

animal sciences



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3
VOLUME
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Preface



Six hundred million years of animal evolution and adaptation have produced a stunning range and variety of life on Earth. From the oldest, single-celled creatures to the most complex mammalian forms, animal diversity defies easy categorization or explanation. The Macmillan *Animal Sciences* encyclopedia provides a clear and comprehensive resource for better understanding this vast domain. By the nature of its interdisciplinary scope, the subject of animal sciences demands an approach that is both specific and general, detailed and thematic. *Animal Sciences* achieves this end in the course of nearly three hundred well-researched, clearly presented entries that explore the wide ranging diversity that exists within the animal kingdom.

Students will learn how animals develop throughout their lives, how they adapt to their changing environments, and how they develop specialized structures over time. Entries in this category explain how animals develop from fertilized eggs to adults. While some forms of development are straightforward—like a puppy maturing to become a dog—other changes are more dramatic—like a caterpillar changing its body forms over the course of its metamorphosis into a butterfly. Other entries study the various forms of animals and how body parts function.

The encyclopedia gives significant attention to animal ecology and behavior. Entries show how animals are part of the world environment while exhibiting unique behaviors within their own particular environments. Animal ecology addresses how animals are a part of ecosystems and how they interact with plants and other animals, both within and beyond their individual species. Given the close relationship of animal behavior and ecology, a number of entries discuss how animals select mates, whether they live alone or as members of groups, or how they share resources within an ecosystem, to give just a few examples.

Finally, *Animal Sciences* surveys the connection between animals and humans. Humans are unique in the animal kingdom because of their ability to alter environments significantly. Agriculture, which includes the domestication of animals and farming, serves as the chief example of such human-inspired environmental change and its impact on animal life worldwide. In addition, humans are the most social of animals and have developed complex social interactions. As human populations grow, habitat once occupied



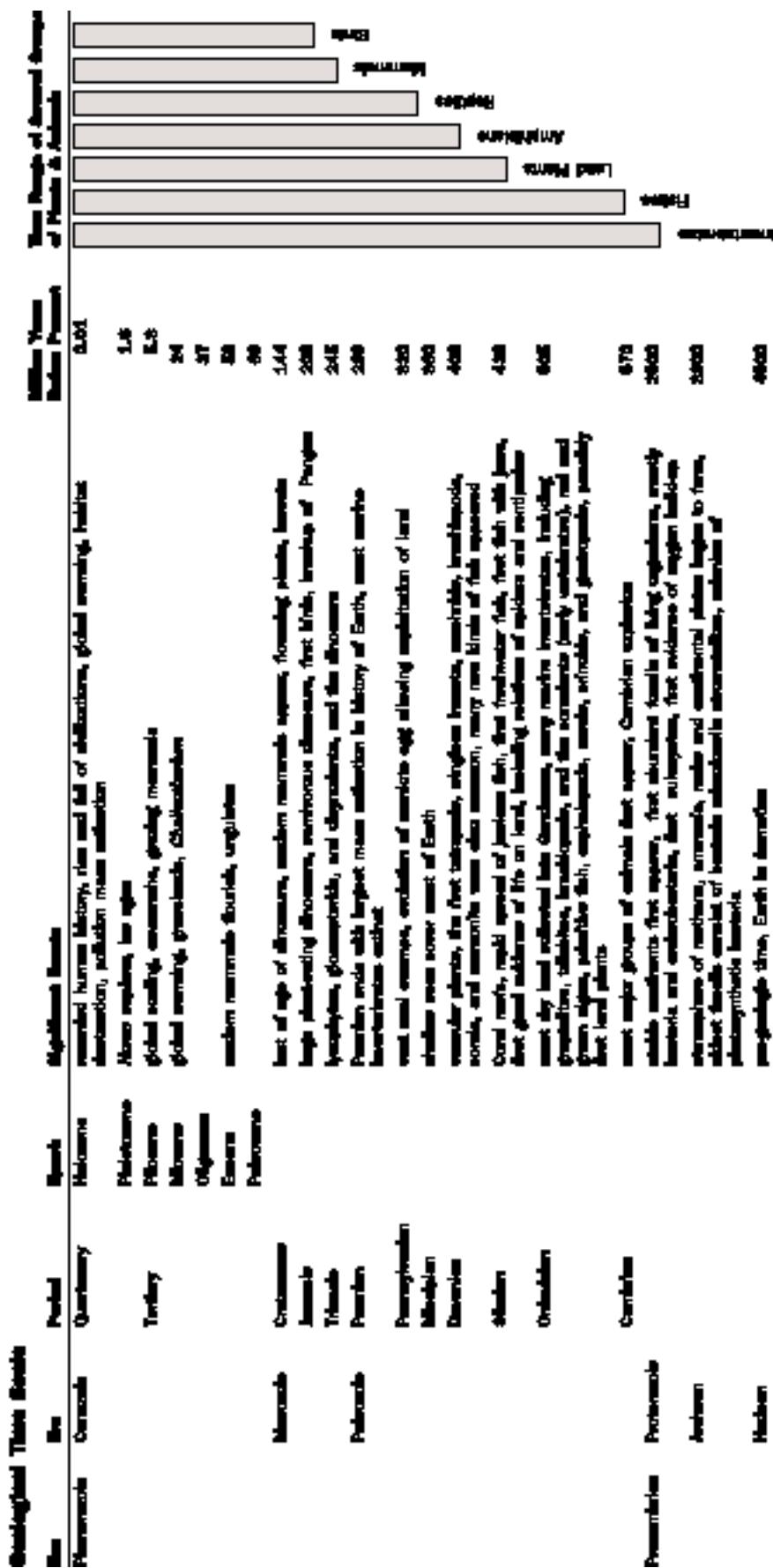
by other animals is converted to human use. One consequence of such socialization is the pollution generated from an expanding human population and its deleterious effect on animal environments.

Animal Sciences also presents biographies of selected scientists who have made significant contributions to the many related fields, and introduces readers to the myriad career opportunities in the discipline.

The authors who contributed entries to *Animal Sciences* represent diverse backgrounds, and include members of academic and research institutions, as well as practicing scientists. The editorial board sought informative, up-to-date, and engaging articles, most of which include cross references, photographs or illustrations that prove helpful in understanding challenging concepts. A generous collection of sidebars accent related subjects. Every attempt has been made to avoid overly technical terms or scientific jargon, and whenever necessary such terms are highlighted and defined in the margin. Selected bibliographies guide readers to additional up-to-date resources, including those found on the Internet. Each of the four volumes also includes a geologic time scale, with particular emphasis on animals, as well as a phylogenetic tree and an alternative table of contents that groups articles under more general topic headings.

I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours in helping guide this project to fruition. I wish to thank the editorial board members—Amy Bryan, Andrew Gluesenkamp, and Marvin Elliot Richmond—for their vast knowledge and hard work. Finally, it is my hope that *Animal Sciences* can spark the interest of the next generation of committed scholars, researchers, and laypersons.

