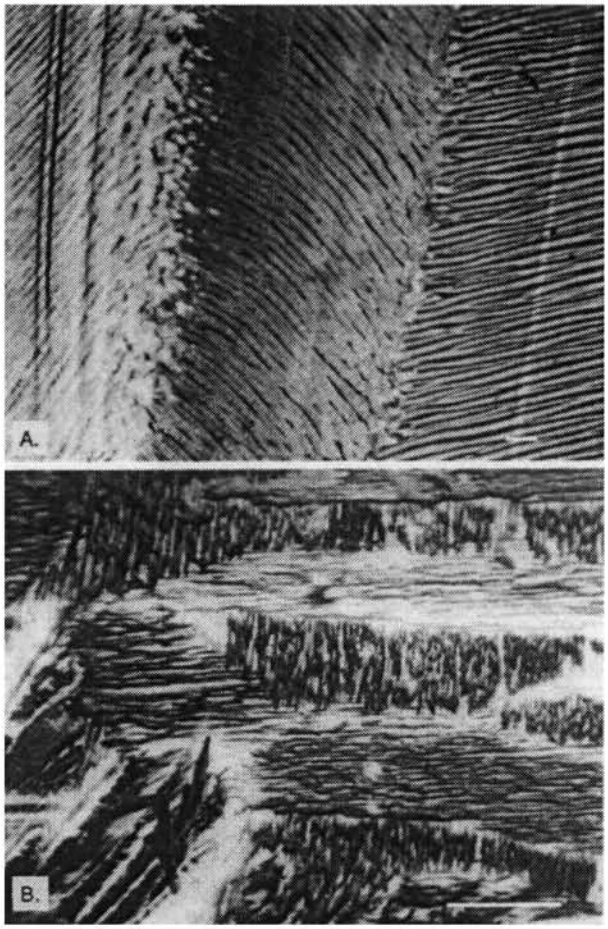

Figure 19-4 Cross lamellar microstructure in molluscs. The scale bars are 0.1 mm. A. Thin section of the modern gastropod *Strombus*. B. Scanning electron micrograph of molluscan shell showing the lamels at various angles. (C. W. Stearn.)

aragonite and calcite in their shells in various proportions in the various orders.

Echinoderms:

Echinoderms secrete high-magnesium calcite exclusively in a distinctive pattern that was described in Chapter 7. Each plate is a single calcite crystal formed as an open network and capable of being changed in shape and size during the growth of the organism by the organic matter that permeates it (Fig. 7–36).

Arthropods:

Arthropods form an exoskeleton that is based on chitin, but in many marine arthropods is reinforced by high-magnesium calcite. The carapaces of most trilobites are usually dark owing to the carbonized organic matter, whose original nature has not been determined, but as preserved they are almost pure calcite. The thin outer layer consists of very small calcite needles perpendicular to the surface and the thick inner layer is finely crystalline calcite marked by laminae parallel to the surface.

Vertebrates:

Vertebrate bone is a combination of the phosphatic mineral dahlite (70 percent) and organic matter that is for the most part the fibrous connective tissue collagen. Like echinoderm calcite it is capable of growth, healing of broken parts, and thickening in stressed areas because it is permeated by living organic matter. Within the vertebrate body bone takes on various microstructures whose description is beyond the scope of this chapter.

FOSSIL DIAGENESIS

Individual fossil particles become rock through processes that are collectively known as diagenesis. Not only are the grains cemented together and voids within and between them filled, but mineralogical and textural changes take place within the grains. These changes often degrade and, if carried far enough, destroy the microstructures of fossils and inhibit the analysis of the paleontologist. When paleontologists refer to fossils as being poorly preserved, they mean that the processes of diagenesis have advanced to a stage of obliterating much of the original structures.

Cementation:

Fossil fragments on the seafloor are bound together in the first stage of diagenesis by very small crystals of aragonite or high-magnesium calcite apparently derived from the ions dissolved in the seawater. Usually the nature of the grain on which this cement is deposited determines which mineral precipitates (Fig. 19–5). For instance, rims of needle crystals of calcite may grow on echinoderm fragments and of aragonite on adjacent scleractinian fragments. The cement crystals usually grow in the same orientation as the crystals in the grain forming what is known as a syntaxial rim. Similar crystals begin the filling of the internal cavities in the fragments reducing the porosity. If cementation takes place in a freshwater environment, such as exists on emerging coral islands, the calcite that initially binds the grains is low-magnesium calcite.

The initial stage in the diagenesis of bone is the infilling of the canals and pores from which the collagen and other organic matter has decayed. This infilling by calcite or silica results in the permineralized condition described in Chapter 1.

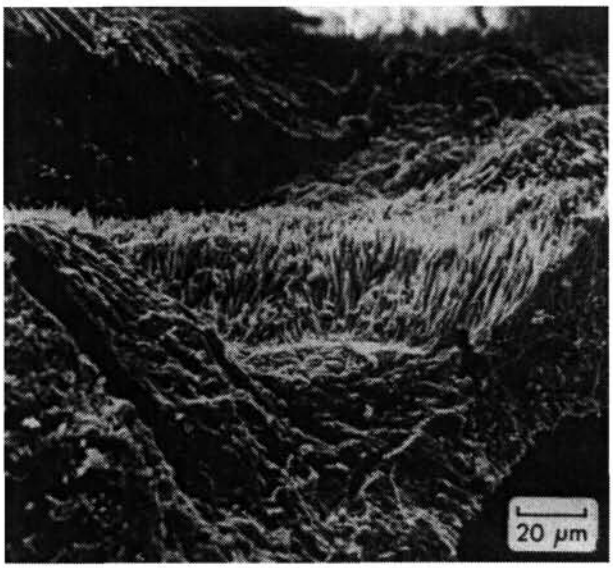

Figure 19-5 Scanning electron micrograph of acicular aragonite cement at the corner of a dissepiment and septum in a recent scleractinian coral. The crystal mass is about 130 micrometers across. (Courtesy of D. Boucher, *Bulletin of Marine Science*, v. 30, p. 500.)

Conversion of Unstable Carbonates:

Both aragonite and high-magnesium calcite are unstable phases of calcium carbonate and in time and in a suitable aqueous environment they convert to the stable phase, low-magnesium calcite. The loss of magnesium from calcite occurs early in diagenesis and releases large quantities of magnesium ions into solutions permeating the nascent limestone. Some of these solutions may be influential in forming dolomites in zones where fresh and salt waters intermix beneath the shorelines of tropical landmasses. Although the conversion is thought to take place by dissolution of one phase and reprecipitaton of the other, the loss of magnesium does not cause obvious textural changes in fossil fragments.

The replacement of aragonite by low-magnesium calcite usually does cause major textural changes in fossils. The replacement is postulated to take place in solution in a thin film that separated the aragonite and calcite. Examination at high magnifications of the scanning electron microscope of the front separating the advancing calcite phase from the original aragonite in partially replaced fossils shows no space between the phases for this film (Fig. 19–6).

Carbonate petrologists disagree on the question of whether such textures of aragonite as spherulitic and trabecular can survive the replacement process. Some claim that all organisms whose calcite fossils show such textures must have secreted them as calcite, and others claim that the textures have survived the calcitization of an originally aragonite skeleton. Possibly the preservation of fossil microstructures only takes place when replacement occurs above the water table (3). The original mineralogy of several Paleozoic groups, such as the stromatoporoids and rugose corals, therefore remains uncertain (4).

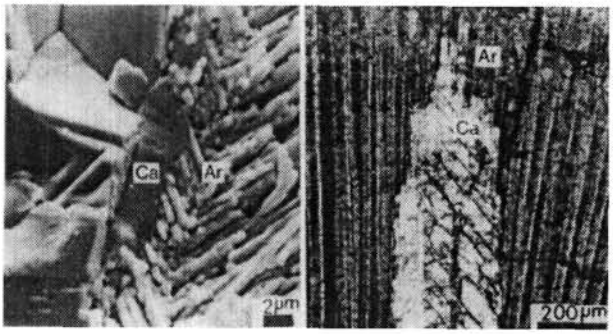

Figure 19-6 Calcite (Ca) replacing aragonite (Ar) in a Pleistocene specimen of the gastropod *Strombus*. Note the abrupt contact between the two minerals. A. Scanning electron micrograph. B. Thin section. (Courtesy of Norman Wardlaw, *Canadian Journal of Earth Sciences*, v. 15, pp. 1861–1866.)

Changes in Grain Size:

Fossil particles in limestones usually have narrow rims that are opaque in transmitted light under the microscope because they are composed of very small grains of carbonate. These opaque borders of grains are termed micrite envelopes. Carbonate grains now being deposited in shallow water show similar envelopes. The rims are formed when algae that bore minute tubes a few micrometers across penetrate the carbonate grain (Fig. 20–8) and are subsequently filled by fine micrite. Some skeletal grains may lose all microstructure in this micritization process.

The processes of carbonate diagenesis that involve substitution of one mineral for another, such as calcite for aragonite, generally result in increase in size of the crystals. The size change is explained by the second law of thermodynamics. Processes of replacement in carbonate diagenesis are collectively termed neomorphism and when they result in crystal growth, they are distinguished as aggrading neomorphism. Larger crystals of low-magnesium calcite, the stable phase, replace smaller ones of less stable phases and eventually the fossil becomes a coarse mosaic of calcite. Many older fossils may be in this state of preservation; the form of the shell is still clear but the original microstructure and mineralogy have been replaced by a coarse calcite mosaic.

Replacement of Carbonates by Other Minerals:

How one mineral replaces another when rocks are buried remains a geological mystery. That it occurs is shown by the common occurrence of fossils, originally formed as carbonates, replaced by silica, pyrite, phosphates, iron oxides, and more rarely by many other minerals. The faithfulness of the replacement is so great that controversy over the original composition of the fossils may arise. For example, in earliest Cambrian rocks fossils are now composed of phosphate (Chapter 5). Whether these minute shells were secreted as calcite or aragonite and replaced during a unique chemical phase of

the sea when such replacement was favored, or were secreted as francolite or a similar phosphate, is a question of current discussion. There is no doubt that pyrite or hematite fossils were not secreted as these minerals, but there is discussion of the time of the replacement and the conditions under which it occurred. Many of these replaced fossils are from micromorph faunas whose small size is indicative of exceptional environments at the time of their entombment (Chapter 17). If exceptional marine conditions were responsible for the size distribution of the fauna, they may also have caused early replacement of the shells before they were buried.

POROSITY

Petroleum geologists study limestones to find oil and gas. About 30 percent of the world's petroleum resources are produced from carbonate rocks. The nature of many limestone reservoirs is determined by the organisms that formed the limestone. Geologists and paleontologists concentrate their attention on grains and cements but to the reservoir engineer the important part of the reservoir rock is the part that is not there—the pore space. The oil in a reservoir is held in the pore spaces within and between grains, and our ability to recover it is related both to the number and size of the pores (the percent porosity) and the degree to which the pores are connected so that oil may flow through the reservoir towards the oil well (the permeability). The average porosity of productive carbonate reservoirs is about 15 percent, but the range of porosity values is great.

We are concerned here only with the porosity produced by, or dependent on, fossils. However, it should be noted that most carbonate reservoirs have had their porosity and permeability enhanced by postdepositional solution, faulting, and fracturing.

Intraparticle Porosity:

Some fossils have internal cavities that are not filled with sediment when they are buried and may later be filled with oil, water, or gas. In some reef reservoirs a significant part of the porosity is made up of cavities within corals, stromatoporoids, sponges, or rudists (Fig. 19–7A). Cavities may be made by boring organisms in skeletal grains before they are buried in sediment.

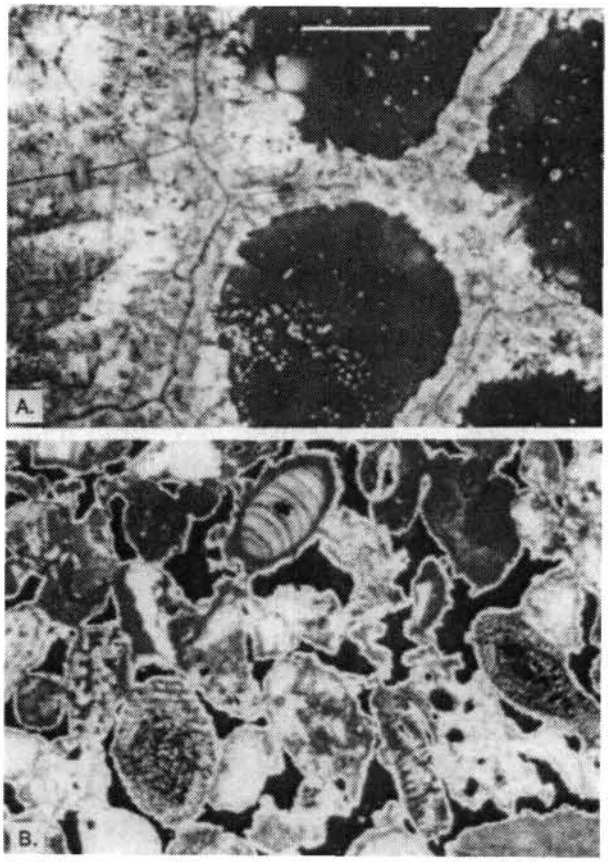

Figure 19-7 Thin sections showing porosity in limestones related to fossils. Scale bar is 1 mm. A. Interfossil porosity. Silurian tabulate coral *Favosites*. The corallites on the left are filled with cement, but those on the right are empty.
B. Interparticle porosity. A Pleistocene grainstone from Barbados, with grains of coralline algae and foraminiferans, cemented by a thin carbonate rim (light tone) leaving large pore spaces which are black in the petrographic microscope with crossed polars.

Interparticle Porosity:

This occurs in limestones composed of coarse, sand-sized grains (Fig. 19–7B). Either the pore space between the grains never filled with cement, or the cement that filled the space early in diagenesis was leached at a subsequent stage of the diagenetic history when unsaturated solutions flowed through the rock. Shelter porosity is a type of interparticle porosity that is formed when large fragments, commonly fossils, prevent cavities below them from being filled with sediment.

Growth-Frame Porosity:

This occurs in reef limestones. Modern corals and their partners in reef building, the coralline algae, tend to overgrow cavities and form overhangs. By shading their neighbors, these light-dependent organisms compete for space on the reef surface. This overgrowing habit leaves large cavities in reefs that may not fill with sediment or cement. When some reef reservoirs have been entered by drilling, the drill has dropped into cavities several meters across. These may not be produced by the overgrowing phenomena alone but may have been enlarged by later solution. Paleozoic reef builders apparently did not have comparable ability to construct frameworks and overgrow cavities (possibly because they were not light dependent), but growth frame porosity may also be important in Paleozoic reefs.

Solution Porosity:

Pores are produced when constituents of a limestone are preferentially dissolved. If the dissolved parts are fossils, molds of fossils are left in the rock and the porosity is said to be moldic. Such moldic porosity is particularly characteristic of limestones that have been replaced by dolomite. The porosity of many reef reservoirs has been greatly enhanced by dolomitization. Solution may open out cavities of all sizes that are potential sites for petroleum accumulation. Smaller solution cavities up to a few tens of centimeters across are called vugs and this type of porosity is referred to as vuggy porosity (Fig. 19–8).

Figure 19-8 Vuggy solution porosity with the cavities stained with oil. An oil well core from the Fenn Oilfield, Alberta.

FOSSIL FUELS

Most of the organic matter of the animals and plants of the past is decomposed by bacteria and recycled into new life. If it escapes bacterial decay it may be stored in sediments as diffuse organic matter or converted to petroleum and coal. Although coal, oil, gas, and oil shale are all fossils in the sense that they are remains of organisms of the past, these remains have been so changed after burial that the form and even the composition of the organisms that accumulated to make them are now obscure. The source of oil and gas is fossil organic matter diffused in buried sediment. When the buried, organic-rich sediment is heated over a sufficient period of time, chemical changes take place that release hydrocarbons that constitute oil. Under pressure of the overlying sediments the minute droplets are flushed out of the source rocks as they are compacted and into the pores of reservoir rocks. Deeper burial results in higher temperatures during the maturation of the organic matter and in the generation of gas rather than oil.

Oil shale is formed when algae increase greatly in numbers producing an ooze rich in waxy hydrocarbons on the bottom of a lake or seaway.

Coal is formed of plants that have not completely

decayed but have been sufficiently changed that little trace of the original structure can be seen. Most coals appear to be amorphous, brown, organic matter when examined in thin section under the microscope. Only when the accumulating plant matter has been permeated with calcite to form a concretion or coal ball is the fine structure of the plants well preserved (Fig. 8–7).