Allan B. Cobb
Editor in Chief

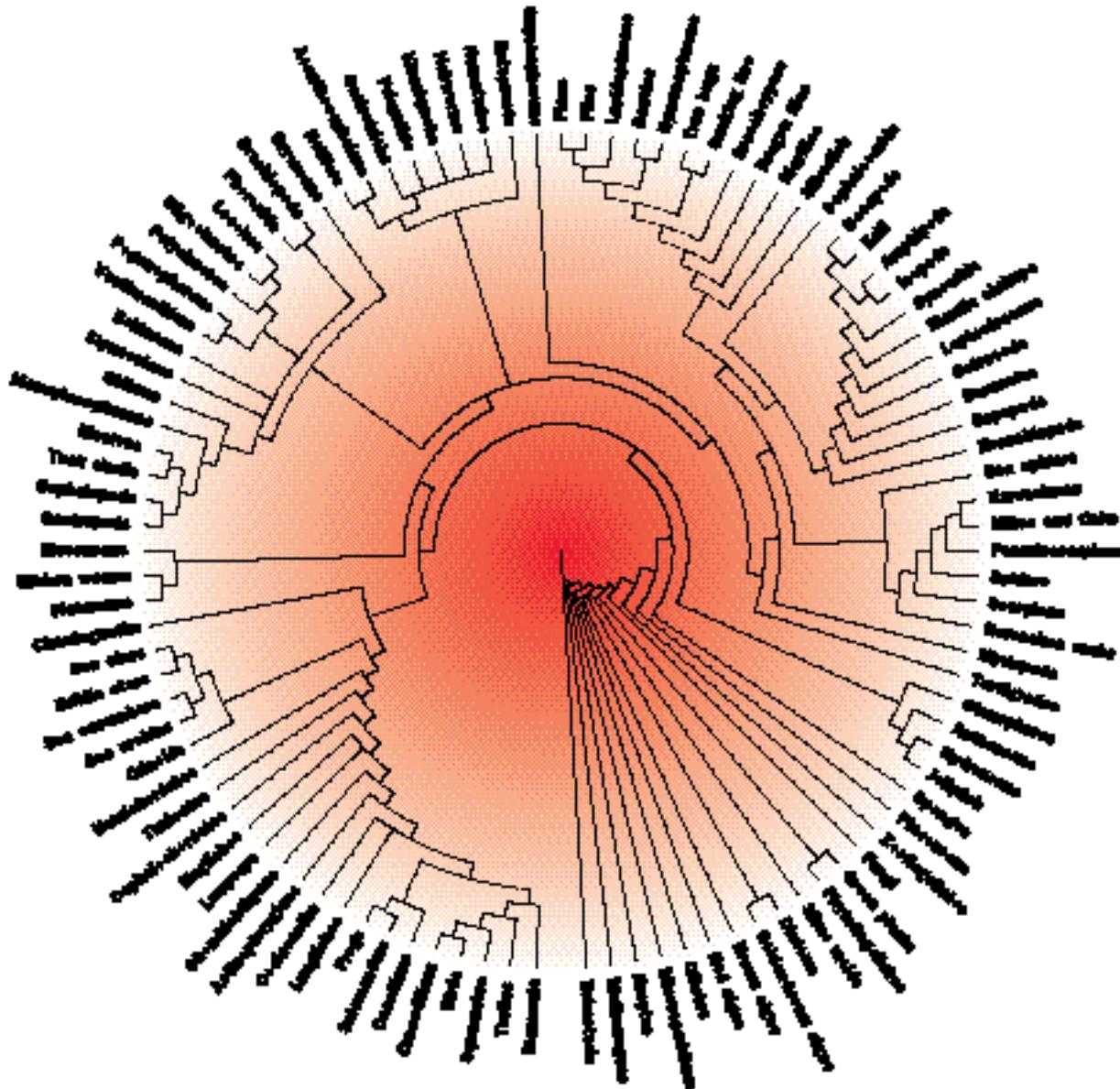


COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom	Six Kingdom
Kingdom: Monera	Kingdom: Archaeabacteria
Phylum: Bacteria	Kingdom: Eubacteria
Phylum: Blue-green algae (cyanobacteria)	
Kingdom: Protista	
Phylum: Protozoans	
Class: Ciliophora	
Class: Mastigophora	
Class: Sarcodina	
Class: Sporozoa	
Phylum: Euglenas	
Phylum: Golden algae and diatoms	
Phylum: Fire or golden brown algae	
Phylum: Green algae	
Phylum: Brown algae	
Phylum: Red algae	
Phylum: Slime molds	
Kingdom: Fungi	
Phylum: Zygomycetes	
Phylum: Ascomycetes	
Phylum: Basidiomycetes	
Kingdom: Plants	
Phylum: Mosses and liverworts	
Phylum: Club mosses	
Phylum: Horsetails	
Phylum: Ferns	
Phylum: Conifers	
Phylum: Cone-bearing desert plants	
Phylum: Cycads	
Phylum: Ginko	
Phylum: Flowering plants	
Subphylum: Dicots (two seed leaves)	
Subphylum: Monocots (single seed leaves)	
Kingdom: Animals	
Phylum: Porifera	
Phylum: Cnidaria	
Phylum: Platyhelminthes	
Phylum: Nematodes	
Phylum: Rotifers	
Phylum: Bryozoa	
Phylum: Brachiopods	
Phylum: Phoronida	
Phylum: Annelids	
Phylum: Mollusks	
Class: Chitons	
Class: Bivalves	
Class: Scaphopoda	
Class: Gastropods	
Class: Cephalopods	
Phylum: Arthropods	
Class: Horseshoe crabs	
Class: Crustaceans	
Class: Arachnids	
Class: Insects	
Class: Millipedes and centipedes	
Phylum: Echinoderms	
Phylum: Hemichordata	
Phylum: Cordates	
Subphylum: Tunicates	
Subphylum: Lancelets	
Subphylum: Vertebrates	
Class: Agnatha (lampreys)	
Class: Sharks and rays	
Class: Bony fishes	
Class: Amphibians	
Class: Reptiles	
Class: Birds	
Class: Mammals	
Order: Monotremes	
Order: Marsupials	
Subclass: Placentals	
Order: Insectivores	
Order: Flying lemurs	
Order: Bats	
Order: Primates (including humans)	
Order: Edentates	
Order: Pangolins	
Order: Lagomorphs	
Order: Rodents	
Order: Cetaceans	
Order: Carnivores	
Order: Seals and walruses	
Order: Aardvark	
Order: Elephants	
Order: Hyraxes	
Order: Sirenians	
Order: Odd-toed ungulates	
Order: Even-toed ungulates	

PHYLOGENETIC TREE OF LIFE

This diagram represents the phylogenetic relationship of living organisms, and is sometimes called a “tree of life.” Often, these diagrams are drawn as a traditional “tree” with “branches” that represent significant changes in the development of a line of organisms. This phylogenetic tree, however, is arranged in a circle to conserve space. The center of the circle represents the earliest form of life. The fewer the branches between the organism’s name and the center of the diagram indicate that it is a “lower” or “simpler” organism. Likewise, an organism with more branches between its name and the center of the diagram indicates a “higher” or “more complex” organism. All of the organism names are written on the outside of the circle to reinforce the idea that all organisms are highly evolved forms of life.



SI BASE AND SUPPLEMENTARY UNIT NAMES AND SYMBOLS

Physical Quality	Name	Symbol
Length	meter	m
Mass	kilogram	kg
Time	second	s
Electric current	ampere	A
Thermodynamic temperature	kelvin	K
Amount of substance	mole	mol
Luminous intensity	candela	cd
Plane angle	radian	rad
Solid angle	steradian	sr

Temperature

Scientists commonly use the Celsius system. Although not recommended for scientific and technical use, earth scientists also use the familiar Fahrenheit temperature scale ($^{\circ}\text{F}$). $1^{\circ}\text{F} = 1.8^{\circ}\text{C}$ or K. The triple point of H_2O , where gas, liquid, and solid water coexist, is 32°F .

- To change from Fahrenheit (F) to Celsius (C):

$$^{\circ}\text{C} = (\text{F}-32)/(1.8)$$
- To change from Celsius (C) to Fahrenheit (F):

$$^{\circ}\text{F} = (^{\circ}\text{C} \times 1.8) + 32$$
- To change from Celsius (C) to Kelvin (K):

$$\text{K} = ^{\circ}\text{C} + 273.15$$
- To change from Fahrenheit (F) to Kelvin (K):

$$\text{K} = (\text{F}-32)/(1.8) + 273.15$$

UNITS DERIVED FROM SI, WITH SPECIAL NAMES AND SYMBOLS

Derived Quantity	Name of SI Unit	Symbol for SI Unit	Expression in Terms of SI Base Units
Frequency	hertz	Hz	s^{-1}
Force	newton	N	m kg s^{-2}
Pressure, stress	Pascal	Pa	$\text{N m}^{-2} = \text{m}^{-1} \text{kg s}^{-2}$
Energy, work, heat	Joule	J	$\text{N m} = \text{m}^2 \text{kg s}^{-2}$
Power, radiant flux	watt	W	$\text{J s}^{-1} = \text{m}^2 \text{kg s}^{-3}$
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	$\text{J C}^{-1} = \text{m}^2 \text{kg s}^{-3} \text{A}^{-1}$
Electric resistance	ohm	–	$\text{V A}^{-1} = \text{m}^2 \text{kg s}^{-3} \text{A}^{-2}$
Celsius temperature	degree Celsius	C	K
Luminous flux	lumen	lm	cd sr
Illuminance	lux	lx	cd sr m^{-2}

UNITS USED WITH SI, WITH NAME, SYMBOL, AND VALUES IN SI UNITS

The following units, not part of the SI, will continue to be used in appropriate contexts (e.g., angstrom):