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Chapter 20

Paleoichnology: The Study of Trace Fossils

DEFINITIONS AND DESCRIPTIONS

What Are Trace Fossils?:

Most of the fossils described in this book are the preserved parts of the bodies of organisms and are called body fossils to distinguish them from tracks, trails, burrows, and borings which are referred to as trace fossils. The study of traces left by living animals is called ichnology; the study of fossil traces, paleoichnology. Because a track or burrow is a partial impression or mold of the exterior of the organism making it, the line between trace fossils and body fossils is not easy to draw. Usually the surface of the animal is not preserved in sufficient detail for identification in a trace fossil because the animal moves as it makes the trace or only a small part of the animal is represented in the impression (typically a foot). Some paleontologists also include in paleoichnology the study of the excreta of animals. The fossils of the droppings of larger animals are coprolites; smaller sandlike particles in which many marine invertebrates package their waste products are fecal pellets.

Most trace fossils or ichnofossils tell us little about the form of the animal or plant that made them but much about its behavior in feeding, moving, escaping, making its home, and resting. The behavior of trace makers can be determined by observing the effect of living animals on sediment in or on which they live, for most trace fossils are the product of organism–sediment interaction. The approach to the interpretation of ichnofossils is uniformitarian, and many of the first ichnological observations were made on animals that inhabit the tidally exposed mudflats of the North Sea on the German coast (1). Intertidal traces are usually removed by the waves at the next high tide and as a result the more easily studied organisms are those whose traces are not apt to be preserved to become ichnofossils. The traces produced by subtidal and deep-water animals can be investigated by SCUBA, coring, and photography but the amount of information available from these sources is relatively limited.

Types of Ichnofossils:

Tracks are the individual impressions of the feet of organisms, and trackways are the assemblage of tracks produced when an individual crosses soft

Figure 20-1 Aerial view of dinosaur trackways on the banks of the Purgatoire River, Colorado. (Courtesy of Martin Lockley, *Geological Society of America Bulletin*, v. 98, p. 1165.)

sediment that will take impressions. The most familiar trackways were made by dinosaurs. Notable North American dinosaur trackways are preserved in the Lower Jurassic sandstones of the Connecticut River Valley in New England, in Cretaceous rocks at Paluxy Creek, Texas, and on the Purgatoire River in southern Colorado (Fig. 20–1). The Texas tracks reveal that the sauropods walked on land on vertical legs, rather than laterally splayed legs and were able to support their weight without the buoyancy of water. The traces formed by epifaunal marine invertebrates, such as trilobites and crabs, are called tracks and trackways when their individual appendages impressed the sediment (Fig. 20–2).

Trails are continuous grooves and ridges formed by the passing of an animal living on the sediment surface. The trace fossil *Cruziana* (Fig. 20–3) was formed by the passage of a trilobite along the surface of muddy sediment. *Aulichnites* is a trail that does not have the transverse ridges that characterize *Cruziana*.

Burrows are made by many infaunal animals either for protection or to find their food in interstitial organic matter in sediment. Burrows may be simple excavations in the sediment or they may be lined by the burrower with grains coated in mucus or with calcareous cement making a tube. *Ophiomorpha* is a burrow lined with pellets that give it a granular

Figure 20-2 Trackways of two large animals, probably arthropods, from the Upper Cambrian to Lower Ordovician Potsdam Sandstone. The track that resembles that of a tire is *Climactichnites*. The track that appears to be a tail impression bordered by foot prints is *Protichnites*. The slab is about 1.5 m in width. (C. W. Stearn, Redpath Museum.)

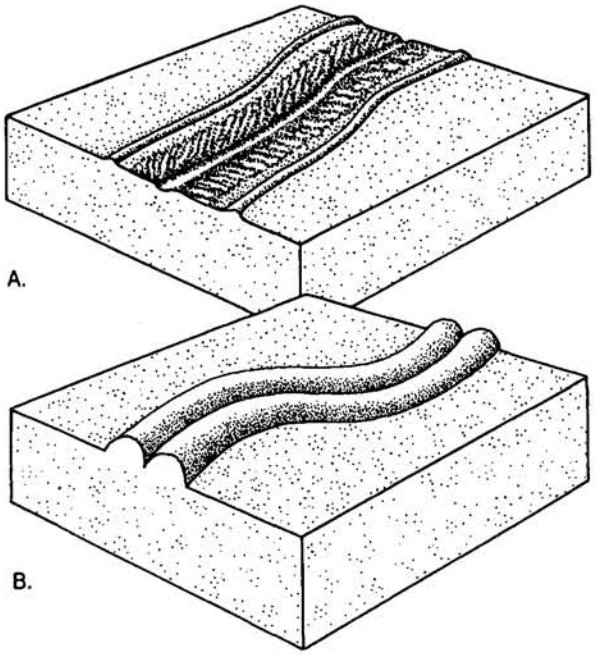

Figure 20-3 A. *Cruziana*, the crawling trace of a trilobite. B. *Aulichnites*, a crawling trace. Both are illustrated as they would appear on the bottom of a bedding plane that had been overturned (reversed relief).

surface (Fig. 20–4A). Similar lined burrows are being formed today by the shrimp *Callianassa* in many areas of the tropics. Many invertebrates make U-shaped burrows so that they can have the protection afforded by living in the sediment yet can filter feed from the water above. At one end of the tube the animal feeds and at the other it passes out excrement. Simple, vertical U-tubes in sandstone are given the name *Arenicolites* (Fig. 20–4B). When the organism periodically moves sideways or vertically and backfills the burrow behind it, the remains of the wall left in the sediment form concentric or parallel layers that are called by the German term spreite (plural = spreiten). The trace fossil genus *Rhizocorallium* consists of a U-tube lying horizontally whose arms enclose a set of spreiten and are bent at their ends to open on the surface (Fig. 20–4C). Species in U-tubes each live at a particular depth below the surface and respond to reestablish this depth when disturbed by sediment burying them or the erosion of sediment bringing them nearer to the surface. If buried, the animal brings the tube upward by

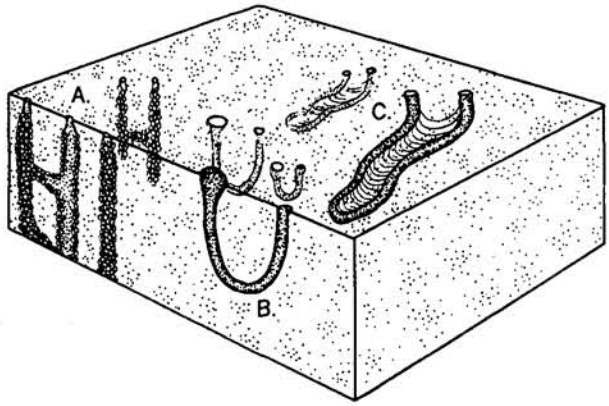

Figure 20-4 Burrows. A. *Ophiomorpha*, a burrow lined with cemented sand grains. B. *Arenicolites*, a simple U-shaped tube. C. *Rhizocorallium*, a U-shaped tube with spreiten. The sediment in which they are embedded is shown here as transparent.

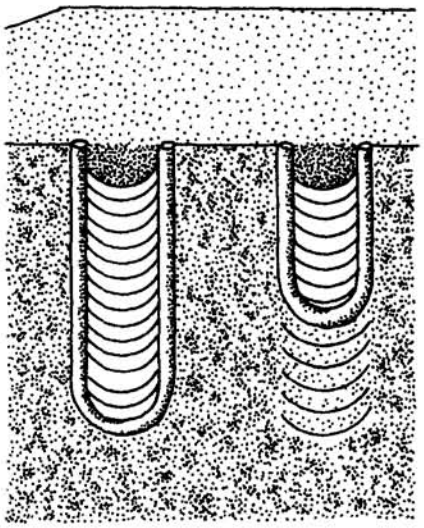

Figure 20-5 *Diplocraterion*. Formation of spreiten by the upward (right) or downward (left) movement of an animal in a U-shaped tube.

taking sediment from the ceiling of the base of the U and plastering it on the floor, and if threatened with exposure by erosion, it does the opposite (Fig. 20–5). In either case, spreiten are left behind as the outlines of the former positions of the base of the burrow. Spreiten may also be formed as an animal progressively samples the sediment for interstitial food in a broad arc and fills the burrow behind with digested sediment (Fig. 20–6).

On rocky coastlines marine animals bore into hard rocks making cavities that are a form of ichnofossil. Some invertebrates penetrate hard substrates by mechanical rasping with claws or shell, others by chemical action, and many by a combination of both. As rocky shorelines are areas of erosion, such cavities are rarely preserved in the fossil record. However, where a hard ground is produced by rapid cementation during a pause in deposition on the ocean floor, borings in that surface may be preserved when sedimentation resumes. Disconformities may also preserve hard rock borers (Fig. 17–17). The cavities of boring organisms are common in the hard tissue of fossils that they attacked. Corals are extensively bored by sponges and bivalves at present (Fig. 20–7) and fossil corals and stromatoporoids also show evidence of hard tissue borers in ancient seas. Predatory gastropods bore neat holes in bivalves, and similar holes drilled by unknown organisms are known from brachiopods as old as Ordovician in age. Algal and fungal filaments a few microns across currently bore through many carbonate skeletons, and did so in the past (Fig. 20–8).

Figure 20-6 *Zoophycus*, a complex feeding trace with spreiten formed in sweeping arcs.

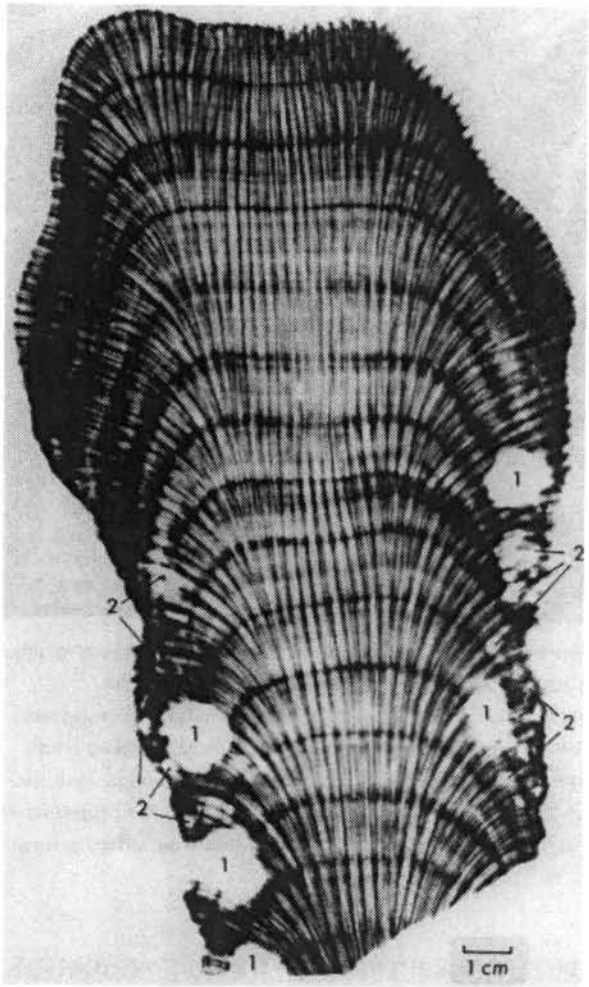

Figure 20-7 X-ray photograph of a slice of the recent scleractinian coral *Montastrea annularis*, showing seasonal growth bands and voids caused by the activity of the boring sponges *Siphonodictyon* (1) and *Cliona* (2). (Courtesy of Kirk MacGeachy, *Bulletin of Marine Science*, v. 30, p. 487.)

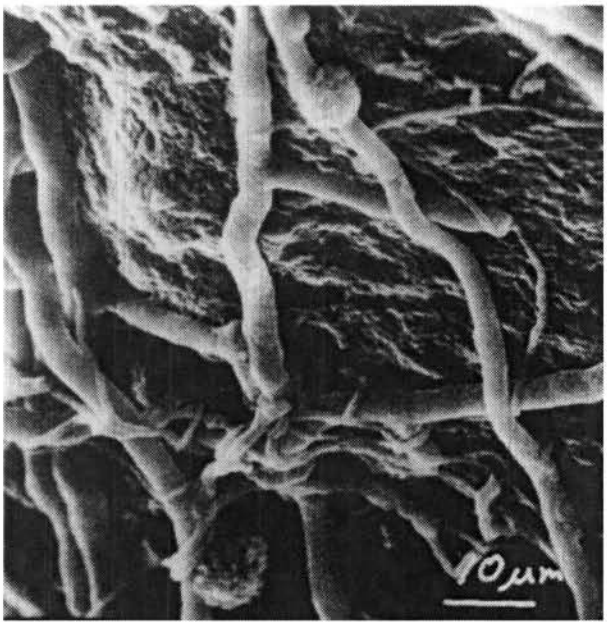

Figure 20-8 Scanning electron micrograph of epoxy molds of borings of microorganisms in the septum of the scleractinian coral, *Montastrea*. The tubes have been injected with the plastic and the carbonate has been dissolved from around them. The large tubes are ascribed to algae and the smaller to fungi. Note the swellings that may be reproductive structures, and the fact that the borings avoid other borings. (C. W. Stearn.)

PRESERVATION OF TRACE FOSSILS

Most traces when originally formed are depressions in the sediment surface or cavities beneath it. Their likelihood of being preserved depends on the firmness of the sediment and the availability of sediment of contrasting color or texture to fill the cavity before it collapses. Many trace makers whose fossils are found in alternating sandstone and shale successions lived in the soft muds represented by the shales and were only preserved when the muds were covered by coarser sands which filled the depressions. When such a deposit is exposed to weathering, the shales are less resistant and are washed away, leaving the bedding planes of the resistant sandstone exposed (Figs. 20–3, 20–9). The sand molds of the grooves of the traces appear in convex relief on the bottom of the sandstone bed. Burrows completely within the shale may be filled with sand, and weather from their matrix as cylindrical, wormlike, or branching bodies. Grooves on the top of the sandstone bed appear in normal relief on its surface. Whether the trace is preserved in true or reversed relief (whether it is a groove or a ridge) may not be obvious unless the orientation of the sample is marked when it is collected.

In carbonate rocks the obvious burrows are filled with coarser grained sediment, usually pelleted either by the trace maker or by other organisms. In the absence of some difference in texture between burrow and matrix, ichnofossils are difficult to detect in carbonates. In many limestones the contrast between matrix and burrow is increased by the introduction of dolomite into the fillings. The dolomite brought in by magnesium-rich solutions percolating along permeable pathways in the burrows is coarser in texture than the limestone matrix and browner in color owing to a higher iron content. Gray limestones mottled with rust-colored burrows of the trace fossil *Thalassinoides* are common in the

Figure 20-9 Under surface of a bed of Lower Silurian sandstone with the trace fossil *Arthrophycus*. (C. W. Stearn, Redpath Museum.)

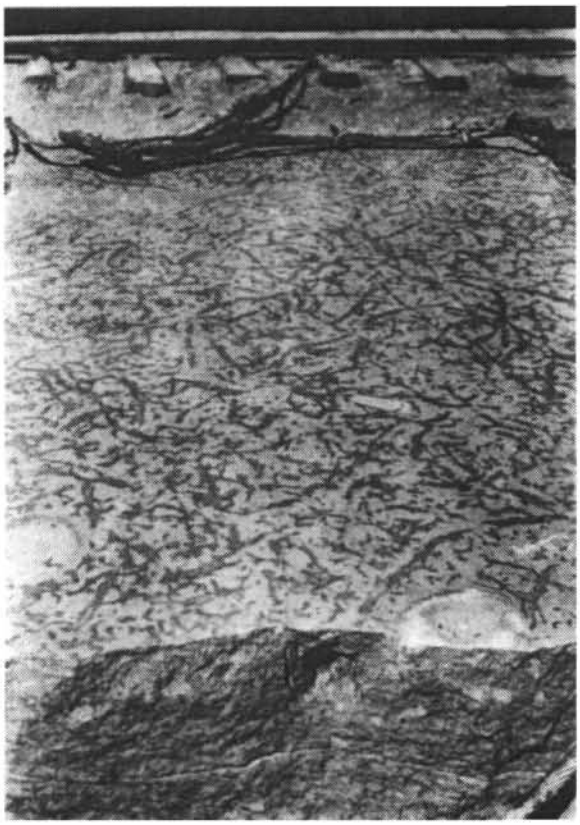

Figure 20-10 Burrows of *Thalassinoides* in lime muds have been partially dolomitized so that they stand out in Late Ordovician limestone. (Courtesy of the Geological Survey of Canada.)