Physical Quantity	Name of Unit	Symbol for Unit	Value in SI Units
Time	minute	min	60 s
	hour	h	$3,600 \text{ s}$
	day	d	$86,400 \text{ s}$
Plane angle	degree	°	$(\pi/180) \text{ rad}$
	minute	'	$(\pi/10,800) \text{ rad}$
	second	"	$(\pi/648,000) \text{ rad}$
Length	angstrom	Å	10^{-10} m
Volume	liter	l, L	$1 \text{ dm}^3 = 10^{-3} \text{ m}^3$
Mass	ton	t	$1 \text{ mg} = 10^3 \text{ kg}$
	unified atomic mass unit	u ($= m_{\text{a}}(^{12}\text{C})/12$)	$\approx 1.66054 \times 10^{-27} \text{ kg}$
Pressure	bar	bar	$10^5 \text{ Pa} = 10^5 \text{ N m}^{-2}$
Energy	electronvolt	eV ($= e \times V$)	$\approx 1.60218 \times 10^{-19} \text{ J}$

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length	Area	Area	
1 angstrom (Å)	0.1 nanometer (nm ²)	1 acre	43,560 square feet (sq ft) (sq yard)
	0.000000004 inch		0.405 hectares
1 centimeter (cm)	0.3937 inches	1 hectare	2.471 acres
1 foot (ft)	0.3048 meter (m ²)	1 square centimeter (sq cm)	0.156 square inches
1 inch (in)	2.54 centimeters (cm ²)	1 square foot (sq ft)	929,030 square centimeters (cm ²)
1 Kilometer (km)	0.621 miles	1 square inch (sq in)	0.4516 square centimeters (cm ²)
1 meter (m)	39.37 inches	1 square meter (sq m)	247.104 acres
	1,094 yards	1 square kilometer (sq km)	0.386 square miles
1 mile (mi)	1,609.344 meters	1 square meter (sq m)	1.196 square yards
	5,280 feet (ft ²)	1 square mile (sq mi)	20,754 square feet
1 astronomical unit (AU)	1.496679 x 10 ¹¹ cm		268,299 kilometers
1 parsec (pc)	268,264,500 AU		
	3.085678 x 10 ¹⁶ cm		
	3.261,663 light-years		
1 light-year	9.460560 x 10 ¹⁷ cm		

MEASUREMENTS AND ABBREVIATIONS

Volume	Units of mass
1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm ³)	0.001 cubic inch
1 cubic foot (ft ³)	7.481 gallons
	28.316 cubic centimeters
1 cubic inch (in ³)	0.464 fluid ounce
1 dram, fluid (or liquid)	16 fluid ounces (oz ²)
	0.021 cubic inch
	0.007 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (in ³)
	3.785 liters
	128 U.S. fluid ounces (oz ²)
1 gallon (gal) (British Imperial)	277.42 cubic inches
	3.203 U.S. gallons
	4.546 liters
1 liter	1 cubic decimeter (dm ³)
	1.067 liquid ounces
	0.209 dry quart
	0.035 cubic feet
1 ounce, fluid (or liquid)	1.000 cubic inches
	29.573 milliliters
1 ounce, fluid (fl. oz.) (British)	0.001 U.S. fluid ounce
	1.734 cubic inches
	28.413 milliliters
1 quart (qt), dry (U.S.)	37.291 cubic inches
	1.000 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (in ³)
	0.946 liter
	1 liter
	0.00092 atmosphere (atm)
	14.2268 pounds/liquid inch (lb/in ²)
	0.00067 bar

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are levied on a barrel of 53 gallons (3.62 liters); many states have the "barrel for liquors" on 33 1/3 gallons (3,030.3 liters); one state taxes a 35-gallon (1,300.5 liters) barrel for whiskey measurements; federal law recognizes a 49-gallon (378 liters) barrel for "spirit of spirits"; by custom, 42 gallons (1,599 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.



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Habitat Restoration

The human race is in a precarious situation as a result of its exploitation of natural **ecosystems**. Humans must balance their current resource needs with the future land-use needs of wildlife and people. As such, it makes sense to care for **habitats** by reducing damage to them and restoring those that have been damaged. With careful planning, healthy habitats can be maintained for people as well as wildlife. The goal of habitat restoration is to identify disturbed habitats and restore the native **flora** and **fauna** that occur there to ensure the continued use of the land by both wildlife and humans.

Historical Background

Habitat restoration is a recent concept in human history. It began in the early 1900s with the recognition that protective measures must be given to wildlife to ensure its survival. A historical landmark is the Pittman-Robertson Act of 1937, which funds wildlife research and habitat restoration. This act was financed by a tax on sporting arms and ammunition. Hunting and fishing continue to provide revenue for wildlife research today. The Endangered Species Act, which was enacted in 1973, provides protection for wildlife, and organizations such as the National Audubon Society and the Nature Conservancy play important roles in habitat acquisition, restoration, and protection.

The Importance of Habitat Restoration

Habitat restoration seeks to repair areas that have been subjected to habitat destruction. Habitat destruction is one of the primary factors involved in causing species of plants and animals to be threatened with extinction. Activities important to maintaining civilization such as agriculture, development, mining, oil drilling, logging, and road building alter natural ecosystems. Habitat destruction can be obvious, such as clearing old-growth forests for timber and draining wetland areas to use the land for raising crops, but it can also be more insidious. Habitat destruction alters the normal abundance and distribution of species in the habitat. All of these types of disturbances require restoration if the land is to be viable in the future.

Ha

ecosystems self-sustaining collections of organisms and their environments

habitats physical locations where an organism lives in an ecosystem

flora plants

fauna animals

population a group of individuals of one species that live in the same geographic area

acidic having the properties of an acid

riparian habitats in rivers and streams

abiotic factors pertaining to nonliving environmental factors such as temperature, water, and nutrients

biotic factors biological or living aspects of an environment

symbiotic relationships close, long-term relationships where two species live together in direct contact

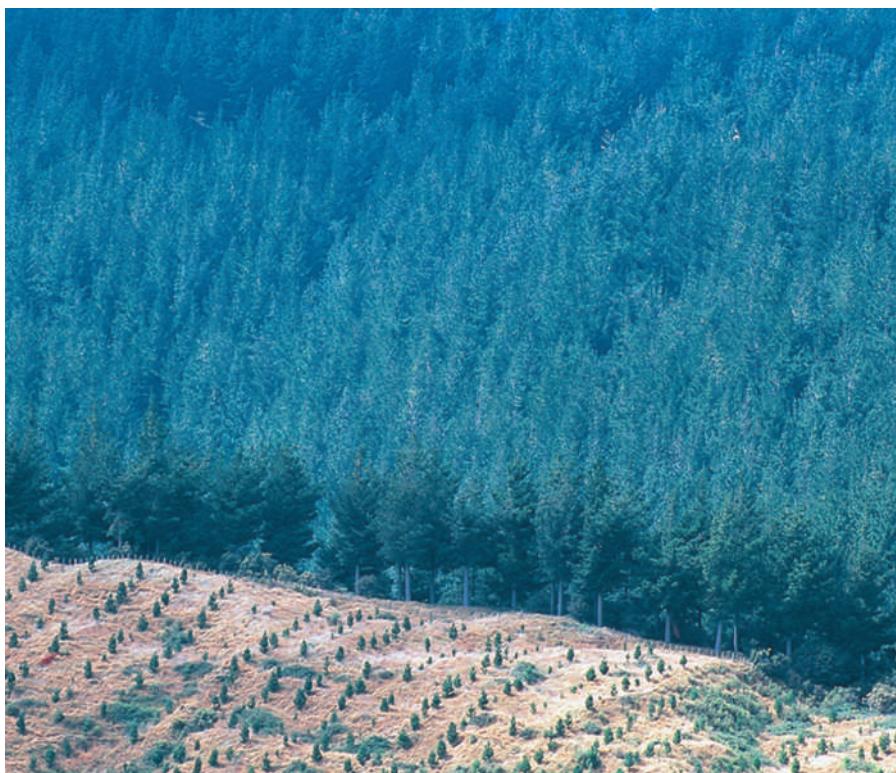
Habitat restoration is important for reasons varying from aesthetic and recreational to economic and pragmatic. Wild lands and wilderness have aesthetic properties that help to maintain mental health for millions of people every year. Restoring habitats can facilitate the return of wildlife to disturbed areas for its own sake or for the sake of recreational activities such as hiking, hunting, fishing, and bird-watching. Returning disturbed land to health can add to existing habitats, making them larger and thereby helping to protect species against the dangers of small **population** sizes. Restoring areas that have been damaged through human use can allow an area to be used again for another purpose. For example, areas that have been mined are often **acidic** and have high heavy-metal concentrations, making it difficult for native plants to be reestablished in the area. Restoring these areas can help to make the habitat healthy again. In the future, the same land could be available for timber harvesting or recreational parkland, or as a wildlife refuge. Healthy forests and **riparian** zones help control erosion and maintain good water quality in streams and lakes. Reforestation and restoring damaged riparian zones helps ensure clean drinking water, control floods, and maintain healthy fish and amphibian populations.