Upper Ordovician of western and arctic North America and are popular as building stones (Fig. 20–10).

NAMES OF ICHNOFOSSILS

Trace fossils are given binomial Latin names just as are body fossils, but since 1930 the names have not been protected by the priority rules of the International Code of Zoological Nomenclature because they are not of the same nature as the names of body fossils. A trace fossil does not represent a unique organism. For example, U-shaped burrows identified as species of the genus *Arenicolites* can be shown by observations of living organisms to be constructed by echiurid worms (annelids or a phylum of their own), enteropneusts (protochordates), holothurians (echinoderms), polychaetes (annelids), amphipods (arthropods), and bivalves (molluscs). Although ichnogenera and ichnospecies are described formally, higher categories, such as families and orders, are not recognized, and in systematic descriptions of taxa, genera are commonly listed alphabetically.

Many trace fossils have names with the suffixes *ichnus* (Greek *ichnos* = trace) or *phycus* (Greek *phucos* = seaweed). The *phycus* names were proposed in the nineteenth and early twentieth centuries when many trace fossils, then called fucoids, were believed to be remnants of soft seaweeds.

We do not know which animals formed most ichnofossils because animals are rarely preserved in tracks and burrows. Most trace makers of the past were soft-bodied and constitute a fauna entirely different from the body fossil fauna. Although trace fossils are commonly found in beds that contain body fossils, they also occur in beds that contain no other fossils. From the first appearance of burrows until the first Ediacara body fossils appear, trace fossils are the only evidence of metazoan life.

INTERPRETATION OF TRACE FOSSILS

Adolf Seilacher (2) proposed a genetic classification into five groups, but these have been expanded by later workers. Fossils illustrative of these divisions are shown in Figures 20–11 and 20–12.

1. *Resting Traces* are made when animals settle to the bottom, leave impressions, or dig shallow depressions, and move off. *Rusophycus* and *Asteriacites* are resting traces ascribed to the impressions of arthropods and asteroids respectively.
2. *Crawling Traces* are linear or sinuous grooves or trackways formed as animals move across sediment surfaces. Some of them end or begin in resting traces. *Climactichnites* is a large crawling trace that resembles a tire track in Cambrian sandstone (Fig. 20–2). It was probably formed by a large trilobite, but no trilobite of this size has been found as a body fossil in these beds. Many other trails, such as *Cruziana* and *Aulichnites* (Fig. 20–3), have been ascribed to trilobites. *Scolicia* is a complex trail apparently made by the passage of a many-legged organism such as an arthropod.
3. *Grazing Traces* are grooves or pits made by mobile deposit feeders or algal grazers at or

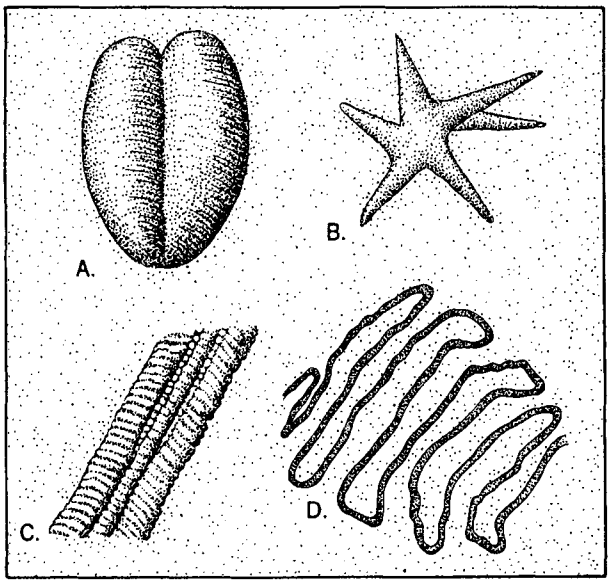

Figure 20-11 Trace fossils on a bedding surface. A. *Rusophycus* (resting trace. B. *Asteriacites* (resting trace). C. *Scolicia* (crawling trace). D. *Helminthoida* (grazing trace).

just beneath the sediment surface. Generally they are unbranched and nonoverlapping grooves made in one plane as the animal efficiently crops algal turf. The meandering grooves of *Helminthoida* are typical grazing traces.

4. *Feeding Structures* are burrows dug by deposit feeders mining sediment for nutrients. They are usually branching galleries with vertical connections that may form intricate networks. *Chondrites* is a typical genus. Feeding traces may be difficult to distinguish from both grazing traces and dwelling structures.
5. *Dwelling Structures* provide more-or-less permanent homes for animals many of which are infaunal filter feeders. Simple or complex vertical tubes, such as those of *Skolithos* and *Diplocraterion*, are typical of this group. The burrow walls are usually lined because they are primarily used for protection, but the walls of feeding structures are not because the burrows are used to gain access to food in the sediment.
6. *Escape Structures* are produced when animals in dwelling structures move vertically to keep their optimum depth in response to sedimentation or erosion at the surface above them. Escape structures show vertically stacked spreiten (Fig. 20–5).

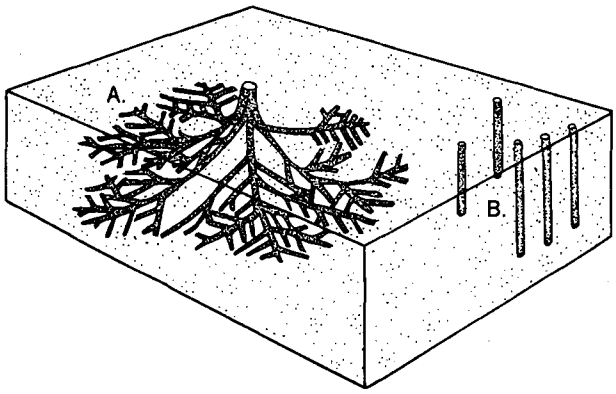

Figure 20-12 A. *Chondrites* (feeding structure). B. *Scolithos* (dwelling structure). (*Source:* Modified from work of T. P. Crimes; courtesy of G. M. Pemberton, *Short Course Notes*, Society of Economic Paleontologists and Mineralogists, 1984.)

Classification of an ichnofossil into these groups defined on the basis of behavior requires an interpretation of the intent of the fossil animal in making the ichnofossil. The paleontologist must also remember that the animal may have had more than one purpose in constructing the trace. For example, it may have served as both a feeding and dwelling structure.

USE OF TRACE FOSSILS

Studies of recent trace makers show that not only can a wide range of animals make the same trace but a single animal can make a variety of traces. Because trace fossils in marine and lacustrine rocks are not the products of specific, evolving organisms but merely reflect the behavior of a whole range of aquatic animals, they do not change much in time and are of little value in biostratigraphic and evolution studies. However, detailed study has shown that they may have value in defining the Proterozoic–Cambrian boundary. Many ichnogenera have ranges extending throughout the Phanerozoic Eras. Improvement in efficiency of grazing appears to have taken place over hundreds of millions of years, but such a change is not comparable in scale or nature to the vast changes in body fossils over the same period.

Trace fossils reveal something about the conditions of life in sedimentary deposits that are otherwise without fossils. In many nonmarine deposits the footprints of terrestrial animals and the impres-

sions of the roots of plants may be the only fossils. The footprints of the dinosaurs from the Connecticut Valley Jurassic sandstones are not accompanied by body fossils and most of the traces cannot be connected to skeletal remains. The footprints of *Cheirotherium* are abundant in Triassic rock of Europe, but skeletal remains of the reptile that made them were not found until recently, 130 years after the footprints were first described.

The tracks of dinosaurs give information, not only on how they walked and ran, but also on their social organization. On a single bedding plane at Mt. Tom, Massachusetts, 19 trackways of the carnivorous dinosaur *Eubrontes* show movement in the same direction. Consistent orientation is also evident in 25 trackways of a large ornithopod dinosaur at Lake Innes, Texas. Both carnivorous and herbivorous dinosaurs must have travelled in herds for otherwise the trackways would trend back and forth across a well-traveled trail. Trackways indicate that, contrary to many reconstructions, sauropods did not drag their tails and some theropods could attain speeds of 40 kilometers per hour. They can also give information on the diversity and local abundance of dinosaur populations, the distribution of age groups, and the geographic ranges of dinosaur types. Most tracks are made on the shores or in the shallow water of lakes and rivers and can be used to recognize shoreline trends, and to estimate water depths, the water content of sediments, and current directions.

For the interpretation of ancient environments trace fossils have two advantages over body fossils. First, they are always found in place, unmoved by currents or wave action. Secondly, the occurrence of a particular genus or species of ichnofossil is almost totally controlled by the suitability of the environment, not by the age of the beds in which they are found. Because trace fossil species and genera have such long ranges, assemblages of ichnofossils recur throughout the Phanerozoic and have been designated as ichnofacies.

ICHNOFACIES

Seven recurrent assemblages of trace fossils have been generally recognized as useful in the interpretation of ancient environments. Their occurrence, like that of other paleocommunities, is dependent on environmental factors such as turbulence, substrate, oxygen availability, and salinity. The assemblages were originally considered to be diagnostic of various depths because these factors change systematically with depth in most marine environments. Further observations have shown that the four fundamental environmental variables previously listed are the primary controls, and that wherever appropriate combinations occur ichnofacies will be present. The facies are illustrated in Figure 20–13.

Scoyenia Ichnofacies:

All nonmarine environments and their trace fossils, from dinosaur footprints, to insect trackways, to burrows of lake-dwelling invertebrates, are included in this ichnofacies. Ichnofossils formed in lake sediments may be similar to their marine counterparts and many genera, such as *Arenicolites* and *Skolithos*, are recognized in both this and marine ichnofacies.

Trypanites Ichnofacies:

Organisms of this facies bore into fully consolidated substrates on rocky coasts, in beach rock, reefs, and hardgrounds. The structures produced by borings cut across the consolidated grains of the host rock.

Glossofungites Ichnofacies:

Members of this facies occur in substrates that are firm but not consolidated into rock. Such substrates are generally intertidal or supratidal. The trace fossils are typically vertical burrows, without linings but with spreiten in the U-tubes. Pouch-shaped burrows called *Gastrochaeonolites*, that are probably formed by bivalves, are typical.

Skolithos Ichnofacies:

This is characteristic of clean, well-sorted sands in nearshore, highly turbulent environments. The animals are infaunal filter feeders inhabiting vertical burrows like the simple vertical tubes of *Skolithos*. Alternating times of deposition and erosion in this rapidly changing environment cause the formation of spreiten.

Cruziana Ichnofacies:

This is a subtidal facies of muddy sediments in offshore areas of low turbulence. Vertically and horizontally branching burrows such as *Thalassinoides*

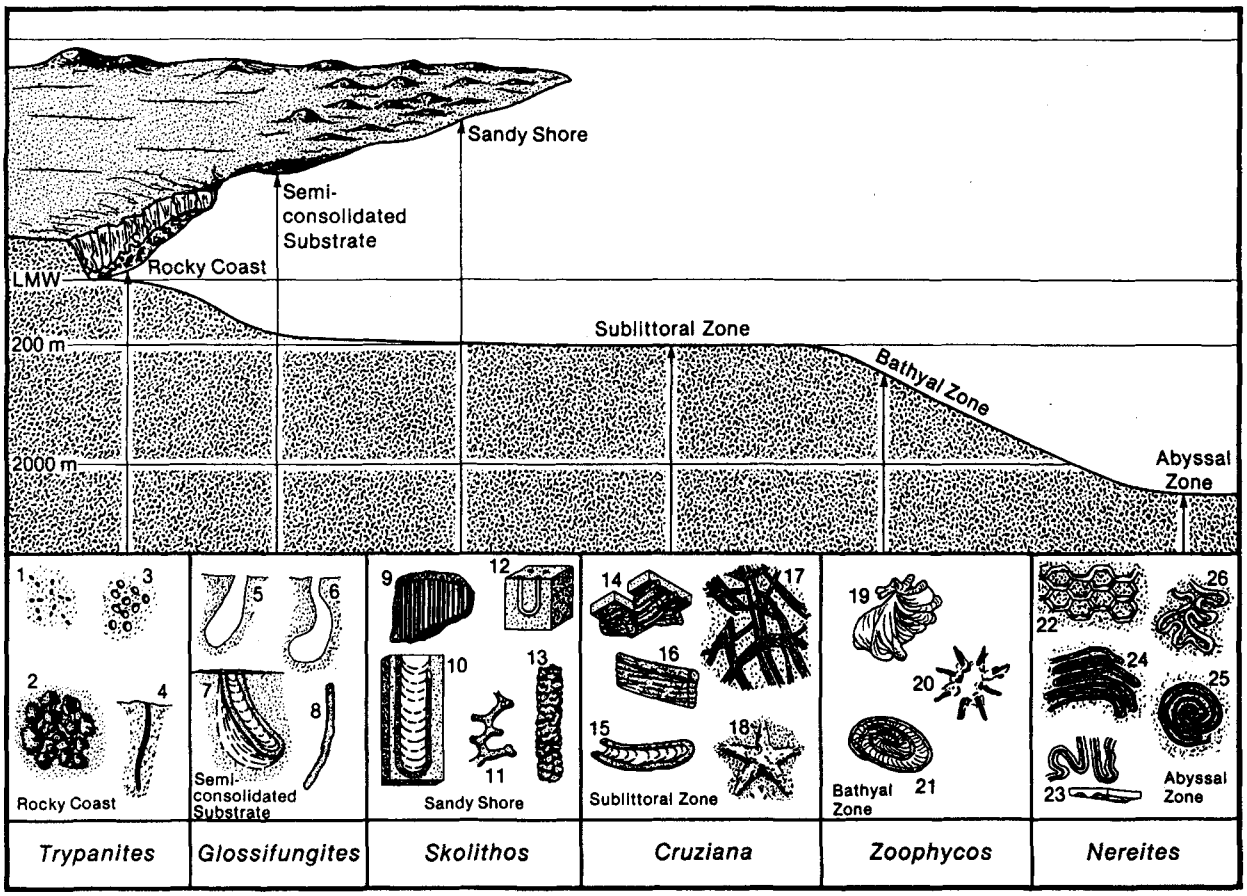

Figure 20-13 Schematic representation of the common marine ichnofacies. Some of the fossils common in these facies are illustrated as follows: 1. *Polydora*. 2. *Entobia*. 4. *Trypanites*. 7, 10. *Diplocraterion*. 9. *Scolithos*. 11. *Thalassinoides*. 12. *Arenicolites*. 13. *Ophiomorpha*. 14. *Phycodes*. 15. *Rhizocorallium*. 16. *Teichichnus*. 17. *Crossopodia*. 18. *Asteriacites*. 19, 21. *Zoophycus*. 20. *Lorenzinia*. 22. *Paleodictyon*. 23. *Taphrhelminthopsis*. 24. *Helminthoida*. 25. *Spiroraphe*. 26. *Cosmoraphe*. (*Source:* Modified from T. P. Crimes; courtesy of G. M. Pemberton, *Short Course Notes*, Society of Economic Paleontologists and Mineralogists, 1984.)

and *Ophiomorpha* are formed by infaunal deposit feeders. Both trails and burrows reach their greatest abundance in this zone which today is developed on the continental shelves.

Zoophycus Ichnofacies:

This occurs in fine-grained, muddy sediments with abundant organic matter in oxygen-deficient environments of low turbulence. These conditions may occur in relatively deep water on continental slopes or in nearshore environments protected from turbulence, where water circulation is restricted. The animals are surface grazers and deposit feeders working a short distance below the surface and making mostly horizontal traces. The facies is of low diversity but some ichnospecies may be abundant.

Nereites Ichnofacies:

Animals of this facies lived in deep water below wavebase, usually in sediments that were deposited from turbidity flows. Planar, horizontal, complex grazing traces are characteristic of the facies. The meandering and spiral grazing traces of *Helminthoida* and *Spiroraphe* are typical. The curious hexagonal grid of *Paleodictyon* is most commonly found in this facies but has also been found in shallow water deposits. Photographs of the modern deep-sea floor have recently shown that an animal that made *Paleodictyon* still lives.

As study of the distribution of ichnofossils continues, these broad facies divisions will be subdivided and new ichnofacies will be introduced. The identification of an ichnofacies and deductions about its ecological significance can be made only after a study of the fossils, the nature of the sediment, and the relationships to adjacent ichnofacies. Identification of a single trace fossil, or even several, is insufficient to place a bed in a particular ichnofacies.