Restoration Methods

Habitat restoration is accomplished through management, protection, and reestablishment of plants by returning **abiotic factors** (e.g., soil chemistry, water content, disturbance) and **biotic factors** (e.g., species composition, interactions among species) to historical levels. Properly restored ecosystems demonstrate the historical species diversity of the area instead of one species in monoculture. Reestablishing plants provides a food source for animals and thus helps restore animal populations.

In reestablishing plants, soil conditions are very important, because they will determine what will grow and where. Soil moisture and mineral content, aeration, and presence of microorganisms are important factors that must be considered. Most plants are associated with fungi called mycorrhizal fungi (also called mycorrhizae), an association that is integral to a plant's system for absorbing nutrients and water. These fungi associate with the roots of the plants and help in gathering and transporting nutrients and minerals to the plant. These **symbiotic relationships** are often species specific, and this makes them essential in reestablishing native plants. Without their symbiotic fungi, many native plants are weak competitors with nonnative species. Therefore, it is often necessary to introduce the correct mycorrhizal fungus into the plants through inoculation. In addition, members of the soil community such as bacteria and earthworms, which create healthy soil food chains and aid in soil aeration, respectively, may also be added to disturbed habitat. Knowledge of the appropriate fungus, bacteria, and worm species for each habitat is necessary. The organisms must also be available for inoculation. In severely disturbed or unique habitats, knowledge of the proper organisms may not exist, or the organisms themselves may unavailable, resulting in an inability to restore the habitat properly.

Situations where the native flora is intact but is not functioning normally because of human activities require management and protection



This forest in Hawkes Bay, New Zealand, had once been cleared for farming purposes, but has been restored to its original composition.

to accomplish restoration. In some cases removal of dense underbrush and thinning young trees is necessary to restore a habitat to health. Another method to restore habitats is controlled fire. In habitats historically subjected to fire, some species require occasional fires to set seed and to thin out young trees that are otherwise stunted as a result of competing for limited resources. Without periodic fire the densely growing trees will be stressed and subject to pest outbreaks that do more damage than the fire.

Drainage patterns and soil water content can be altered to facilitate natural reestablishment of native vegetation. Large earthmoving machines can alter drainage patterns while smaller tools can help shape water movement in the soil. Wetlands can be restored by flooding drained areas. Once the water is in place, revegetation can proceed with species appropriate for the area. Waterfowl and wetland bird species may assist in seed dispersal from nearby wetlands.

Stream habitats may also be restored through appropriate management. For example, flooding can be problematic for inhabitants of small streams, particularly the eggs and young of salmonid fishes in the northwestern United States. Large-scale timber harvesting can add silt to streams, and with fewer trees, heavy rains reach streams more rapidly and with more force. This can lead to the covering of fish eggs by silt, which suffocates them, and the removal of young fish and eggs from protected areas into the main stream channel, which results in increased rates of predation. Restoration projects aimed at redirecting the streambed to slow floods and the placement of in-stream obstructions such as large rocks and logs can prevent these problems while creating spawning habitat at the same time.



Maintenance of adequate riparian zones can eliminate the need for such restoration measures by reducing the impact of floods.

Restoration Difficulties

Habitat restoration is difficult and problems are often encountered. Exotic and invasive species, problematic soils, and variation in populations can make habitat restoration a challenge. Exotic or invasive species may out-compete natives for nutrients in the early stages of restoration. Inoculation with mycorrhizal fungi can alleviate this by helping the natives absorb nutrients, but often the problem persists. This is because habitat destruction releases nutrients into the soil that may be used by the exotic species. Sometimes, fertilizers are added with the intent of helping the native species grow, but the excess nutrients encourage exotic species to grow instead. One solution to this problem is to limit the nutrients available to the exotic species by removing excess nutrients. Removing excess nutrients, not adding them, allows the native species to persist with assistance from their mycorrhizal associates, while not giving the invasive species the nutrients they require to compete with the natives. Subtle differences in moisture, altitude, slope aspect, and other variables over species' ranges may make some restoration projects difficult. Individuals of a species from one area may be difficult to establish in another area because they may be adapted to local conditions.

abiotic nonliving parts of the environment

biotic pertaining to living organisms in an environment

A caveat of habitat restoration is that to do it properly one must have a thorough understanding of the ecological requirements, both **abiotic** and **biotic**, for the species involved. Also necessary for proper restoration is an understanding of historical land-use patterns coupled with the knowledge of what locally similar, pristine habitat looks like. This knowledge can be difficult to collect and can require substantial investment of money, time, and energy. The result, however, is a better understanding of ecosystems, and with this, one can make educated decisions about how to restore habitats. Habitat restoration is important for the health of the planet and the human race, and continued research on ecosystems and restoration techniques is vital.

Restoration need not only take place in rural settings. Suburban gardens of native plants encourage beneficial native insects and bird species that can act as biocontrol for pests. Gardening with native species also conserves water, increases awareness and appreciation of regional diversity, and can create small islands of habitat for local species to use as gateways to larger habitat areas. This type of habitat restoration can be done individually on a local level and can turn the tide from wildlife in a sea of people to people in a sea of wildlife. **SEE ALSO** Ecosystem; Environment; Habitat; Habitat Loss.

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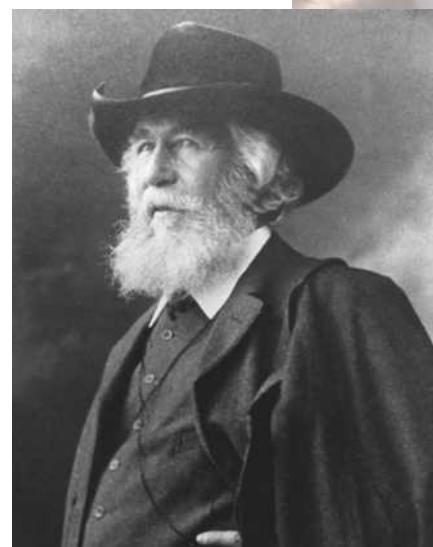
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Haeckel's Law of Recapitulation

German zoologist Ernst Haeckel famously—and inaccurately—uttered, "Ontogeny recapitulates **phylogeny**." While investigating the developing embryos of a variety of **vertebrates**, Haeckel thought they all closely resembled one another. This observation led to his conclusion that embryonic development echoed **morphological** evolution. Specifically, gill depressions in human embryos led Haeckel to conclude that humans were derived from fishes. He therefore felt that the study of embryonic development, or **ontogeny**, retold the story of evolution, or phylogeny. As he wrote in 1866, "During its rapid evolution, an individual repeats the most important changes in form evolved by its ancestors during their long and slow paleontological development." (Haeckel)

There are a number of flaws with Haeckel's theory. For example, Haeckel confused a fish embryo with a young human one. Haeckel's drawings strongly suggest that a variety of vertebrates share a common developmental phase, but he does not account for the entire process of development, nor does he compensate for size differences. His drawings were grossly oversimplified and ignored or obfuscated many salient differences. This did not stop Haeckel's law from being widely accepted for the majority of the twentieth century. Many otherwise up-to-date textbooks, such as *Molecular Biology of the Cell*, written in 1994 by Nobel laureate James Watson and National Academy of Sciences President Bruce Alberts, continue to cite Haeckel.

In 1997 a group headed by Michael Richardson of St. George's Hospital Medical School in London published a serious investigation of Haeckel's claims. Photographs of a variety of vertebrate embryos showed conclusively that, despite some similarities, there is no stage in vertebrate development when all embryos are identical. That said, there are definitely some common features among developing vertebrates. In the nineteenth century, embryologist K. E. von Baer wrote, "The embryo of the mammal, bird, lizard, and snake and probably also the turtle, are in their early stages so uncommonly similar to one another that one can distinguish them only according to their size" (Richards 1992). Common structures do not imply that vertebrate development retells the story of evolution.



Ernst Haeckel incorrectly stated, "Ontogeny recapitulates phylogeny."

phylogeny the evolutionary history of a species or group of related species

vertebrates animals with a backbone

morphological the structure and form of an organism at any stage in its life history

ontogeny the embryonic development of an organism





natural selection

process by which organisms best suited to their environment are most likely to survive and reproduce

fertilization the fusion of male and female gametes



John Burdon Sanderson Haldane made several important discoveries about human physiology and respiration.

Haeckel was a strong supporter of evolution, particularly after reading Charles Darwin's *The Origin of Species*. However, Darwin argued that **natural selection** was the mechanism that advanced evolution. Haeckel's view was that developing embryos strove to meet the needs of their environment by adding more and more complex structures. Examining Haeckel's law, one could conclude that it is possible to reach backwards through development and find the alleged evolutionary forerunner of all vertebrates. In normal development, a ball of cells known as a gastrula develops soon after **fertilization** and eventually becomes the gut. As each embryonic stage was supposed to represent another species, Haeckel postulated the existence of a "gastraea"—an organism that resembled the gastrula and was, by extension, the ancestor of all the vertebrates.

Despite mainstream acceptance of Haeckel's ideas, gastraea do not exist. Nor does evolution advance by adding traits to developing embryos. While there are definite similarities among developing vertebrates, Haeckel's famous utterance can be safely dismissed. Despite the acceptance he found elsewhere, scientists in Haeckel's native Germany considered his findings suspect. He was accused of academic fraud and pled guilty, claiming that many of his drawings were reproduced from memory. When comparing photographs of actual embryos to the drawings, however, one could conclude that Haeckel remembered only one embryo and claimed that all vertebrates looked just like it. As Michael Richardson said, "These are fakes. In the paper, we call them 'misleading and inaccurate,' but that is just polite scientific language" (*Times* London, August 11, 1997). SEE ALSO ONTOGENY; PHYLOGENETICS SYSTEMATICS.

Ian Quigley

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Times (London), August 11, 1997.

Haldane, J. B. S.

Geneticist

1892–1964

John Burdon Sanderson Haldane was born on November 5, 1892. His father, John Scott Haldane, was a physiologist at Oxford University who worked on respiration and contributed to the safety of miners. The elder Haldane encouraged his son to assist him, and he was soon bringing the child down mine shafts during his experiments to prove that the air in them was breathable.

Haldane attended New College at Oxford on a mathematical scholarship and worked with the rediscovered laws of Mendelian **genetics**. It was while experimenting on his sister Naomi's guinea pig colony that he discovered genetic linkage. About the same time, in 1912, Haldane published his first of some 400 scientific articles, on **hemoglobin** binding of carbon monoxide.

One of Haldane's specialties was the **physiology** of gas **absorption** and binding in humans. He frequently experimented on himself and his second wife, Dr. Helen Spurway. To assess carbon dioxide regulation of blood pH, for example, he ingested large quantities of sodium bicarbonate to make his blood basic or ammonium chloride to make it more **acidic**. He inhaled the highly toxic carbon monoxide and described its effects.

Aside from his work in human physiology and respiration, Haldane created the discipline of population genetics nearly single-handedly, starting with the publication of *The Causes of Evolution*, in 1932. He laid down the foundations for **enzyme** kinetics in 1930 with *Enzymes*. He also studied biochemical genetics and human genetics, discovering what effects ionizing radiation had on humans.

Haldane postulated that the early Earth might be able to produce life-supporting molecules such as nucleic acids from **abiotic** processes. The theory was later shown to be true. At New College, he was a fellow in physiology. And he occupied the chair of **biometry** at University College, London, for twenty years (1937–1957). Haldane also served as an editor for the influential *Journal of Genetics* for seventeen years (1947–1964). Before his death, in 1964, he studied tropical biology in India. Despite his monumental contributions to physiology, genetics, enzyme kinetics, and biochemistry, Haldane never held a science degree or any scientific certification from Oxford.

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Many of Haldane's gas absorption experiments were designed to help the British Navy and its divers. Haldane lost two teeth, which exploded due to the rapid decompression in his sinuses, during one experiment.

genetics the branch of biology that studies heredity

hemoglobin an iron containing protein found in red blood cells that binds with oxygen

physiology the study of the normal function of living things or their parts

absorption the movement of water and nutrients

abiotic nonliving parts of the environment

enzyme a protein that acts as a catalyst to start a biochemical reaction

acidic having the properties of an acid

biometry the biological application of statistics to biology

Herpetology

Herpetology is the study of amphibians and reptiles. The scientists who study these animals are called herpetologists. They research the structure, physiology, and behavior of these animals, as well as how they live and are related to one another. Medical researchers have been able to gain valuable knowledge from the study of these animals because they are able to survive well in captivity and they can survive operations that would kill many birds and mammals. Herpetological research also includes the extraction and biochemical study of venoms—a growing subspecialty. Because of their unique biochemistry, some venoms hold great promise as therapies for incurable or chronic diseases.

The field of herpetology appears to stem from the ancient tendency to group all creeping animals together. The Greek word *herpeton* means “crawling thing.” Modern herpetology, as a popular and important science, tends



to focus more narrowly on issues specific to orders or suborders of animals (e.g., the global decline of frog populations). Most technical research in herpetology is carried out in the field or at universities.

Herpetologists may work in zoos or for wildlife agencies, do environmental assessments, care for museum collections, or teach the public in a museum setting. Some herpetologists work as writers, photographers, or animal breeders. The majority of herpetologists work as professors or researchers in colleges and universities. While most herpetologists do have a doctorate, there have been some cases where novices were so renowned for their expertise, that they were invited to teach at the college and university level. Smaller colleges may hire teachers with a master's degree. Herpetologists with an entrepreneurial spirit may go into business for themselves, breeding and selling amphibians and reptiles, or marketing related herpetological merchandise and publications. **SEE ALSO** AMPHIBIA, REPTILIA.

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Heterochrony

allometry relative growth of one part of an organism with reference to another part

somatic having to do with the body

Heterochrony—literally, “different timing”—describes the occurrence of a change in the timing of the development of different body parts between an ancestor and its descendants. The concept of heterochrony is intimately associated with **allometry**, which describes the relationship between the size of different structures or organs of an organism throughout its life; both concepts involve the study of growth patterns.

Describing Heterochrony

Heterochronic phenomena may be described with respect to **somatic** (body) and gonadal (reproductive) maturation and may be global (affecting the entire individual) or local (affecting only one structure, organ, or system). Further, the growth of a structure or organ may be isometric with respect to other structures (shape does not change with growth) or it may follow either a positive or negative allometric path (shape changes with growth). Finally, different kinds of heterochronies can occur in different parts of the body, producing ontogenies (courses of development in an organism) that are “dissociated” or “mosaic.” That is, some aspects of development are accelerated while others are retarded. Any change in a body part’s growth rate relative to that of other structures is described as either acceleration or retardation (also called neoteny).

Classes of Heterochronic Development

Developmental heterochronic phenomena result in either paedomorphosis or peramorphosis. Paedomorphosis describes the retention of juvenile traits in a structure (the trait in the descendant resembles that of juveniles in the ancestor). Peramorphosis describes cases where a trait in the descendant has a more extreme morphology than in its ancestor.



The axolotl, a type of salamander, has feathery appendages that have evolved from its ancestors by heterochrony.

Heterochrony can be further classified in terms of changes in the length of the duration, rate, or timing of events in **ontogeny**. Change in the duration of growth without any change in rate or timing is described as hypermorphosis (increased period of somatic growth with respect to gonadal development) or progenesis (decreased period of somatic growth with respect to gonadal development). Change in the timing at which growth of a structure occurs is described as predisplacement (onset of growth occurs earlier in ontogeny) or postdisplacement (onset of growth occurs later in ontogeny).

ontogeny the embryonic development of an organism

Effects of Heterochronic Changes

Heterochronic changes are often driven by selection on life history traits. For example, some species may be under selection to reproduce at an earlier age than others and correlate with paedomorphic or hypermorphic results. Paedomorphosis by means of progenesis (structures stop developing at an earlier stage than in the ancestral ontogeny) may occur when there is selection for rapid maturation. Paedomorphosis is frequently associated with small adult size in many groups of animals (some tiny **salamanders** have simplified skeletons that are reminiscent of earlier developmental stages in their ancestors). Paedomorphosis via neoteny often results from selection operating under particular stable larval environments.

salamanders four-legged amphibians with elongated bodies

Peramorphosis via hypermorphosis can result from selection for increased body size or **sexual selection** and may result in exaggerated features. The relatively more elaborate antlers of some large deer species compared to those of smaller, ancestral species are hypermorphic. Peramorphosis by acceleration can result from selection for acceleration of prenatal growth. An example of peramorphosis via acceleration is the rapid larval development of many desert-adapted frogs (including the spadefoot toads of the American Southwest), which breed in temporary pools of water. Some species can transform from egg to froglet in less than three weeks compared to the three months required in many species whose tadpoles live in more stable environments.