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Index Term **Links**

Index

Aardvark	305	306		
Acanthaster	379			
Acanthocephala	69			
Acanthochaeletes	90			
Acanthodii	198	199	200	
Acanthostyle	104			
Accleration	356			
Accreted terranes	406-405			
Acipenseriformes	199	200		
Acoelomate	55	69	75-101	
Acritarch	218	219		
Acropora	222			
Acrotretida	109			
Actinoceratoidea	123			
Actinopteria	121			
Actinopterygii	198-201			
Actinostroma	89	90		
Actinostromatida	88			
Adapidae	290	291		
Adapiformes	289			
Adaptation	327-329			
Adaptive radiation	363-364			
Adductor muscle:				
bivalve	117	120	223	224
brachiopod	109	111	112	
Aegyptopithecus	291			
Aeluroidea	295	296		
Aerobes	42	43		
Aerobic zone (in sea)	387-388			
Aestivatation	204			
Aetosauria	249			
Agaricia	170	222		
Agelas	82			
Agelocrinites	156			

Index Term	Links				
Agglutinated test	77				
Agnatha	29	186-192			
Agnostida	138	139	140		
Ahermatypic corals	220	221			
Aigialosaurs	248				
Aistopoda	205	207	208		
Albatrosses	263				
Alberstadt L.	395				
Alcohols	42				
Aldanella	126	128			
Algae	54	169			
endolithic borers	425	426			
green	171	172			
phylloid	171				
red	169	170	171		
reef	393				
skeletons	412	413			
Alievium	219				
Allogenic succession	395				
Allogromia	76				
Allogromiina	77	78			
Allometry	330-332				
Gryphaea	342				
Allopatric speciation	408				
Allosaurus	253				
Allotheria	270				
Alphadon	278				
Alternation of generations:					
forams	76	78			
plants	173				
Alveolinidae	215				
Ambonychia	121				
Ambulacral area	146	147	154	236	237
Amiiformes	199	200			
Amino acid	42				

Index Term	Links				
sequences	29	30	43		
Ammobaculites	214				
Ammodiscus	77	213	214		
Ammonia-atmospheric	46				
Ammonite	8	34			
habitat	231-232				
heteromorph	231	232			
history	232-233				
shell	375				
shell form	335-334				
temperature	385				
zone	318	319	322		
Ammonitic suture	229				
Ammonitida	232	233			
Acipenseriformes	199	200			
Ammonoidea	119	123	125	126	232
Mesozoic	229-233				
Paleozoic	125-727				
shell form	335-336				
suture	126-727	229	360		
Amniota	27	29	205	209	
Amoeboid cell	80	81			
Amorphognathus	162				
Amphiaspidae	187	189			
Amphiaerobes	42	43	49		
Amphibia	205-209	277			
evolution from fish	353				
Amphicyonidae	296				
Amphioxus	164	184-186	192		
Amphizona	141				
Amplexizaphrentis evolution	357				
Ampulla	146	236	239		
Anabarites	65				
Anaerobes	42	43			
Anaerobic zone (in sea)	387-388				

Index Term	Links				
Anagale	298				
Anagalida	284	289-294	297		
Anagenesis	346	347	348	349	362-363
Anakosmoceras	343				
Anal plate	148	149			
Analogous structures	23	335			
Anapsida	187	189	190	191	211
Anaptychus	231				
Anarcestida	123	232	233		
Ancestor identification	25	26			
Anchiceratops	258				
Anchitherium	311				
Ancyloceras	232				
Ancyloceratina	231	233			
Ancylopoda	310				
Ancyrochitina	220				
Andrewsarchus	312				
Anemone	220				
Aneurophyton	175	180			
Angiosperm	173	179-183			
Animalia	54				
Anisoceras	232				
Anisograptid	160	161			
Ankylosauria	251	253	256		
Annelida	56	57	61	68	143
Annularia	175				
Anomalodesmata	223				
Anoxic events	388				
Antarctodolops	281				
Antelopes	306	307-309			
Antennule	140				
Anthophyta	173	179-183			
Anthozoa	95-101				
Anthracobundidae	304				
Anthracosauria	205	207	210		

Index Term	Links				
Anthracotheriidae	307				
Anthropoidea	289	290			
Antiarchi	195				
Antilocapridae	308	309			
Antler	310				
Antorbital fenestra	249	251			
Ants	285				
Anura	205	207			
Aortic arches	25	354			
Apatemyidae	283				
Apatosaurus (*Brontosaurus)*	255				
Aperture gastropod	129	131			
Apes	290				
Aplacophora	116	165			
Aplodontoidea	297				
Apomorphy	24				
Appendages					
arthropod	131				
trilobite	136	137			
Apternodontidae	287				
Aptychus	231				
Arachnida	132	133			
Araeoscelida	245				
Aragonite	75	411-418			
solubility	379				
Arandaspis	187	188			
Araucarioxylon	178	181			
Arca	223	225			
Archaebacteria	43	54			
Archaeocyathida	65	68	70	78	82
	83	84	85		
Archaeogastropoda	128-130	228			
Archaeohippus	311				
Archaeopteris	175	180			
Archaeopteryx	263	341	353		

Index Term	Links		
Archaic *Homo sapiens*	293		
Archanodon	121		
Archean:			
divisions	39	40	
environment	40	41	
fossils	43		
sediments	410-411		
Archeoceti	313		
Archimedes	106		
Archosauria	249-259		
Archosauromorpha	245	246	249-259
Arctinurus	139		
Arctocyonidae	301		
Arctoidea	295	296	
Arctostylopidae	302		
Arenicolites	424	427	430
Argon	15		
Argyrolagidae	281		
Argyrolagus	281		
Aristotle	5		
Aristotle's lantern	237	238	
Arkansas novaculite	220		
Arkarua	61		
Armadillo	285	406	
Armenoceras	125		
Arms race	351		
Arthrodira	195		
Arthrophycus	426		
Arthropoda	56	57	61
biology	130-133		
classification	132-133		
microstructure	417		
Arthrostylus	106		
Articulata (crinoid)	148	151	
Articulata (brachiopod)	108	109	

Index Term	Links				
Artiodactyla	284	306-310			
Ascocerida	123	125			
Asioryctes	282				
Assemblage:					
fossil	390				
transported	379-388				
Asteriacites	427	428	430		
Asteroidea	145	146	147		
Asterophyllites	175	179			
Asteroxylon	174				
Asterozoa	145				
Astraeospongium	85	86			
Astragalus	306				
Astrapotheria	284	301	302		
Astraspis	187	188			
Astrohippus	311				
Astroites stellis	5	6			
Astrorhizae	88	89	90		
function	332-333				
Astrosdera	414				
Astybspongia	87				
Astylospongiids	85	87			
Atdabanian Stage	65				
Atelostomata	235				
Atlantic ocean development	407				
Atmosphere development	40	73	464-466		
Atrium	186				
Atrypa	113	400			
Atrypella	32-34				
Atrypida	109	112	113		
Auditory bulla	280	290	295	296	302
Auks	263				
Aulacophore	156				
Aulacophyllum	100				
Aulechinus	239	240			

Index Term	Links			
Aulichnites	423	424	427	
Auloporid	97			
Auricle bivalve	225	226		
Australasian realm	402	403		
Australopithecus afarensis	291	292	294	
africanus	292	294		
boisei	292			
robustus	292	294		
Autapomorphy	24			
Autogenic succession	395			
Autozooecium	104			
Avalon terrane	406			
Aves	29	209	262-265	
Ax P.	26			
Axolotl	355-366			
Aysheaia	132	143		
Bactritina	123	233		
Baculites	231	232		
Bairdia	141	367		
Bakker R.	337			
Balancing shells	123-125			
Baleen whales	313			
Baltic salinity	385-356			
Baluchitherium	310			
Bambach R.	363			
Bandicoots	280	281		
Barbados reef	93			
Barbourofelis	296			
Barghoorn E. S.	45			
Barnacle	133			
Barriers to migration	323	404		
Barunkstes	282			
Basal plate	148-149	153	154	155
Basilosauridae	313			
Basilosaurus	313			

Index Term	Links			
Bathyurus	393			
Batoidea	187	195		
Batostoma	105			
Bats	287			
Beak bivalve	117			
Bear-dogs	296			
Bears	293	296	297	
Beavers	297	298		
Behrensmeyer A.	377			
Belcher Is.	46			
Belemnitella	234			
Belemnitida	232	233-235		
Belemnoidea	119			
Belemnopsis	234			
Bell A.	334			
Bellerophontina	128	129		
Benthic assemblage	397-398			
Beresford L.	51			
Bering land bridge	278			
Bermuda	92			
Beyrichia	141			
Biarmosuchidae	266-268			
Biarmosuchus	268	269		
Bias fossil record	11-12	167	371	
Billingsaria	97			
Bindstone	93			
Bioerosion	7	92	237	425
Biofacies	319			
Biogenetic law	355			
Biogeographic theories	407	408		
Bioherm	92			
Biostratigraphic unit	326			
Biostratigraphy	4-5	60	317-326	
ammonite	232			
Biozone	319	326		

Index Term	Links		
Bird	27	246	262-265
ancestry	353		
of prey	264		
Bison	309	310	
Biston melanism	351		
Bitter Springs chert	45	46	
Bivalvia:			
biology	116-118		
borer	227-228		
byssate	224-225		
cemented	225		
classification	222-223		
freshwater	122		
Mesozoic	221-228		
microstructure	416		
Paleozoic	119-122		
rudist	225-228		
shell form	334		
survivorship	368		
swimming	225		
Bivariate plot	33		
Black chert fossils	43-46		
Blastoidea	153	154	155
Blastozoa	145		
Blood circulation amphioxus	186		
Blue-green algae	45		
Bolandiceras	126		
Bone origin and function	188		
Bony fish	277		
Borer	425	426	
bivalve	222	227	228
Borhyaenidae	279	281	
Botanical Code	22		
Bothriocidaris	239		
Bothriocidaroidea	235		

Index Term	Links				
Bothrieolepis	194				
Bottjer D.	388				
Boucot A	167	397	399		
Bovidae	309				
Bovoidea	307				
Brachial:					
plate	148	149			
valve	107	108			
Brachiole	151	153			
Brachiopoda	56	107-114	222		
biology	107-109				
Cambrian	109				
microstructure	415	416			
Ordovician	110-112				
shell form	334				
shell function	332				
silicified	8				
Silurian/Devonian	112-113	324			
Brachyceratops	258				
Brain size	269	270	273	292	293
	300	352			
Braincase	269				
Branchiopoda	132	133			
Branchiostoma	164	184			
Brasier M. D.	73				
Bretsky S. & P.	343	367			
Brinckmann R.	342				
Brongniart A	17	317			
Brontosaurus	255				
Brontotheria	357				
Brontotherioidea	310	311			
Brood pouches	102	103	240	241	
Brooksella	60				
Brouillon index.	394				
Brown body	102				

Index Term	Links				
Bryophyta	169	173			
Bryozoa	56	101-107	240		
biology	101-104				
Mesozoic/Cenozoic	240				
mineralogy	415	416			
Paleozoic	104-107				
Bufo-subspecies	31				
Buildup	92				
Bulk sampling	380				
Bullfrog subspecies	31				
Bunodont	308				
Buoyancy nautiloids	124-125				
Bur	310				
Burgess Shale	137	142-144	150	338	
Burgessochaeta	143				
Burne R.	46				
Burrow	423	424			
Burrower bivalve	222	223	224		
Busycon	229				
Byssal notch	225	226			
Byssus	121	222	224	225	226
Cache Creek Group	220				
Caecilia	207-209				
Caenolestoidea	280				
Cairns-Smith A. G.	42				
Catamites	175	178	179	181	
Calcarea	82	85	86	87	
Calcichordata	154-157				
Calcification zooxanthellae	387				
Calcite	75	411-419			
carbonate solubility	387				
varieties	411	418			
Calice	98				
Calippus	311				
Callianassa	424				

Index Term	Links			
Calyx (crinoid)	146	148		
Cambrian fauna	65-67			
Camelidae	308			
Cameloidea	307			
Camenella	66			
Camerate crinoids	151			
Canadia	143			
Cancrinella	114			
Canidae	296			
Caprina	226	228		
Captorhinidae	211			
Carapace of turtle shell	243			
Carbon isotopes	49			
and salinity	385			
Carbon dioxide:				
atmospheric	42	365		
oceanic	387	410	412	
Carbonate minerals	411-419			
in diagenesis	418			
Carbonate production	221			
Carbonization	9	11		
Carcharodon	196			
Cardinal teeth	223			
Cardinal process	109-112			
Cardiocephalus	206			
Cardioceras	231	375		
Cardium	359	360		
Cardonia	302	303		
Carnassial teeth	295			
Carnivora	284	293	295-297	313
Carnivores	282			
Carnosaurs	251			
Carpoidea	154-157			
Carroll R.	208			
Cartilaginous fish	195	277		

Index Term	Links			
Caruthers R. K.	357			
Caryocrinites	151			
Caseidae	265	266		
Caspian sea cockles	349			
Cassian Formation	85			
Cassiduloidea	235			
Cassowaries	265			
Castorimorpha	297			
Castoroides	298			
Catarrhini	289	290		
Cattle	306-309			
Caviomorpha	297	299		
Cellularia	82			
Cellulose digestion	288	308		
Cement aragonite	417			
Cementation	417			
Cenozoic name	17			
Census assemblage	377	379		
Centipede	132			
Cephalaspidomorpha	187	189	191	
Cephalaspids	189	191		
Cephalochordata	155	157	164	184
Cephalon	134	135		
Cephalophytarion	45			
Cephalopoda	116			
biology	119	122-123		
early Paleozoic	123-125			
late Paleozoic	125	126		
microstructure	416			
shell form	334			
Cephalothorax	131	133		
Cerastoderma	223	349		
Ceratites	230			
Ceratitic suture	229			
Ceratitida	232	233	242	

Index Term	Links			
Ceratocystis	155	156		
Ceratomorpha	310			
Ceratoporella	414			
Ceratopsia	251	253	256	
Ceraurus	139	380		
Cercopithecoidea	289	291		
Cervidae	308	331		
Cervoidea	307			
Cetacea	284	312	313	
Chaetetes	89			
Chaetetida	82	89	90	91
Chaetognatha	164			
Chalicotheres	310	311		
Chalicotherium	311			
Chalk	216	227	225	
Chama	226	227		
Champlain sea salinity	385-356			
Chancelloria	66			
Character state	24			
Charadriiformes	263			
Charniodiscus	61	63		
Chasmatosaurus	249	251	252	
Chasmosaurus	258			
Cheilostomata	102	104	240	241
Cheirotherium	429			
Chelicerata	132-133			
Cheliped	131			
Chelonia	2	243-246		
Chelonioidea	244			
Chimaeroids	195	196		
Chimpanzee	289	291	292	
Chiniquodontidae	266	270	271	
Chiroptera	284			
Chitin	130	140	412	417
Chitinozoa	220			

Index Term	Links				
Chiton	116				
Chlamys	226				
Chlorbphyta	169	171-172			
Choanocyte	81				
Chondrichthyes	29	187	195		
Chondrites	428				
Chondrostei	199	200			
Chonetida	114				
Chonostrophia	114				
Chordata	55	57	184		
origin	157				
Chromosome plant	173	181			
Chron	19				
Chronostratigraphic unit	326				
Chrysochloroidea	287				
Chrysophyta	169	217			
Cidaris	238				
Cidaroidea	235	240			
Cirripedia	132	133			
Cirrus	147	148	149		
Civets	296				
Clade-shape	363	364	372		
Cladistics	23-29				
Cladodus	196				
Cladogenesis	346	347	348	349	352
	362	363			
Cladogram	28	29			
Cladoselache	196	197			
Clark R.	68	71			
Clarkson E.	357				
Classification	22	26-31			
Clathrochitina	220				
Clathrodictyida	88				
Clathrodictyon	89				
Climacograptus	160				

Index Term	Links			
Climactichnites	424	427		
Climatic change	289			
Climax community	395			
Cliona	425			
Clonal organisms	94	102		
Cbnograptus	159			
Cformda-assemblage	324			
Cloud P.	52	60	73	
Cloudina	62			
Cluster analysis	391-392			
Clydagnathusl	164			
Clymeniina	123	233		
Clypeaster	239			
Clypeasteroidea	235	239		
Cnidaria	56	68	69	70
biology	94-96			
Coal	420			
ball	174	175		
swamps	174-178			
Coal forest environment	381			
Coccolith	169	217		
Coccosphere	217			
Coccosteus	194			
Codaster	153	155		
Coelacanthini	199	200	204	205
Coelenterata	94			
Coelobites	390			
Coelolepida	191	192		
Coelom	55	56		
development	57-59	69-70		
Coelomate	55	57		
Coelophysis	252	254		
Coelurosauravidae	245	246		
Coelurosauravw	247			
Coelurosaurs	252			