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

Predisplacement (initiation of development of a structure occurs earlier in development in the descendant than in the ancestor) may occur in



aquatic living in water

metamorphose to change drastically from a larva to an adult

metamorphosis to change drastically from a larva to an adult

gills site of gas exchange between the blood of aquatic animals such as fish and the water

lungs sac-like, spongy organs where gas exchange takes place

terrestrial living on land

genetics the branch of biology that studies heredity

mutations abrupt changes in the genes of an organism

response to selection in unstable larval environments. In some frog species, adult skull structures may begin to form during the larval stage depending on the availability of food. The presence of these structures allows the tadpoles to eat larger food items, including other tadpoles. This development expands the range of food the tadpole is capable of consuming, therefore increasing its chances of survival.

Perhaps the best known example of heterochrony in nature is the axolotl, an **aquatic** salamander from Mexico. Axolotls were not thought to be salamanders until 1863, when some individuals on display at the Natural History Museum in Paris began to **metamorphose** (probably because of some environmental stress associated with their conditions in captivity). Ordinarily, amphibians undergo **metamorphosis** from egg to larva, and finally, to the adult form. The axolotl, along with a number of other amphibians, remains in its larval form, meaning that it retains its **gills** and fins and doesn't develop protruding eyes, eyelids, and characteristics of other adult salamanders. It reaches sexual maturity in the larval stage. The axolotl is completely aquatic, and although it possesses rudimentary **lungs**, it breathes primarily through its gills and to a lesser extent, the skin. This species descended from a **terrestrial** ancestor with an aquatic larval stage (probably the tiger salamander, *Ambystoma tigrinum*). These salamanders were historically found in lakes with relatively constant temperatures, abundant food sources, and no competition from or predation by fish. Unfortunately, introduced predatory fish and heavy pollution threaten most wild populations. The unusual life history and large eggs of this species make it an excellent organism for studies of **genetics** and development, and large colonies are maintained in universities and research institutions throughout the world.

Conclusion

Identification of heterochronic phenomena requires a hypothesis of relationships among the life-forms being considered and information on the development patterns of the ancestor and descendant. Detailed information on the duration, timing, and rate of developmental phenomena in both the ancestral and descendant ontogeny may be required to discriminate between various types of paedomorphosis and peramorphosis. **Mutations** causing heterochronic changes play an important role in evolution and developmental constraints and can result in powerful relationships between the processes of embryonic development and the resulting evolutionary history. **SEE ALSO** ALLOMETRY; EMBRYONIC DEVELOPMENT; ONTOGENY; PHYLOGENETICS SYSTEMATICS.

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Home Range

In the course of its daily activities, an animal travels through familiar places to obtain food, seek shelter, or find mates. The actual physical area covered in the course of these regular movements is the animal's home range. An animal's familiarity with the features of its home range allows it to forage efficiently and escape predators when necessary. For example, a house cat in its home range may begin to stalk as it approaches a familiar birdfeeder even if it cannot tell whether there are birds on the feeder. The cat has learned that the birdfeeder is a reliable source of prey and behaves accordingly. An individual animal, a mated pair, a family, or a group of families may occupy a given home range, and home ranges of several individuals or groups may overlap. Animals do not defend the boundaries of their home ranges against intruders of their own species. An area that is defended is called a territory, and is usually a smaller area within an animal's home range. Some species may carry out all their daily activities within a defended territory, especially during the breeding season. In this case, territory is equivalent to home range.

An animal's need for resources and the distribution of resources in the environment determine the size of its home range. This general ecological trend is known as the resource dispersion hypothesis. When resources are sparsely distributed, an individual must travel farther to obtain the same amount of food as an individual of the same species living in a **habitat** where food resources are concentrated. Variation in the sizes of home ranges within species reflects the quality of the habitat; home ranges will be smaller in resource-rich habitats and larger in those that are resource-poor.

The size of an animal's home range is directly affected by its body size. Large animals generally require large amounts of food and therefore have larger home ranges than individuals or species that are smaller but eat the same types of food. The type of resources an animal requires also greatly influences the size of its home range. For example, **herbivores** have smaller home ranges than omnivores of the same size: The leaves and grass that herbivores eat tend to be easier to find than the fruits and seeds more common in an **omnivorous** diet. Similarly, omnivores have smaller home ranges than carnivores of the same body size. The prey of carnivores are distributed even more sparsely than the food of omnivores, so carnivores must cover greater distances to meet their resource needs.

Social systems can also influence the size of a home range. In some species, such as voles (*Microtis* sp.), males do not care for offspring but instead travel among the home ranges of multiple females seeking mates. In a classic experiment testing the factors that determine home ranges, researchers placed female voles in movable enclosures mimicking a home range and then monitored the movements of uncaged males. When the females were close together, males had small home ranges. When females were farther apart, males increased the size of their home range. Another experiment showed that free-ranging females do not change the size of their home ranges when caged males are close together or far apart. The home range size of female voles is determined by the dispersion of resources, but the home range size of males is determined by the dispersion of females.



A grizzly bear debarks a tree in the La-Sal Mountains in Utah. Animals move about in their home range, a comfortable environment in which to forage and evade predators efficiently.

habitat physical location where an organism lives in an ecosystem

herbivores animals who eat plants only

omnivorous eating both plants and animals





habitat requirement
the necessary conditions or resources needed by an organism in its habitat

ecology the study of how organisms interact with their environment

In general, scientists measure a home range by plotting the movements of an individual onto a map over an extended period of time, often several months or years. This plotting can be done by watching the movements of an animal, capturing and recapturing marked individuals in a grid of traps, or by monitoring individuals with radiotelemetry. Radiotelemetry is a tracking technique in which a scientist attaches a signal-emitting transmitter to an animal which is then released. Using an antenna and receiver, the scientist can then locate the unique signal frequency emitted by an individual's transmitter and follow that animal's movements in the wild. The resulting map of points shows the major activity areas of the study animal, but is not completely precise. An animal will not necessarily visit all areas of its home range during the observation period, and not all areas of the home range will be equally important. For example, a bobcat might spend very little time at a pond in its home range, indicating that fresh water is not very important, yet the availability of fresh water is a key **habitat requirement** of the species. Many mathematical approaches can be used to analyze home range data, but all approaches have the underlying goal of estimating the probability that an animal will be found in a particular place. Studies of home range are an important part of the science of **ecology** and can provide insight into the social organization, foraging behavior, limiting resources (those resources that limit the number of individuals that can live in a particular area), and habitat requirements of animals. SEE ALSO **FORAGING STRATEGIES; HABITAT**.