Index Term	Links			
Coenostele	88			
Coenostrom	88			
Coenozone	319			
Coleoidea	119	123	232	233
Collagen	29	417		
Collar cell	81			
Collection bias	12	380-381		
Collins D.	142			
Colonial organism	94			
Colonization stage	395	396		
Color alteration index	161			
Columella	100			
Columnal plates	149	150		
Comatulid crinoid	147	149		
Community	376			
Community:				
depth controlled	323-324	397	399	
descriptors	397			
paleoecology	390-400			
replacement	395			
Compensating sack	241			
Compsognathus	263			
Computer simulation of form	333-335			
Conception Group	62			
Condensed assemblages	377			
Condylarthra	284	300	301	306
evolution	347-348	353		
Conies	305	306		
Coniferophyta	173	178		
Coniform element	161	163		
Connecting ring	122			
Conodonta	161-165			
affinity	164			
biostratigraphy	165			
color	161			

Index Term	Links		
zones	321		
Constellaria	104	105	
Continental drift	259	405	406
Contortothrix	45		
Conus	228	229	
Convergence	279	290	304
Convergent evolution	23	328-329	351
Conway Morris S.	142		
Cooksonia	173	174	
Cope's law	354		
Coprolites	422		
Corallinacae	170		
Corallite	95	96-100	
Corallium	96		
Corallum	98		
Corals	94-101		
see Scleractinia,			
Rugosa, Tabulata.			
Cordaites	178	181	
Cormohipparion	311		
Correlation	319	321-324	
lithostratigraphic	321		
oxygen isotope	384		
quantitative	322-323		
time	321		
Cortex (graptolite)	158		
Corthurnocystis	156	157	
Corynexochida	138	139	140
Coryphodon	283		
Cosmoraphe	430		
Cotylorhynchus	266		
Cowrie shell	229		
Crab	133		
Craniida	109	111	
Cranioceras	310		

Index Term	Links				
Craniopsida	109				
Crassostrea	227				
Crawfordsville IN	149				
Crawling traces	427				
Crayfish	131				
Creodonta	284	295			
Cribilina	241				
Cribrilaria	241				
Crick R.	343				
Cricoconarids	67	68			
Crinoidea	68	145	146	148-151	
Crinozoa	145				
Crises extinction	166-168				
Crocodylia	29	211	246	249	250
metabolism	336	338			
Croizat L.	408				
Crompton A.	274				
Cross lamellar microstructure	416				
Crossopodia	430				
Crossopterygii	200	202	204	205	
Crustacea	132	133			
Cruziana	423	424	427		
Cruziana ichnofacies	429	430			
Cryptodira	243-246				
Cryptolithus	135	139			
Cryptonella	113				
Cryptostomata	104	106			
Cryptozoon	48				
Ctenacanthiformes	195				
Ctenacanthoidea	187	195			
Ctenidodinium	219				
Ctenophora	94				
Ctenostomata	104	107			
Cuckoos	264				
Currie P.	208				

Index Term	Links				
Cuttlefish	119				
Cuvier G.	17	317			
Cyanobacteria	45	46	47	49	51
	52	171	412		
Cyathaxonia	393				
Cycadeoidophyta	173	179	182		
Cycadophyta	173	178			
Cyclammina	77				
Cycles:					
eustatic	366				
in earth history	364-366				
Cyclocystoidea	154				
Cyclomedusa	61				
Cyclonema	130				
Cyclostome bryozoan	104				
Cyclotella	218				
Cylindromphyma	87				
Cylindroteuthis	234				
Cymbospondylus	261				
Cynodontia	265	266	267		
Cypraeidae	229				
Cypridina	140				
Cyrtodonta	392	398			
Cyrtonella	128				
Cystiphragm	104				
Cystiphyllida	100	101			
Cystiphyllum	100				
Cystoidea	68	145	151-152	155	391
Cystoporata	104	105			
Cytochrome-c	30				
d'Orbigny A.	317	325			
Dahlite	412	417			
DallW.	403				
Darwin C	18	23	26	183	318
	327	328	347	367	

Index Term	Links			
Darwin unit	362			
Dasypoidea	285			
Dasyuridae	281			
Dasyuroidea	280	281		
Dawson W.	209			
Death assemblage	377	379		
Deep sea cores	384			
Deer	306-308			
Degassing	41			
Deinitheroidea	304			
Deinonychus	253	254		
Deltoblastus	155			
Deltoid plate	153	154	155	
Demiplate	236			
Demospongia	82	85	87	
Dendrogram	391-392			
Dendrograptus	159	160		
Dendroidea	157	159	160	
Dentalina	77			
Dentition mammals	277	278		
Derived character	24	28		
Dermoptera	284	288	289	
Desmostylia	284	301	304	305
Deuterostome	56	58	59	71
Devonian System founding	325			
Dextral gastropod	118			
DiaboUchthys	203			
Diacodexis	306	307		
Diadema	236	237	377	
Diadematacea	235			
Diadiaphorus	302			
Diagenesis of fossils	417-419			
Diaphragm	104			
Diapsida	244-265			
Diastema	274			

Index Term	Links				
Diatom	169	217	218		
Diatomite	217				
Diatremiformes	264				
Diatryma	264				
Dice coefficient	322				
Dice diagram	32	33			
Diceras	228				
Dichobunidae	307				
Dichrometra	147				
Dickinsonia	61	63	68	71	
Dicranograptus	160				
Dictyonema	160				
Dicynodon	268				
Dicynodontia	265	266-268			
Didductor muscles	109	111	112		
Didelphidae	279				
Didelphis	367				
Didelphoidea	280-282				
Didolodontidae	301				
Didymograptus	160				
Diexallophasis	219				
Digitigrade posture	295				
Dimeropyge	138				
Dimetrodon	181	266	267	268	
Dimorphism:					
ammonite	34	230	343		
Foraminiferida	34	76-75			
sexual	34				
Dineley D.	189				
Dinocerata	283	303			
Dinoflagellate	169	217	218	219	221
symbionts	221	386	387		
Dinohippus	311				
Dinophyllum	100				
Dinosaur	250-258				

Index Term	Links		
extinction	338		
metabolism	336-338		
movement	337		
posture	336		
size and temperature	337		
trackway	423	429	
Dinosauria	246		
Diplocraterion	425	428	430
Diplodus	196		
Diplograptid fauna	161		
Diplograptus	160		
Diplopore	152		
Diploporita	145	151	
Diplorhina	187		
Diplmia	221	222	
Dipnoi	199	200	
Diprotodonta	280		
Diprotodontidae	282		
Diprotodontoidea	281		
Dipterus	202		
Discocyclina	215		
Disconformity	320		
Discovery Bay Jamaica	221		
Dispersal theories	407		
Dissepiment	88	96	98
Dissolution of shells	379		
Dissorophidae	208		
Diversification:			
causes	72-74		
invertebrate	72		
metazoan	68-73		
stage	396		
Diversity	216	368	
ammonite	233	370-371	
anthophytes	182		

Index Term	Links		
archaeocyathid	85		
Cambrian	68	69	75
community	393-394		
curves	166-167		
index	394		
latitudinal variation	381	382	
Ordovician	91		
Paleozoic	165	166-167	
and salinity	385-356		
and stability	382		
stromatoporoid	370	371	
DNA and phylogeny	29		
Dobb's Linn Scodand	326		
Docodonta	270	274	
Dogs	293	296	
Dolomite	411		
Dolomitization	420		
Dolphin	328	329	
Domestic fowl	264		
Domination stage	396		
Dormice	297		
Dorsal hollow nerve cord	184		
Doublure	135	136	
Draco	245	247	
Drepanoistodus	163		
Dromomerycidae	308	310	
Dryopithecus	291		
Dsungaripterus	259		
Ducks	263		
Dusisiren	305		
Dwelling structures	428		
Dysaerobic zone (in sea)	387-388		
Dysodont dentition	223		
Earth origin	40		
Earthworm	71		

Index Term	Links			
Eastern Americas realm	403	404		
Echidna	271			
Echinacea	235			
Echinocardium	238			
Echinochimaera	198			
Echinocorys	238			
Echinocystitoidea	235	239		
Echinodermata	56	57	145-157	
see also its classes				
biology	145-148			
microstructure	417			
skeleton	145			
Echinoidea	145			
evolution	358			
irregular	237-239			
Mesozoic/Cenozoic	235-240			
Paleozoic	239-240			
regular	235-237			
Echinozoa	145	147		
Echinus	236			
Echolocation	287			
Ecoclinal	391			
Ecophenotype	390			
Ecosystem	374	376		
Ecotonal	391			
Ecphora	228	229		
Ectoconus	300			
Ectoderm	55-58	69	70	94
Ectoprocta	101			
Edaphosauridae	265	266		
Edaphosaurus	181	266	267	
Edentates	285-287			
Ediacaran fauna	60-63	95		
interval	60	64		
Edmontosaurus	256			

Index Term	Links				
Edrioasteroidea	61	145	153	154	156
	391				
Edrioblastoidea	154				
Eggerella	77				
Eglonaspis	189				
Ektopodon	281	282			
Ektopodontidae	281	282			
Elasmobranchii	195				
Elasmosauridae	260				
Eldredge N.	344	349			
Electrosensory structures	189	201			
Eleganticeras	34				
Elephant birds	264	265			
Elephant shrews	287	288	289		
Elephantidae	304				
Elephants	301	304	305		
Elk Irish	331	332			
Elliot L. Mines	50				
Embrithopoda	301				
Embryology:					
and ancestors	354-360				
human	354	355			
and polarity	25				
relationships	59				
Emiliana	217				
Enaliarctos	297				
Endemic fauna	404				
Endler J.	351				
Endocasts	258				
Endoceras	125				
Endoceratoidea	123-125				
Endoderm	55-58	69	94		
Endolithic algae	425	426			
Endothyra	79				
Endothyrida	213	413			

Index Term	Links			
Enopleura	156			
Entahphora	104			
Entelodont	308			
Entelodontidae	307			
Entelodontoidea	307			
Enterocoel	108			
Enterocoelomate	55	58	59	145-165
Enteropneusta	157			
Entobia	430			
Eoastrion	44	45		
Eocene Epoch name	17			
Eocoelia	400			
Eocoelia assemblage	324	325		
Eocrinoidea	154			
Eofletcheria	97			
Eoharpes	139			
Eospermatopteris	180			
Eosphaera	44	45		
Eosuchia	245	246	250	
Eosynechococcus	46			
Eotitanosuchia	266			
Epifauna	389	390	392	
Epihippus	311			
Epiphyses	246			
Epiphyton	171			
Epipterygoid	269			
Equidae	311			
Equisetum	175	367		
Equitability	394			
Equoidea	310			
Equus	311	312		
Erinaceomorpha	287			
Ernietta	62			
Estuarian environments	385-386			
Ethiopian realm	402	403		

Index Term	Links				
Eubacteria	54				
Eubrontes trackway	429				
Eucalyptocrinites	149				
Eucidaris	236				
Eudimorphodon	259				
Euechinoidea	235				
Euhoplites	231				
Eukaryotes	42	43	50-53	54	72
	169				
Euphemites	130				
Euplectella	86				
Eurotamandua	286				
Eurymylus	298				
Eurypterida	132	141-142			
Eurypterus	142				
Euselachii	195				
Eustatic cycles	366				
Eusthenopteron	204				
Eusuchia	250				
Eutheria	270	282-313			
Event magnetic	19				
Evolution:					
convergent	328-329				
definition	351				
explosive	73				
fossil evidence	4				
mechanisms	340-361				
rates	362-367				
Evolutionary systematics	23	24			
Excurrent pore	80	81			
Exogyra	225	227			
Exoskeleton	130-132				
Extinction:					
ammonite	232-233				
background	368-369				

Index Term	Links		
causes	368-371		
climatic	371		
Cretaceous	240	242	
cyclic	369		
impact hypothesis	369-370		
mass	346-372		
Paleozoic	166-168		
Extraembryonic membranes	209		
Eye trilobite	135		
Fabrosaurus	255		
Facial suture	135	138	
Facies	319		
Facies fossil	319		
Falites	10		
Fallotapsis	65		
Faunal realm barriers	404		
Favistina	99	101	
Favosites	97		
Favosites porosity	419		
Favositida	96		
Feathers evolution	353		
Fecal pellets	422		
Feeding structures	428		
Feigel's solution	411		
Felidae	296		
Fenestella	106	393	
Fenestrata	102	104	106
Fermentation	43	51	
Ferns	173	175	
Figured stones	5-6		
Filter feeding	185	187	389
Fischer A.	365		
Fistulipora	105		
Fistuliporid	104		
Fitness	327	328	

Index Term	Links			
Flamingos	263			
Flatfish	195			
Flatworms	69	117		
Flexicalymene	102	136	380	
Flinders Ra.	60			
Flood Biblical	6			
Flying foxes	287			
Flying lemurs	287	288	289	
Flying reptiles	257-259			
Food grooves	153			
Foraminiferida:				
benthonic	213-215			
biology	76-78			
diversity	382			
evolution	343-345			
Mesozoic	213-216			
mineralogy	413			
Paleozoic	78-80			
planktonic	215-276	387		
reproduction	76	78		
test	76	77-80		
zones	318	322		
Fordilla	121			
Formaldehyde	42			
Formation	321			
Formic acid	42			
Fortey R.	334			
Fossil fuels	420-421			
Fossil Gardens N.Y.	48			
Fossil record bias	11	12	167	371
inadequacy	11	12	341	
Fossil:				
chemical	49			
definition	3			
living	175	367		

Index Term	Links				
mineralogy	411-417				
practical value	4-5				
preservation	6-11				
range	319-321				
relative value	321-322				
Fossula	100	101			
Framebuilders	93				
Framestone	93				
Franciscan Formation	220				
Francolite	419				
Frequency distribution	33				
Freshwater turtles	244				
Frigilaria	218				
Frogs	207	209	266		
Fucoid	427				
Functional morphology	329-332				
Fungi	54				
boring	425				
Funnel (cephalopod)	120				
Fusulinina	77-50	79	213	387	322
mineralogy	413				
Galeaspida	187	189	190		
Galeoid	187	195	196		
Galesauridae	266				
Gallon P.	255				
Gametophyte	173	176			
Gas exchange	186				
Gases:					
limiting	387-389				
sea	387				
Gastrochaeonolites	429				
Gastropoda	68	116			
biology	118-119				
drills	119	229			
Mesozoic	228-229				

Index Term	Links			
microstructure	416			
Paleozoic	126-130			
shell form	333-334			
Gene pool	31	341		
Gene flow	31	341		
Gene	31	52		
Genetic drift	372			
Genital plate	236	237	238	
Genus name	21			
Geochemistry	4			
Geochronology	14-16			
Geolabididae	287			
Gibbons	291			
Gilinsky N.	363			
Gill:				
bivalve	117			
echinoid	237	239		
Gill slits	155	156	184-186	354
embryology	354			
Gingerich P.	346			
Gingkophyta	173			
Giraffe	308	310		
Giraffidae	309			
Girtycoelia	87			
Glabella	135			
Glaciation:				
cycles	365			
late Proterozoic	60			
Varangian	65			
Glaessner M. F.	60			
Glauconite	16			
Glenobotrydion	45			
Gliding possum	281			
Gliroidea	297			
Gbbigerina	214	216	382	

Index Term	Links				
Gbbigerina-ooze	216				
Globigerinidae	215				
Globogerinoides	216				
Globorotaliidae	215				
Gbssofungites ichnofacies	429	430			
Gbssopteris	405				
Glycogen	337				
Glyptodont	406				
Glyptodontoidea	285				
Glyptorthis	110				
Gnathostomata	29	186	193	235	
Goat	309				
Gobiconodontidae	274				
Golden mole	287				
Golden Lane Mexico	226				
Goldschmidt R.	347				
Gomphonema	218				
Gomphotheriidae	304				
Goniatitic suture	229				
Goniatitida	123	126-127	232	233	
Goniograptus	160				
Gorgonopsia	266-268				
Gorilla	289	291			
Gorsline D.	388				
Gould S.	328	330	340	344	349
	370				
Gracihsuchus	249				
Granuloreticulosa	78				
Graphite	48				
Graptolithina	57	157	158-161		
alteration	161				
Dendroidea	11	159-160			
Graptoloidea	157	159	160-161		
polyphyletic	161				
zones	321				

Index Term	Links			
Grass	183	311		
Grazers	183	392		
Grazing traces	427			
Great Barrier Reef	92			
Greenhouse effect	364	365		
Greenhouse phase	412			
Greenops	135			
Greererpeton	206			
Growth in ostracoderms	188			
Gryphaea	225	227		
evolution	342	349	354	355
Guard (belemnite)	234			
Gubbio Italy	370			
Gulls	263			
Gunflint chert	44-45			
Gymnolaemata	103	104		
Gymnophonia (caecilians)	205	207		
Gymnosperm	176	179	180	
Gypsina	215			
Hadean:				
environment	40	41		
time	39	40		
Hadrosauridae	255			
Haeckel E.	355			
Hagfish	186	187	190-292	
Half-life	15			
Halimeda	171			
Hallam A.	347	366		
Halbpora	104	105	400	
Hallucigenia	338			
Halysites	97	400		
Halysitida	97			
Hammatostroma	414			
Hanthenina	214			
Haplohippus	311			

Index Term	Links			
Haramiyidae	274			
Hard parts	11	12		
Hardground community	390-397			
Hearing in vertebrates	208			
Hebertella	380			
Hedgehogs	287			
Hegetotheroidea	301	302		
Helicoplacoidea	154			
Heliolites	97			
Heliolitida	98			
Heliopora	96			
Helminthoida	428	430		
Helodontidae	262			
Hemichordata	157-161	184		
biology	157			
Graptolites	158-161			
Hemiphragma	105			
Hemoglobin and phylogeny	30			
HennigW.	24	25	26	
Henodus	262			
Heomys	298			
Hercynian ocean	407			
Hermatypic corals	220	221		
Heroditus	215			
Hesperornis	263	264		
Hesperornithiformes	263	264		
Heteractinida	82	83	85	87
Heterocercal caudal fin	199	202		
Heteroconchia	223	227		
Heterodont dentition	223			
Heterodontosauridae	253			
Heteromorph ammonite	231	232		
Heterostraci	187	188	189	
Hexactinellida	82	84-86	87	
Hexagonaria	101			

Index Term	Links			
Hibbardella	163			
Hildoceras	231			
Hindiids	85			
Hipparion	311			
Hippomorpha	310			
Hippopotamidae	307			
Hippopotamoidea	307			
Hippos	306			
Hippurites	226	228		
Histogram	33			
History of paleontology	5-6			
Hog	307			
Holarctic realm	402	403		
Holaspid	138			
Holasteroidea	235			
Holectypoidea	235			
Holmes R.	208			
Holmesina	286			
Ghnobotrydion	45			
Holocephali	187	195	196	198
Holochroal eye	135			
Holosteans	200			
Holotheca	101			
Holothuroidea	145	147		
Holotype	35			
Holzmaden Shale Germany	233			
Homagnostus	139			
Homalozoa	154-157			
Homeoplastic structure	23			
Hominidae	289	291-294		
Hominoidea	289	291		
Homo	289	293		
Homo erectus	293	294		
Homo habilis	293			
Homo sapiens	292	294		

Index Term	Links			
Homologous structure	23	24	335	
Homotrema	215			
Homotryblium	219			
Hoofed mammals	300-313			
Hopson J.	337			
Hormatoma	129	130		
Horn core	310			
Horner J.	255			
Horses	309	310		
Horseshoe crab	132	133		
Huayangosaurus	257			
Human paleontology	30			
s*ee* Primates				
Hunsruck Slate	8	9		
Huroniospora	44			
Huxley T. H.	341			
Huxley J.	341			
Hyaenas	293			
Hyaenidae	296			
Hyaenodon	295	296		
Hyaenodontidae	295			
Hyaenodontinae	295			
Hybodontoidea	187	196		
Hybodus	197			
Hydnoceras	87			
Hydrospire	152	153	154	155
Hydrozoa	95	96		
Hylobatidae	289	291		
Hylonomus	210	211	245	
Hyolithellus	65	67		
Hyolilhelminthes	67			
Hyolithes	66	116		
Hyolithida	65	67		
Hyopsodus	347-348			
Hypermorphosis	356			

Index Term	Links			
Hypersaline environments	385			
Hyperstrophic gastropods	127			
Hypohippus	311			
Hypopetraliella	102			
Hypostome	135	136		
Hypsilophodon	252			
Hypsodontidae	301			
Hyracoidea	284	305		
Hyracolherium	311	312		
Hyraxes	305	306		
Hystricognathi	297			
Hystricognathous	298			
Iapetus ocean	406	407		
Icaronycteris	288			
Ice Age distributions	407	408		
Icehouse phase	365	412		
Ichnofacies	429-430			
Ichnofossils	10	11	60	422-431
Ichnogenera	427			
Ichnospecies	427			
Ichthyornis	263			
Ichthyomithiformes	263			
Ichthyosaur	328	329		
Ichthyosauria	246	259-261		
Ichthyostega	204			
Ichthyostegalia	205	207		
Idioprionoidus	163			
Idmonea	104			
Igneous rocks	4	16		
Iguanodontidae	255			
Illumination limiting	386-387			
Imitoceras	127			
Impact hypothesis	369-370			
Impedance matching middle ear	246			
Inarticulata	108	109		

Index Term	Links		
Incurrent pore	80	81	
Incus	269	270	271
Infauna	389	390	
Information loss	376		
Infrabasal plate	148	149	
Iniopterygiformes	195-197		
Innes L. TX	429		
Inoceramus	225	227	
Insecta	132		
Insectivora	282	284	287
Interambulacral area	146	236	237
Interatherium	303		
Interbrachial plate	148	149	
Intercentrum	207		
Intraspecific combat	255		
Invertebrates	55	56	
Iridium anomaly	370	371	
Irish Elk	331	332	
Iron formation	50	51	52
Iron ores	4		
Iron-rich soil	50		
Ischadites	171	172	
Ischyromyoidea	297		
Isocrinoid	147	148	
Isofilibranchia	223		
Isometric growth	330	331	
Isotope	15		
carbon	49	385	
corals	221		
dating	14-16		
fractionation	382-385		
oxygen	382-385		
stable	49		
Isua Group	41	49	50
Jablonski D.	366		

Index Term	Links		
Jaccard coefficient	322		
Jasper	50		
Jaw muscles:			
Adductor mandibulae externus	209		
Deep masseter	269		
Masseter	269		
Superficial masseter	269		
rodents	299		
Jaws origin in vertebrates	193		
Jefferies R.	156	157	
Jellyfish	11	60	
Jenkins F.	274		
Johnson M.	324		
Juvenile faunas	395		
Kakabekia	44	45	46
Kangaroo	281		
Kannemeyeria	268		
Kauffman E.	60	366	390
Kayentachelys	244		
Kellogg D.	344		
Kennalestes	282	283	
Kenyapithecus	291		
Keratosa	82		
Kerogen	48	49	
Kielanjaworowska Z.	274		
Kingdom	54		
Kingfishers	264		
Kirk N.	161		
Kiwi	265		
Klonk Czechoslovakia	325		
Koala	280	281	
Koch C.	379		
Komodo dragon	248		
*Kosmoceras*evolution	342	343	344

Index Term	Links		
Krause D.	274		
Kronosaurus	260		
Kuehneotheriidae	274		
Kuehneotherium	272		
Kyptoceras	309		
LaBarbera M.	72		
Labechia	88	89	
Labechiida	88	367	
Labyrinthine enfolding	207		
Labyrinthodontia	205	207	
Lacertilia	245	246	
Lagena	77		
Lagenina	78		
Lagomorpha	284	297	
Lagosuchidae	249	252	253
Lagosuchus	252		
Laguna Madre TX	378		
Lambeophyllum	101		
Lambeosaurus	256		
Lamellibranchia	117		
see Bivalvia			
Lamels	416		
Lamina	88		
Laminar microstructure	415	416	
Lamprey	185-187	190-193	
Land bridges	405		
Laoporus	12		
Lapis stellaris	5	6	
Lappets	230	231	
Lapworthella	64-66		
Larva:			
adaptation	360		
dispersal	322	323	
Larval stage amphibians	209		
Lateral line canals	189		

Index Term	Links				
Lateral teeth	223				
Lateral temporal openings	265				
Latimeria	201	202	204	205	367
Lawn mower ecology	275				
Lawrence D.	376				
Lead	15				
Lecanospira	127	130			
LeGrand Iowa	150				
Lemuriformes	289				
Lemurs	289	290			
Lenticulina	214				
Leperditiids	140				
Lepidocyclus	113				
Lepidocystis	153				
Lepidocystoidea	154				
Lepidodendron	174	176	178	181	
Lepidolina	343	345			
Lepidophloios	174				
Lepidosauria	29	245			
Lepidosauromorpha	245	246			
Lepidosiren	204				
Lepidotes	201				
Lepisosteiformes	199	200			
Lepospondyli	205	207	208		
Leptagonia	393				
Leptoceratops	258				
Leptolepids	200				
Leucetia	82				
Lewontin R.	328				
Lichen	172				
Lichenaria	96	97			
Lichiida	138	139	140		
Life:					
assemblage	377	379			
definition	6				

Index Term	Links			
origin	42	51		
Light limiting	386-387			
Lima	225			
Limestone	410			
fossil fragment	91			
reef	92			
reservoirs	419			
Limiting factors	381-390			
Limnoscelis	206			
Limnosceloids	210			
Limpet	12			
Limulus	133			
Line transect sampling	381			
Lingula	367			
Lingula assemblage	324	325		
Lingulata	108	109	415	
Lingulida	110	109		
Linnaeus	21			
Linné Carl von	21	22		
Linsley R.	129			
Lion	293			
Liopleurodon	262			
Liquidambar	182			
Lissamphibia	207	208		
Lithisuda	82	83	85	
Lithofacies	319	321		
Lithophaga	227	228		
Lithophyllum	170			
Lithostrotion	99	101		
Litopterna	284	301		
Living fossil	26	110	175	367
Lizards	211	245		
Lobe (suture)	229			
Lobe-finned fish	198	201		
Lobster	133			

Index Term	Links			
Loligo	120			
Lonsdaleia	99	101		
Loon	263	264		
Lophophorate	59	71	101-115	
Lophophore	56			
brachiopod	107	108	113	
bryozoan	102	103		
graptolite	157	158	161	
Lophospira	130			
Lorenz D.	367			
Lorenzinia	430			
Loricata	285			
Lorisids	290			
Loxonema	131			
Loxoplocus	393			
Lucy	291			
Lung	199			
Lungfish	201-204	375		
Lycaenops	267	268		
Lycophyta	173-175			
Lycopod	209			
Lysocline	387-388			
Archean	410	411		
Lystrosaurus	267			
Lytoceratida	232	233		
Machaeroidinae	295			
Maclurites	127	130	398	
Macluritina	128-230			
Macraucheniidae	301	302		
Macroevolution	352-354	363		
Macroscelidae	287	289		
Madreporite	146	236	237	238
Magellania	108			
MaglioV.	304			
Magnetic reversals	18	19		

Index Term	Links				
Magnetism remanent	19				
Magnetopolarity unit	326				
Malacostraca	132				
Malleus	269	270	271		
Mammalia	27	29	209	265	270
	277-313				
diversification	349				
evolution	346-347				
origin	353	354			
Mammal-like reptiles	265-271	278			
Mammary glands	271				
Mammoth preservation	7				
Mammutidae	304				
Manatee	305				
Mancini E.	394				
Manis	286				
Manitounuk I.	46				
Mantle overturn	365				
Mantle brachiopod	107	108			
Manton.S.	132				
Marlin	259				
Marmot	298				
Marrella	143				
Mars	39	42			
Marsupial mammals	265	274	277	278	406
Marsupialia	279				
Mastondontosaurus	206				
Mature community	395				
MayrE.	23				
McGhee G.	167				
McKenna M.	278	285			
McKerrowW.	397				
McNamara K.	359				
Medullosa	175				
Medusa	95				

Index Term	Links			
Medusoid	61	62	68	144
Megaceros	310			
Megachiroptera	287			
Megahippus	311			
Megaloceros	332			
Megalodon	122			
Megalodont bivalve	225			
Megalonychioidea	285			
Megalosauridae	253			
Megalospheric test	34	77	78	
Megaspore	176			
Megatherioidea	285			
Melanism industrial	351			
Mellita	239			
Melonechinus	236	240		
Meniscotheriidae	301			
Meraspid	138			
Mercenaria	117	223		
Meryceros	310			
Merychippus	311	312		
Merycoidodontidae	307			
Merycoidodontoidea	307			
Mesaxonic	310			
Mesentery	95	96		
Mesoderm	55-58	69	70	
Mesogastropoda	128	129	131	228
Mesohippus	311	312		
Mesonychia	284			
Mesonychidae	301	313		
Mesosauria	259	260		
Mesosaurus	260	405		
Mesosuchia	250			
Mesozoic mammals	270-275			
Mesozoic name	17			
Mesozooecium	104			

Index Term	Links				
Messel fauna	286				
Metabolic rate	266	268	271	273	
Metabolism:					
bird	337				
dinosaur	336-338				
mammal	337				
unicellular	43				
Metacheiromys	286				
Metacone	272	278			
Metamerism	56	58	70	71	185
Metamorphic rocks	4	16			
Metatheria (marsupials)	270	279-282			
Metazoa	52				
early	60-68				
Meteorite impact hypothesis	370	372			
Methanogens	43	45	49	51	54
Methylacetylene	42				
Methylamine	42				
Miacidae	295				
Miacoidea	295				
Mice	297				
Michelinia	393				
Micraster	238	239			
Micrite	411				
Micrite envelope	418				
Micritization	418				
Microbiolite	46				
Microbiotheriidae	280				
Microchiroptera	287				
Microevolution	342-349	352			
rate	347	349			
Micromorph fauna	394-395	419			
Microsauria	205	207			
Microspheric test	34	77	78		
Microspore	176				

Index Term	Links		
Microstructure of fossils	412-417		
Middle ear	269	271	
Migration and correlation	322	323	
Miliolina	77	78	389
Milkpora	95	389	
Milleratia	141		
Mimia	200		
Mimicry	351		
Mimolagus	298		
Mineralogy of fossils	411-417		
Miocene Epoch name	17		
Miocidaris	240		
Miohippus	311	312	
Mistassinia	40		
Mistiaen B.	90		
Mixopterus	142		
Mixosaurus	261		
Moas	264	265	
Modern Synthesis	341		
Modiolus	224	225	
Moeritherioidea	304		
Moeritherium	304	305	
Molds and casts	9	10	
Molecular clock	30		
Moles	287		
Mollusca	56	116-130	
biology	116-119		
mineralogy	415	416	
Monaxon	83		
Monera	42	54	
Mongoose	296		
Monkey	290		
Monoclonius	258		
Monograptid fauna	161		
Monograptus	160	161	

Index Term	Links				
Monophyletic groups	23	26			
Monophyletic (plants)	183				
Monoplacophora	68	116	117	124	127
	128	129			
Monorhini	187	189			
Monotremata	270				
Monotremes	265	271	273	282	
Montastrea	222	425			
Monterey Formation	217				
Moon	40	41			
Moore L.	46				
Moores E.	73	408			
Morganucodon	272	273	274		
Morosovella	214				
Mosasaur	375				
Mosasauridae	248	249			
Mother-of-pearl	416				
Mount Tom MA	429				
Mountain beaver	297	298			
Mountain goat	309				
Mountain sheep	309				
Mourlonia	130				
Mouth embryonic	58				
Murchison R.	325				
Multimembrate assemblage	163				
Multituberculata	265	270	272	280	
Murchisoniina	128-130				
Murex	228	229			
Muroidea	297	299	300		
Muscles:					
invertebrate	70	71			
reptilian	337				
Musk ox	309				
Mustelids	296	297			
Mutation chromosomal	347				