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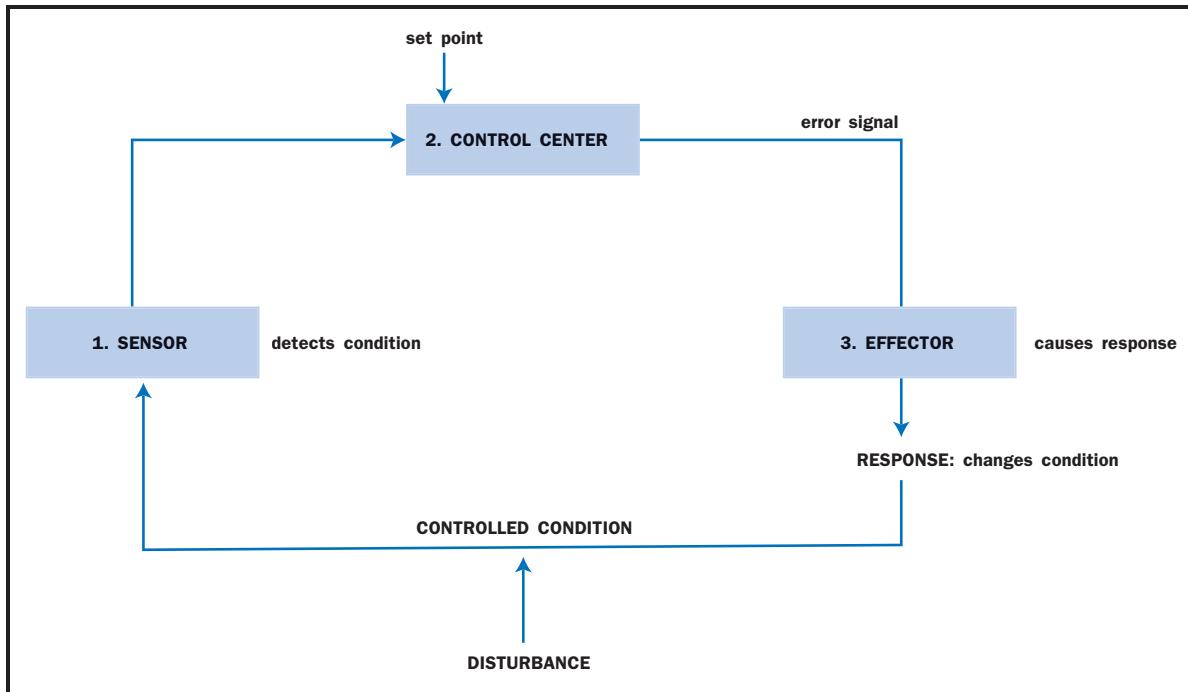
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Homeostasis

In 1865 French physiologist Claude Bernard pointed out that in order for an organism to survive, a constant, or stable, internal environment was required. Based on this insight, and more than half a century later, in 1929, a physiologist from Harvard University, Walter B. Cannon, coined the term "homeostasis." Homeostasis means a stable state of the internal environment that is maintained by regulatory processes despite changes that may occur in the external environment.

Like the first animals to evolve, simple animals such as sponges and jellyfish have a body wall that is only a few cell layers thick, and each cell has direct access to the external environment. As a result, cells can take up nutrients and dispose of wastes by direct exchange with the external environment, but they are also directly exposed to fluctuations in that external environment. Such fluctuations (e.g., in ion concentrations or temperature),



will affect the ability of the cells to perform the chemical processes necessary for survival, and therefore restrict the occurrence of these simple animals to more favorable environments.

Homeostatic feedback diagram.

When animals evolved that had a bulkier shape (like earthworms, fish, or humans today), only some of their cells were still in contact with the external environment. This required specializations such as a digestive system to bring food inside the body for digestion, and a circulatory system to disperse the nutrients to all the cells. The big advantage was that these internal cells were no longer directly exposed to the external environment but were surrounded by extracellular fluid creating an internal environment. Living cells can thrive in certain kinds of conditions and not in others. Various homeostatic control mechanisms regulating the internal environment can now cooperate to maintain the optimal conditions, independent from the external environment. This allows these animals to thrive in areas with less favorable external conditions. Homeostatic regulation of the extracellular fluid can include ion composition, pH levels, oxygen and carbon dioxide levels, nutrient and waste product levels, as well as temperature.

When studying the physiology (structure and function) of animals, scientists are often concerned with the question of how the animals maintain homeostasis. Homeostatic control relies on negative feedback. This means that any deviation from the desired state of the internal environment will be reduced (hence negative) as a result of homeostatic control and bring the internal environment back to the desired state (e.g., regulation of body temperature).

This is in contrast to positive feedback that would enhance (hence positive) the difference leading to an escalation (e.g., child birth). Positive feedback is not useful for the homeostatic control of the internal environment.

There are three main structures that are part of all homeostatic control systems (see homeostatic feedback diagram): (1) sensors that sense the



endocrine system the grouping of organs or glands that secrete hormones into the bloodstream

enzymes proteins that act as catalysts to start biochemical reactions

neurons nerve cells

hypothalamus part of the upper end of the brain stem that regulates activities in the nervous and endocrine systems

action potentials rapid changes in the electric charge of the cell membrane

skeletal muscles muscles attached to the bones; are responsible for movement

actual state of the condition that is being controlled. This information is passed on to the (2) control center, which compares the information from the sensors with the stored information, or set point, about what the condition should be. When the information from the sensors differs from the stored set point, the control center will send an error signal to (3) effectors to trigger an adequate response that will lead to a change in the controlled condition and bring it closer to the set point. When a difference between the controlled condition and the set point is no longer registered by the control center, the error signal ceases, and homeostasis is maintained until another disturbance causes a change in the controlled condition.

The nervous system and the **endocrine system** play a major role in homeostatic control by relaying the signals from the sensors to the control center and from the control center to the effectors.

An important example of homeostatic control is temperature regulation. Cellular processes are temperature dependent. For example, protein **enzymes** that catalyze the chemical reactions in cells have a preferred temperature range at which they perform optimally. Lower temperatures will slow them down, higher temperature may destroy them. Mammals and birds are two animal groups that have evolved the ability to maintain a stable body temperature independent of the environmental conditions (endothermy). This allows them to be active in environments over a wide temperature range. Humans normally regulate their body core temperature in a relatively narrow range (between 36 and 39°C [96.8° and 102.2°F]). To maintain this temperature, heat production has to balance heat loss. Homeostatic control of body temperature ensures that heat production and heat loss are approximately equal.

For example, when humans exercise, the muscle activity generates a lot of heat as a byproduct of muscle contraction. This additional heat (disturbance) will increase the body core temperature (controlled condition). The temperature is monitored by temperature sensors, and this information is passed on by **neurons** to a specific brain region, the **hypothalamus** (the temperature control center). If the core temperature exceeds the desired temperature (set point), an error signal is generated by the control center. This error signal in the form of **action potentials** (electric signals that travel along neurons) triggers sweat glands (effectors) to secrete sweat over the body surface (response). The evaporation of sweat leads to cooling off of the body surface. When heat loss through evaporation balances heat gain through exercise, a stable core temperature (and temperature homeostasis) will be maintained.

When humans experience severe heat loss (disturbance), the body temperature (controlled condition) monitored by the sensors drops below the desired temperature (set point). As a result, the hypothalamus (control center) sends action potentials (error signal) to **skeletal muscles** (effectors) to trigger muscle contractions and cause shivering (response). As a byproduct of this muscle activity heat is produced. When heat gain through shivering balances heat loss a stable core temperature (and temperature homeostasis) will be maintained. SEE ALSO ALLOMETRY; CELLS; FUNCTIONAL MORPHOLOGY.

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Homology

The term “homology” was defined in 1843 by Richard Owen, a noted British paleontologist, as the “same organ under every variety of form and function.” Thus **homologous** structures can be defined in an evolutionary context as elements whose similarity in various **taxa** derives from their common origin in a shared ancestor. Homology may be based on:

1. similarities in structure, or how an organ is shaped;
2. topography, or the location of an organ;
3. associations with other structures, an example of which would be bone–muscle relationships;
4. development, including shared expression patterns of homologous **genes**.

The concept of homology is fundamental to comparative biology and **phylogenetics** systematics. Homology has historically been defined in terms of inheritance of a structure, with more or less modification, from a common ancestor. In this sense, attributes of two organisms are homologous when they are derived from an equivalent characteristic of the common ancestor. For example, whale flippers, bat wings, and human hands are homologous with respect to one another despite obvious differences in size, structure, and function. Whales, bats, and humans are descendants of a common mammalian ancestor, and their specialized appendages are simply modifications of the ancestral forelimb.

If two or more species have a similar trait that was not inherited from their common ancestor, the traits are said to be **homoplastic**. For example, insect wings, bird wings, and bat wings are considered to be homoplastic with respect to one another despite that they are all specialized appendages used for flight. The common ancestor of insects and **amniotes** (terrestrial vertebrates, including mammals and birds) did not have wings. Specialized appendages used in flight have evolved several times independently in the history of **metazoans** (multicellular animals). The developmental origins and underlying structural patterns are very different in these two groups of organisms. Insects and amniotes acquire wings in different ways during development and, despite similarities in the early development of bats and birds, the common ancestor of birds and bats did not have wings but rather some other type of forelimb. In addition, insect wings are foils made up primarily of **chitin**, a type of tissue, while bird and bat wings are highly complex with various tissue types organized into different structures such as feathers, skin, bone, muscle, and nerves.