Index Term	Links				
Mya	223	224			
Mylagaulidae	298	299			
Mylodontoidea	285				
Myomorpha	297				
Mysticeti	313				
Mytilus	223	224	225		
Mytilus salinity control	385				
Myxiniformes	187				
Nacreous microstructure	416				
Nama Group	62				
Names:					
fossils	21	22			
ichnofossils	427				
Nance D.	365				
Nannippus	311				
Nannofossil zone	318				
Nasohypophyseal opening	191				
Natural selection	329	350-352	368	370	372
Nautiloidea	119	123	124	125	
Nautilus	119	120	122	123	231
	334	335-356			
Neanderthals	5	293	294		
Nearshore/offshore communities	367				
Necrolemur	291				
Nectridea	205	207			
Nemakit-Daldym Fm.	65				
Nematocyst	94				
Nematode	57	69			
Neoceratodus	204				
Neodarwinism	341				
Neodymium	15				
Neoflabellina	214				
Neogastropoda	128	228	229		
Neogene System name	17				
Neogloboquadrina	382-383				

Index Term	Links			
Neohipparion	311			
Neomorphism	418			
NeopiUna	367			
Neopterygii	200			
Neoselachians	196			
Neostromatoporoid	89			
Neoteny	356			
Neotropical realm	402	403		
Neritopsina	128			
Neural arch	207			
Neutralist position	372			
New World monkeys	290	299		
Niche	376	381		
Nimravidae	296			
Nobel A.	217			
Nodosinella	79			
Norm Pole Australia	44			
Notharctus	291			
Nothosauria	245	246	260	262
Notochord	155	184		
Notoprongonia	301	302		
Notosaria	359			
Notoungulata	284	301	302	
Novacek M.	282	285		
Nuculites	343	345		
Nuculmdea	121			
Numees tillite	62			
Numerical taxonomy	23	24		
Nummulites	215	387		
Nummulitic Epoch	215			
Nyctitheriidae	287			
Nyctosaurus	259			
Obturator process	252			
Ocean history	4			
Oceanic Formation	220			

Index Term	Links		
Octocoralla	96		
Octopus	119		
Ocular plate	236	237	238
Odontella	218		
Odontoceti	313		
Odontopleura	139		
Odontopleurida	138	139	140
Oil glands	271		
Oil shale	420		
Oil well zonation	320		
Old World:			
monkeys	291		
realm	403	404	
Oldest rocks	40	41	
Olenellus	134	139	140
Olenoides	136	137	
Oligomerism	58	71	
Oliver W.	403		
Omomyidae	290	291	
Ontogeny	354-360		
coral	100		
trilobite	137-135		
Onychophora	132		
Opal	412		
Operculum bryozoan	240		
Operculum gastropod	118	119	
Ophiacodon	267		
Ophiacodontidae	265	266	
Ophiocystoidea	154		
Ophiomorpha	423	424	430
Ophiomorphus	248		
Ophiuroidea	145	147	
Opisthobranchia	119	128	
Opossum	279	406	
OppelA.	318		

Index Term	Links			
Orangutan	291			
Orbitolites	215			
Oreodont	307			
Organic matter (dispersed)	48	49		
Organs	55	56		
Oriental realm	402	403		
Orientation of fossils	380			
Origin of Species book	18	341		
Ornithischia	249	251	253	254-257
Ornithomimidae	253			
Ornithopoda	251	252	253	
Ornithosuchia	249			
Orodus	196			
Orohippus	311	312		
Orthida	109	110		
Orthoceratoidea	124			
Orthograptus	160			
Orthosphaeridium	219			
Osculum	80	81	86	
Osmosis	385			
Ossicones	310			
Osteichthyes	195	198-201		
Osteolepiformes	205			
Osteolepis	202	206		
Osteostraci	187	189-190		
Ostracoda	132	133	140-141	
replacement	10			
stunted	395			
Ostracoderms	187			
Ostrich dinosaurs	253			
Ostriches	265			
Ostrom J .	253			
Otarioidea	295			
Otoites	231			
Otsuka coefficient	322			

Index Term	Links			
Ovary	180			
Owls	264			
Oxyaenidae	295			
Oxygen:				
atmospheric	42	49-52	73	364
isotope (temperature)	382-385			
isotope (salinity)	385			
in sea water	387-388			
Oyster	117			
community	376			
Ozawa T.	343			
Ozone shield	51			
Pachycephalosauria	251	253	255	256
Pachyphyllum	415			
Pachypleurosaurus	262			
Pachyrhachis	248			
Pachyrukhos	303			
Pacing	308			
Paddle fish	200			
Padian K.	257			
Paedomorphocline	359			
Paedomorphosis	354-360	395		
Paired fins origin of	190			
Pakicelus	312			
Palaeanodonta	285	286	287	
Palaeodonta	307			
Palaeomerycidae	308			
Palaeomyrmedon	286			
Palaeonisciformes	199	200		
Palaeoniscoidea	199	200	202	203
Palaeoparadoxia	305			
Palaeotheriidae	310	311		
Paleobiogeography	93	402-408		
Paleocommunities	390			
Paleodictyon	430			

Index Term	Links				
Paleoecology	5	374-401			
Paleofavosites	97				
Paleofelids	296				
Paleogene System name	17				
Paleogeography	5				
Paleoherpeton	206				
Paleoichnology	422-431				
Paleophonus	142				
Paleophyllum	99	101			
Paleotaxodonta	223				
Paleozoic history	165-168				
name	17				
Paliguana	248				
Pallial:					
line	117				
sinus	223				
Palynomorph zone	318				
Panama isthmus	403				
interchange	406				
Panda's thumb	330				
Panderodus	164				
Pangaea	213	278	365	405	408
Pantodonta	283				
Pantolestidae	283	285			
Pantotheria	265	270	272	275	
Paracone	272	278			
Paracrinoidea	154				
Paradigm method	332				
Parahippus	311	312			
Paranyctoides	287				
Paraphyletic groups	27	28			
Parapuzosia	230				
Parasaurolophus	256				
Parasitism	375	392			
Paratoceras	309				

Index Term	Links	
Paraxonic	310	
Parrots	264	
Parsons T.	208	
Parvancorina	71	
Passerines	264	
Pasteur Point	50	
Patellina	128	
Paterina	66	
Patterson B.	275	
Peccaries	307	
Pecopteris	11	
Pecora	307-309	
Pecten	225	227
Pectinacea	225	
Pectiniform element	161	163
Pectinirhomb	152	
Pedder A.	167	
Pedicellate teeth	208	
Pedicle:		
brachiopod	108	
valve	107	108
Pelagiella	128	
Pelecypoda	117	
see Bivalvia		
Pelicans	264	
Pelleted sediment	426	
Peloidal limestone	411	426
Peloids	411	422
Pelycodus	346	
Pelycosauria	265-267	
Pen (squid)	120	
Penguin	264	
Penicillus	171	
Pentaceratops	258	
Pentacrinites	150	

Index Term	Links			
Pentamerida	109	111	112	415
Pentamerus	112	400		
Pentamerus assemblage	324	325		
Pentremites	153	154		
Perameloidea	280	281		
Peramorphocline	358			
Peramorphosis	355-359			
Perignathic girdle	237			
Period	17			
Peripatric speciation	347			
Periptychidae	301			
Perischoechinoidea	235			
Perissodactyla	284	309-312		
Permeability	419			
Permian System founding	325			
Permineralization	7	8		
Peronidella	85	86		
Petalodont	196			
Petalonamae	62			
Peterson C.	377	379		
Petrel	263			
Petrified wood	7	8		
Petrified forest Ariz.	7	178	181	
Petrolacosaurus	245	246		
Petroleum	93	420		
Petromyzontiformes	187			
Pflug H. D.	62			
Phacopida	138	139	140	
Phacops	136			
eye evolution	349			
Paedomorph iocline				
Phaenopora	106			
Phaeophyta	169			
Phalangerids	281			
Phalangeroidea	280			

Index Term	Links			
Pharetronida	82	85	87	
Pharyngeal pouch	354			
Pharynx	186			
Phascolarctoidea	280			
Phenacodontidae	301			
Phenacolophidae	301	304		
Phenetics	23			
Phillipsastrea	101			
Phillipsia	139			
Pholas	227	228		
Pholidophoroids	200			
Pholidota	284-286			
Phoronida	71	109		
Phoronis	71			
Phorusrhacidae	264			
Phorusrhacus	264			
Phosphate:				
Cambrian	65			
replacement	8	10	417	419
skeletal	412	417		
Photic zone	386			
Photodissociation	51			
Photosystem-I	42	52		
Photosystem-II	42	52		
Phragmoceras	126			
Phycodes	430			
Phylactolaemata	103	104		
Phyletic gradualism	347	350	352	
Phylloceras	230			
Phylloceratida	232	233		
Phylloid algae	171			
Phylloporina	106			
Phylogenetic systematics	23-25			
Phylogeny	28			
adaptation	329			

Index Term	Links			
molecular	29	30		
Phylozone	320			
Phytoplankton	217			
Phytosauria	249			
Pigeon	264			
Pig	306	307		
Pilina	128			
Pillar	88			
Pilosa	285			
Pinna	224			
Pinnipedia	297			
Pinnularia	218			
Pinnule	148	150		
Pioneer community	395			
Pistosaurus	260	262		
Placental mammals	265	274	277	278
Placodermi	29	187	194	195
Placodontia	246	262		
Plagiolophus	306			
Plagiomenidae	288	289		
Planktonic forams	213	215-276		
Planktonic microorganism	216-220			
Plantae	54			
Plantigrade posture	295			
Plants	169-183			
early Paleozoic	173			
flowering	179-183			
late Paleozoic	174-178			
Mesozoic	178-183			
Planula larva	69	70		
Plasmopora	97	98		
Plastron of turtle shell	243			
Plate tectonics	278			
Plateosauria	251			
Platyceras	129	130	375	

Index Term	Links			
Platycrinites	149			
Platyhelminthes	59	70	117	
Platypus	271			
Platyrrhini	289	290		
Plectodina	162			
Plesiadapiformes	289	290		
Plesiadapis	290			
Plesiomorphy	24			
Plesiosauria	245	246	260	262
Plesiosauroidea	245	260		
Plethodon subspecies	32			
Pleurocentra	207			
Pleurocystites	151			
Pleurodira	243-245			
Pleurosaurs	247			
Pleurotomariina	128-130			
Pliocene Epoch name	17			
Pliohippus	311	312		
Pliosauroidea	245	260		
Pneumatic foramina	258			
Point count sampling	381			
PojetaJ.	119			
Polacanthus	257			
Polarity:				
of characters	24	25		
commonality	25			
outgroup comparison	25			
Pollen	180			
Polychaete annelid	144			
Polydolopoidea	280	281		
Polydora	430			
Polygnathus	163			
Polyp	95			
Polyphyletic groups	26			
arthropods	132			

Index Term		Links
graptolites	161	
Polyplacophora	116	
Polypteriformes	199	200
Polypterus	200	
Polyzoa	101	
Pongidae	289	
Pongo	291	
Porcupine	298	
Pore-rhomb	152	
Porifera	56	69
biology	80-83	
mineralogy	413	
Paleozoic	83-91	
skeleton	81-83	
Pontes	377	
Porolepiformes	205	
Porosity	419-420	
growth frame	420	
interparticle	419	
intraparticle	419	
moldic	420	
shelter	419	
solution	420	
vuggy	420	
Portugese man-of-war	94	
Post-displacement	356	
Potamotherium	297	
Potassium-	40	15
Potsdam sandstone	424	
Pound quartzite	60	
Prasopora	105	
Pre-displacement	356	
Pre-Paleozoic life	39-53	
Precambrian life	39-53	
Predation	351-352	375

Index Term	Links		
Predator	392		
Predentary bone	254		
Prepubic process	252		
Preservation	6-11	209	
potential	12		
trace fossils	426		
Priapulid annelid	144		
Primary producer	374	375	
Primary rocks	16		
Primates	282	284	289
evolution	346		
Primitive character	24		
Prioniodus	163		
Prismatic microstructure	415		
Prismatophyllum	99		
Proboscidea	284	304	305
Procellariiformes	263		
Procerberus	278		
Procheneosaurus	256		
Proconsul	291		
Procynosuchidae	266		
Procyonids	296		
Productida	114		
Proetida	138	139	140
Profusulinella	80		
Proganochelydia	244	246	
Proganochelys	244	245	
Progenesis	356		
Progress in evolution	340		
Progymnospermophyta	173	175	180
Prokaryotes	42	43	52
Prolecanitida	232	233	
Pronghorn antelope	310		
Prorichlofenia	114		
Prosauropoda (Plateosauria)	251	253	

Index Term	Links				
Prosimii	289	290			
Prosobranchia	119	128			
Prosoma	141	142			
Protaspid	138				
Protective coloration	351				
Proteins	29	30			
Protenaster	358	359			
Proterosuchia	249	250			
Proterotheriidae	301	302			
Proterozoic:					
divisions	39	40			
fossils	45-48				
Proteutheria	283				
Protichnites	424				
Protista	54	75	78		
Protoceras	306	309			
Protoceratidae	308	309			
Protoceratops	258				
Protocetidae	313				
Protochordate	56	57	184		
Protocone	272	275	278		
Protoconodonts	165				
Protohertzina	65				
Protohippus	311				
Protopterus	204				
Protorosauria	246	249	*250*		
Protostome	56	58	59		
Protosuchia	249				
Prototheria	270				
Protozoa	55	75	78		
Protrogomorpha	297				
Protungulatum	301				
Provinces faunal	403	404			
Proviverinae	295				
Pseudocoelomate	55	57	58	69	70

Index Term	Links		
Pseudocubus	344	345	
Pseudohipparion	311		
Pseudometamerism	58		
Pseudonuclei	46		
Pseudopods	76		
Pseudopunctate microstructure	416		
Psibphyton	173	174	
Pteranodon	259		
Pteraspidae	187	189	
Pteraspidomorphi	187	188	
Pteraspis	189		
Pteria	226		
Pteriacea	225		
Pteridinium	62		
Pteridophyta	173	175	
Pteridospermophyta	173	176	177
Pteriomorphia	223	227	
Pterobranchia	157	158	
Pterocanium	219		
Pterodactyloidea	246	249	
Pteropoda	119		
Pterosauria	249	257-259	
Pterygoid muscle	210		
Pterygoideus	269		
Pterygotus	141	142	
Ptychopariida	138	139	140
Ptycnodontida	195		
Ptyonius	206		
Pulchrilamina	93	94	
Pulmonata	119	128	130
Punctuated equilibrium	349-350	352	
Purgatoire R. CO	423		
Pygidium	134	135	
Pygmy possums	281		
Pyramids Eygpt	215		

Index Term	Links				
Pyrite replacement	8	9	419		
Pyrotheria	284	301	302		
Pyrrhophyta	169				
Quadrat sampling	380				
Quahog	223				
Quaternary rocks	16				
Quetzalcoatlus	258	259			
Quinqueloculina	77				
Rabbits	297	282			
Raccoons	296				
Radial plate	148	149	153	154	155
Radial water canal	236	237			
Radiation adaptive	363-364				
Radioactivity	14	15			
Radiolaria	76	219-220			
Radiolites	226	*228*			
Radula ammonite	231				
Ramapithecus	291				
Ramiform element	161	163			
Range fossil	319-321				
Rangea	62				
Rates of evolution	362-367				
Ratfish	195	196			
Rats	297				
Raup D.	222	333	334	343	369
	372				
Ray-finned fish	198				
Rays	195				
Realms faunal	402-409				
Recapitulation	355				
Receptaculites	171	172			
Recrystallization	7				
Recycling of life	6	7			
Red Queen hypothesis	328				
Redbeds	50	52			

Index Term	Links			
Redlichiida	134	138	139	140
Reef	91-94			
archaeocyathid	84			
builders	381			
community Paleozoic	91-94			
definition	92	93		
limestones	420			
organism shapes	88	94	387	
patch	92			
succession	396-397			
Reflected lamina of the angular	266	268	269	260
Regression:				
and correlation	324			
and evolution	366			
Relationship of organisms	22-26			
Relief reversed	426			
Renalcis	83	171		
Replacement	7	8		
in carbonates	418			
phosphate	8	418		
pyrite	419			
Reproduction:				
amphibians	209			
early mammals	271	273		
ichthyosaurs	260			
placental mammals	282			
reptiles	209			
Reptiles (paraphyletic)	27			
Reptilia	209	277		
Respiratory canal	238			
Resting trace	427			
Revolution in earth history	317			
Rhabdinopora	11	159	160	367
Rhabdopleura	157	158	159	
Rhamphorhynchoidea	246	249	258	

Index Term	Links				
Rheas	265				
Rhenanida	195				
Rhenops	9				
Rhinocerotoidea	310	311			
Rhinoceros	7	309			
Rhipidistia	122	199	200	203	205
	207				
evolution	353				
Rhizocorallium	424	430			
Rhodophyta	169-171				
Rhombifera	145	151			
Rhopahnaria	107				
Rhynchonellida	109	112	113	114	332
	416				
Rhynchosauria	246	249	250		
Rhynia	174				
Rhynie Scodand	173				
Rhyniophyta	173				
Richtofeniidae	114				
Ring canal	146	148	236	237	
Riojasuchus	251				
Rodentia	282	284	297-300		
Romer.A.	205				
Rose K.	285				
Rostricellula	397	398			
Rostroconchia	116	120	129		
Rostrum	233				
Rotaliina	78	213-216	413		
Rotifer	57	69			
Rubidium	15				
Rudist	225-227	387			
Rudwick M.	72				
Ruga	*98*				
Rugosa	98-101				
biogeography	403	404			

Index Term	Links			
microstructure	415			
ontogeny	100			
Ruminantia	307-309			
Runnegar B.	73	117	119	
Rusophycus	427	428		
Russell D.	242			
Saddle (suture)	229			
Saetograptus	158			
Sagenocrinites	149			
Salamander	32	207-209		
Salinity controls	385-556			
Salmon	195			
Salterella	380			
Samarium	15			
Sampling method	380-381			
Sand dollar	239			
Sandberg P.	412			
Sanitary canal	238			
Sansabella	141			
Santa Monica basin CA	388			
Saratoga Springs N.Y.	48			
Sarcinulida	98			
Sarcodina	78			
Sarcomastigophora	78			
Sarcopterygii	198	199	201-205	
Sarkastodon	295			
Saurischia	249	251-254		
Sauropoda	251	253		
Sauropodomorpha	251	255		
Sauropsida	29			
Sauropterygia	245	260	262	
Saurornithoididae	253			
Savrda C.	388			
Scallop	117	225	226	330
Scaly pangolins	286			

Index Term	Links			
Scandentia	284			
Scaphites	231	232		
Scaphopoda	116			
Scatter diagram	33			
Schaeffer B.	192			
Schindewolf O.	347			
Schizochroal eye	135	136		
Schizocoel	108			
Schizocoelomate	55	58	59	116-142
Schopf J.	44	50		
SchopfT.	347	372		
Sciuroidea	297			
Sciurognathi	297			
Sciurognathous	297	298		
Sciuromorpha	297			
Scleractinia	220-222	387	425	
cement	417			
microstructure	415			
origin	360			
radiation	364			
symbiosis	220	221	363	
Scleromochlus	257			
Sclerospongea	82	414		
Scolecodont	57			
Scolicia	427	428		
Scolithos	428	429	430	
Scorpionida	132	141		
Scott R.	390			
Scoyenia ichnofacies	429	430		
Scrutton C.	97			
Scutellosaurus	255	257		
Scutellum	139			
Scyphozoa	95	96		
Sea horse	195			
Sea lion	296	297		

Index Term	Links				
Sea otter	283				
Sea turtle	244				
Sea-fan	61	96			
Sea-pen	61	96			
Seal	296	297			
Secondary palate	267	268			
Secondary rock	16				
Sedimentary rock	4	15	410-421		
Seed-fern	175	176	178		
Seed origin	176	178			
Segmentation	58				
Segmented invertebrate	184				
Seilacher A.	329	427			
Selection:					
intraspecific	351				
natural	329	341	350-352	354	
sexual	329	341			
species	352				
Selenodont	307	308			
Semicircular canals	188	189			
Semiorbis	218				
Sensory input	273				
Sepkoski J . J.	68	91	165	366	369
Septal insertion	220				
Septal neck	122				
Septum:					
ammonite	229				
archaeocyathid	83				
cephalopod	119	120	122	125-126	
coral	96	98			
rugosan	100				
Serial sections	100				
Series definition	11				
Serpentes.	245	246			
Sewellel	298				

Index Term	Links			
Sexual dimorphism	267			
Sexual reproduction	52			
Shannon-Weaver index	394			
Shark Bay Australia	46	47		
Shark	193	195		
convergence	329			
Sheehan P.	91			
Sheep	306	307	309	
Shonisaurus	261			
Shrew	287			
Sicula	158	160		
Side-necked turtle	244			
Siderastrea	415			
Sigillaria	174	176	177	209
Signor P.	166			
Silicification	8			
Similarity coefficient	322			
Simons E.	291			
Simpson G.	23	347		
Simpson coefficient	322			
Simpson index	394			
Sinistral gastropod	118			
Sinohippus	311			
Sinuites	130			
Siphon:				
bivalve	117	222	223	
gastropod	118	127-129		
Siphonodictyon	425			
Siphuncle	120	122-125		
ammonite	229	231		
belemnite	234			
function	335	336		
Sirenia	284	305		
Sister group	24			
Sivapithecus	291			

Index Term	Links				
Sivatherium	310				
Size increase trend	354				
Size distribution	394-395				
Skates	195				
Skeletal tissue:					
carbonate	73	75	84		
metazoan	73				
mineralogy	412-417				
phosphatic	73				
Skolithos ichnofacies	429	430			
Skunks	296				
Sloan R.	371				
Sloth	285	406			
Smibdon	296				
Smith W.	17	317			
Snakes	211	245	248	249	277
Sneath P.	23	24			
Soft-shelled turtles	244				
Sohl N.	379				
Sokal R.	23	24			
Solenodontidae	287				
Solenopora	170				
Solenoporacae	170				
Somasteroidea	154				
Sonar	313				
Songbirds	264				
Sorauf J.	167				
Soricidae	287				
Soricoidea	287				
Soricomorpha	287				
South American anteaters	285				
South American ungulates	301-304				
Spatangoidea	235				
Speciation	347				
Species:					

Index Term	Links			
biogeographic	31	32		
concept	341			
definition	31-35			
Linnean	32-35			
name	21			
new	22			
paleontological	35			
selection	352			
variation	33-35			
Sphaeractinoid	89			
Sphenacodontia	265			
Sphenacodontidae	266			
Sphenodon	210	211	244-247	
Sphenodontida	245-247			
Sphenophyta	173	175		
Sphenosuchia	250			
Spherulitic microstructure	413	414		
Sphinctozoa	82	85	86	87
Spicule	81-83	88		
Spider	132	133		
Spine echinoid	235	236	238	
Spinocyrtia	113			
Spiracle	153	154		
Spiriferida	109	113		
Spiroraphe	430			
Spondylium	112			
Sponge	56	68		
see also Porifera				
biology	80-83			
boring	425			
Spongocoel	80	81	83	
Spore (plant)	173	176		
Sporophyte	173	176		
Spotila J. R.	337			
Spreite	424	425	428	

Index Term	Links			
Spriggina	61			
Squalomorpha	187	195		
Squamata	245	247-249		
Squid	119			
Squirrel	297	298		
Stabilization stage	396			
Stabilizing shells	123-125			
Staff G.	379			
Stage	317	318	325	
Standard deviation	32			
Stanley G.	221	387		
Stanley S.	352	369		
Stapes	208	246		
Staurikosauria	251	253		
Staurikosauridae	253			
Staurikosaurus	250	252		
Stegodontidae	304			
Stegosauria	251	253	255	
Stegosaurus	255			
SteidtmannJ.	60			
Stellar's sea cow	305			
Stellispongia	85	87		
Slenacanthus	197			
Stenolaemata	103	104		
Stephanozyga	131			
Stephen Formation	142			
Stictopora	106	393	398	398
Stigmaria	174			
Stigmatella	105			
Stolon (graptolite)	157	158		
Stomatopora	104			
Stone canal	146	237		
Stratigraphic Code	326			
Stratigraphic Guide	326			
Stratotype	324-325			

Index Term	Links				
Strebulus	77				
Streptelasma	100	101			
Streptorhynchus	393				
Streptostyly	248				
Stricklandinia-assemblage	324				
Stromatolite	40	46-48	51	52	93
	366	412			
Stromatopora	89				
Stromatoporella	89				
Stromatoporellida	88				
Stromatoporida	88				
Stromatoporoidea	82	86	88-90	93	94
	332-333	414			
mineralogy	88				
Strombus	416	418			
Strongylocentrotus	145	236	237		
Strontium	15	16			
Strophodonta	111				
Strophomena	393	397	398		
Strophomenida	109	111	112	114	416
Stunted faunas	395				
Sturgeon	200				
Stylar shelf	278				
Styliolina	67	*68*			
Stylohipparion	311				
Styracosaurus	258				
Subcephalic muscle	203				
Subspecies	31				
Subulites	131				
Succession	395-397				
level bottom	397	398			
reefs	396				
Suidae	307				
Suina	307				
Suiodea	307				

Index Term	Links			
Sunnaginia	66			
Supraorbital bone	254			
Survival of the fittest	327	351		
Survivorship	347	349	362	368
Suspension feeder	73	389	392	
Suture:				
ammonite	229	230		
ammonoid	336			
goniatite	126-127			
Sweat glands	271			
Swifts	264			
Swimming invertebrate	71			
Swordfish	195	259	329	
Symbiosis:				
algal	386			
bivalve	226			
zooxanthellae	220	221	386	
Symmetrodonta	265	270	274	
Symplasma	82			
Synapomorphy	21	28		
Synapsida	211	265-271		
Syndactyly	281			
Syndyoceras	309			
Synplesiomorphy	24	28		
Syntaxial rim	417			
Synthetoceras	309			
Syringopora	97			
System definition	17	319		
Systematics:				
evolutionary	23	24		
phylogenetic	23	24-29		
Tabula	95	96	98	
Tabulata	96	*97*	98	
Taeniodonua	283			
Talonid basin	272			

Index Term	Links			
Talonid	272	275		
Talpidae	287			
Tanystropheus	250			
Taphonomy	6	7	376-381	
Taphrhelminthopsis	430			
Tapiroidea	310	311		
Tapir	309			
Tarsiiformes	289			
Tarsoidea	290			
Tasmanian devil	279	281		
Tasmanian wolf	279	281		
Taxodont dentition	223			
Taxon	22			
Taxonomy	22	21-22	31-35	
numerical	23	26		
Tayassuidae	307			
Tegmen	148			
Tegulorhynchia	359			
Teichichnus	430			
Teleostei	199	200	207	277
Teleostomi	29			
Telson	131	133	142	
Temnospondyli	205	207	208	
Temperature limiting factor	381-385			
Tempo and Mode in Evolution	347			
Temporal openings	210	211		
Temporalis	269			
Tenrec	287			
Tenrecoidea	287			
Tentacullites	67	68	116	
Terebratulida	109	113	114	
Teredo	227			
Termite	285			
Terrestrisuchus	*252*			
Tertiary rocks	16			

Index Term	Links			
Testudinata	243-245			
Testudinoidea	244			
Tethyan faunal realms	403	408		
Tethys ocean	278	403	405	407
Tetraclaenodon	306			
Tetracoral	98-101			
Tetradium	97	98		
Tetragraptus	160			
Tetrapoda	29			
Tetraxon	83			
Teuthida	232	233		
Texlularia	77			
Textulariina	77-79	213	214	
Thalassinoides	426	427	429	430
Thecideacea	114			
Thecodontia	246	249		
Thelodontida	187	191	192	
Theocampe	219			
Theologian natural	328			
Theosodon	302			
Therapsida	265	266		
Theria	270			
Therian mammals	274			
Theropoda	251	253		
Thomson K.	192			
Thorium	15			
Thrinaxodon	268	269		
Thylacinidae	281			
Thylacoleo	281			
Thylacoleonidae	281			
Thylacosmilidae	281			
Thylacosmilus	296			
Ticinella	214			
Tiering in communities	392			
Tiers in evolution	370			

Index Term	Links				
Tiger	293				
Tillodontia	283				
Time scale:					
relative	16-18				
standard	19-20				
Time averaging	377-379				
Time measurement	14-20				
Tissue rejection	282				
Tissues	55	56			
Tommotian Stage	64-67				
Tommotid	65	66			
Tooth:					
formula	278				
occlusion	268	270	272		
replacement	268	277	278		
Toothed whale	313				
Torosaurus	258				
Torsion gastropod	119				
Tortoises	244				
Toxodontia	301	302			
Trabecular microstructure	413	415			
Trace fossils	422-431				
Tracheophyta	169				
Tracks	9	10	12	60	422
Trackway	120	422	*423*	424	
dinosaur	423	429			
Tragulidae	308				
Traguloidea	307				
Trail productid	112	114			
Trail	423-424				
Transgression:					
and correlation	324				
and evolution	366				
Transition rocks	17				
Translation rate	333				

Index Term	Links				
Transported assemblages	379-380				
Transverse flange of pterygoid	210				
Tree shrews	287	288			
Trematosaurs	259				
Trepostomata	102	103	104	105	416
Triadobatrachus	209				
Triarthrus	139				
Tribosphenic tooth	272	275			
Tribrachidium	61	63	72		
Triceratops	258				
Triconodonta	265	270			
Tridacna	226	387			
Trigonia	223	224			
Trilete spores	173				
Trilobita	65	68	132	133-140	
appendages	136	137			
classification	138-139				
history	139-140				
onotgeny	137-138	360			
replacement	9				
zones	321				
Trilobitoidea	133				
Trilobitomorpha	132	138			
Trimerella	111				
Trimerellida	109	111			
Trimerophytophyta	173				
Trionychoidea	244				
Triops	367				
Trithelodontidae	266	270			
Triticites	80				
Trituberculata	270				
Tritylodontidae	266	269-271			
Trivial name	21				
Trochiina	128	130			
Trophic role	374	375			

Index Term	Links		
Trophic structure	391-393		
Trophoblast	282		
Trout	195		
Trueman A.	342		
Trypanites ichnofacies	429	430	
Tryposlega	241		
Tube foot	146	238	239
Tubipora	96		
Tubulidentata	284		
Tubuliporata	104	240	
Tuna	259		
Turbulence limiting	389-390		
Turgai Strait	278		
Turkana L. molluscs	350		
Turrilites	232		
Turtle	211	243-245	
Tyler S. A.	45		
Tylopoda	307		
Tympanic ring	269	270	
Tympanum	246		
Type section	17	324	
Type specimen	35		
Typotheroidea	301	302	
Tyrannosauridae	251		
Tyrannosaurus	251	253	254
Ubaghs G.	156		
Uintathere	283		
Ulrichia	141		
Ultradextral gastropod	127		
Umbo bivalve	117	223	
Umbo brachiopod	108		
Ungulates	282	300-313	353
Unicellular life	42-52		
Uniformitarianism	375		
Unimembrate assemblage	163		

Index Term	Links			
Unionoida	224			
Uniramia	132			
Uranium	15	16		
conglomerate	50			
ores	4			
Urochordata	157	184		
Urodela (salamanders)	205	207		
Uscia	241			
Utatsusaurus	261			
Vaceletia	86			
Vail curve	366			
Valentine J.	73	166	404	408
Van Valen's law	368	372		
Van Valen L.	328	368	371	
Varangian glaciation	65			
Varanus	248			
Vascular tissue	172-173			
Vascular plants	169	172-174		
Vendian System	62			
Venus	39	42		
Vermeij G.	222	228		
Vermilingua	285			
Vertebrae	207			
Vertebrata	29			
Vertebrates origin of	186			
Vicariance biogeography	408			
Vieraella	209			
Vinella	107			
Virgella	158	160		
Vis plastica	5			
Viverravidae	295			
Viverrids	296			
Vombatoidea	280			
Von Baer E.	59	354	355	
Walchia	181			

Index Term	Links		
Walcott C.	142		
Walker K.	392	395	
Wallabies	281		
Wallace A.	402		
Walrus	296	297	
Walter M.	44		
Warrawoona Group	44	47	48
Water vascular system	146		
Wavebase	389		
Weasel	296		
Wedges metaphore	328		
Westermann G.	336		
Whalebone	313		
Whale	301		
Whittington H.	142		
Whorl expansion	333		
Williams E.	208		
Williamson P.	349		
Witwatersrand Mines	50		
Wombat	281		
Woodpecker	264		
Wynyardiidae	281		
Xanthos of Sardis	5		
Xenacanthida	195	196	
Xenarthra	284	285	
Xiphosura	132		
Zalambdakstes	282	283	297
Zalambdodonta	287		
Zangerl R.	195		
Zeigler A.	324	397	
Zoantharia	96-101		
Zone	317	318	
assemblage	319		
concurrent range	319		
interval	319		

Index Term	Links	
phylozone	320	
range	319	
Zooecium	101	103
Zoogeography	278-280	
Zoological Code	22	
Zoophycus	425	430
Zooplankton	216	
Zooxanthellae	221	386-387
Zosterophyllophyta	173	175
Zugokosmoceras	343	344