The question of whether an identical trait shared by two or more taxa is the result of homology or homoplasy usually cannot be decided based on a single character alone. In the above examples, one might be misled by grouping organisms based solely on the presence or absence of “wings.” Rather, multiple characters are needed to provide an accurate hypothesis of relationships. Whales, bats, and humans have many more traits in common than are shared by bats, birds, and insects despite the fact that the latter three have wings. Therefore, mammals are considered to be a natural group and the forelimbs of mammals are considered homologous, whereas the wings of birds, bats, and insects (an unnatural group whose members do not

homologous similar but not identical

taxa named taxonomic units at any given level

genes segments of DNA located on chromosomes that direct protein production

phylogenetic relating to the evolutionary history of species or group of related species

homoplastic similar but of different origins

amniotes vertebrates that have a fluid-filled sac that surrounds the embryo

metazoans a subphylum of animals that have many cells and some are organized into tissues

chitin a complex carbohydrate found in the exoskeleton of some animals



share a common, winged ancestor) are considered homoplastic. It is the pattern of relationships among taxa with the trait in question that determines the nature of the similarity. **SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS; PHYLOGENETICS SYSTEMATICS.**

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Hormones

A hormone is a chemical that is produced in one tissue and transported via the circulatory system to a different target tissue. There, it causes a physiological change in the target.

endocrine system the grouping of organs or glands that secrete hormones into the bloodstream

equilibrium a state of balance

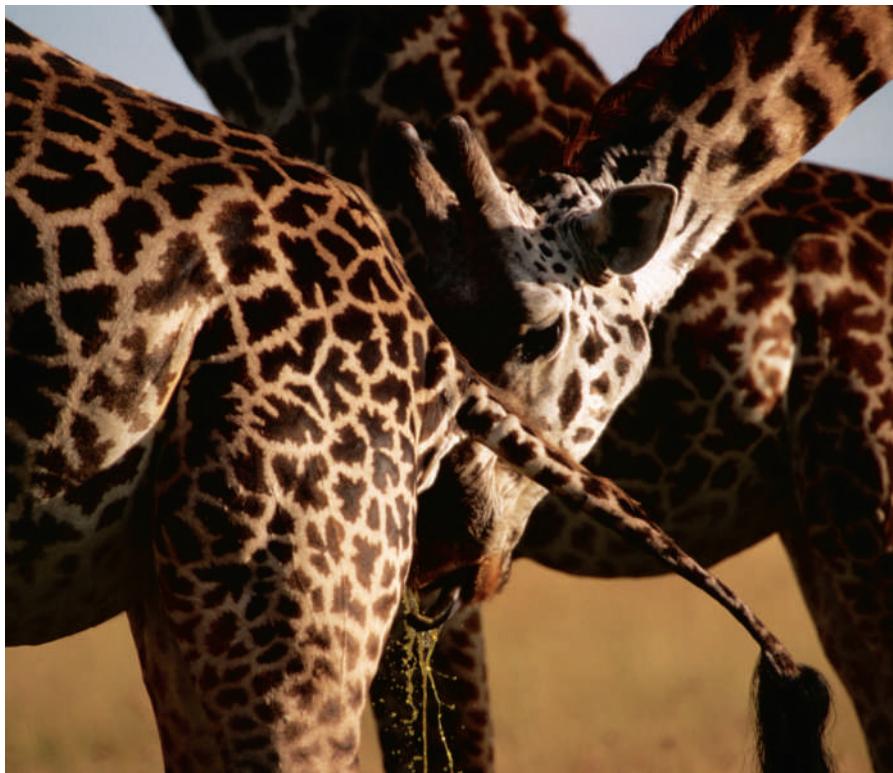
Hormones are the chemical messengers of the **endocrine system**. The endocrine system also includes the ductless glands that synthesize and secrete hormones, and incorporates the responding target cells as well. Hormones are secreted by endocrine glands directly into the circulatory system, from which they contact nearly all cells of the body. Some endocrine glands, such as the adrenal glands, form organs of their own, while others are just parts of organs. The brain, for example, performs certain critical endocrine functions.

The endocrine system is one of two physiological systems responsible for the control of all biological processes. The other is the nervous system. While the nervous system controls specific, rapid biological responses, often to external stimuli, endocrine control generally involves comparatively broad, long-term, gradual physiological processes.

The endocrine system is essential to diverse aspects of an organism's biology, including its development, growth, reproduction, metabolism, water and ionic balance, and maintenance of homeostasis (internal **equilibrium**). In general, animal species that are characterized by well-developed nervous and circulatory systems also possess endocrine control systems.

Because hormones are transported through the circulatory system, they come into contact with all cells and are able to affect numerous tissues simultaneously. Some hormones affect a wide variety of tissues. The sex hormone testosterone, for example, affects multiple parts of the body, whereas others have a considerably more limited effect.

Only cells that possess receptors specific to a hormone will respond to its presence. In addition, depending on the hormone receptor and the pathway coupled to it, different tissues can respond to the same hormone in different ways. Thus, despite their relatively low concentrations in the bloodstream, hormones can have dramatic effects on an organism's physiology.



A male giraffe sniffs a urinating female giraffe to test the hormone level of the female in the wilderness of Kenya.



The Two Major Hormone Groups

Hormones have been divided into two major groups that differ in their biochemical attributes, as well as in the mechanisms by which they affect the activity of target cells. These are steroid hormones and peptide hormones.

Steroid hormones are synthesized by endocrine glands in the gonads (ovaries and testes) and adrenal cortex. They are not stored but, rather, secreted into the circulatory system as soon as they are synthesized.

Steroid hormones are derived from cholesterol and are lipid soluble. Lipid solubility enables steroid hormones to cross cell membranes and enter directly into the **cytoplasm**. Once there, hormone molecules bind to cytoplasmic receptors, cross the nuclear membrane, and interact directly with DNA to affect cellular activity. Some well-known steroids are estrogen and testosterone.

cytoplasm a fluid in eukaryotes that surround the nucleus and organelles

Peptide hormones, on the other hand, are proteins and composed of amino acids. Peptide hormones are water soluble and range greatly in size. They are synthesized in endocrine cells and then stored in vesicles within the cell for secretion later.

Peptides are the more diverse group of hormones by far. Unlike steroids, peptide hormones are not lipid soluble and do not penetrate their target cells directly. Instead, they function via what is referred to as a second messenger pathway. The hormone binds to a receptor protein on the target cell membrane, which then signals a second messenger within the cellular cytoplasm. This second messenger initiates an **enzyme** cascade, which affects

enzyme a protein that acts as a catalyst to start a biochemical reaction



anterior pituitary the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

circadian rhythms
daily, 24-hour cycles of behavior in response to internal biological cues

posterior behind or the back

the activity of the cell. Examples of second messengers involved in peptide hormone function include cyclic AMP and inositol triphosphate.

Endocrine Control

The maintenance of appropriate hormone concentrations in the bloodstream is absolutely critical. Numerous diseases result from hormone levels that are too high or too low. Diabetes is one well-known example.

Feedback systems are often used to regulate hormone synthesis and secretion. Some of these cycles can be extremely complex, involving numerous hormones and endocrine glands.

A particularly well-studied example is the control of thyroid hormone levels. The hypothalamus, an endocrine organ in the brain, secretes a hormone called the thyroid-releasing hormone (TRH). TRH targets the **anterior pituitary**, which responds by secreting thyroid-stimulating hormone (TSH).

TSH targets the thyroid, inducing it to secrete the thyroid hormones known as T3 and T4. However, when T3 and T4 reach a certain concentration in the bloodstream, they act on the hypothalamus, inhibiting it from secreting more TRH. As a result, TSH is no longer secreted, and T3 and T4 secretion is also terminated. This type of negative feedback is common in endocrine regulation. When the levels of thyroid hormones fall below a certain concentration in the bloodstream, the inhibitory, or restraining, effect on the hypothalamus is removed.

The hypothalamus and the anterior pituitary (which is often referred to as the master gland) are critical to endocrine control because many of the hormones they produce affect the activity of other endocrine glands. The hypothalamus is located at the base of the middle portion of the brain, and the pituitary lies immediately below it. The two are directly connected by blood vessels, an unusual organization of the circulatory system referred to as a portal system. The portal system allows for the direct and efficient transport of hormones from the hypothalamus to targets within the pituitary.

Other hormones are under cyclical control. Cycles can be short, lasting hours, or much longer, spanning several months. Melatonin is a hormone produced by the pineal gland whose level follows a daily cycle. It establishes **circadian rhythms**. Hormone cycling over longer periods is responsible for the control of activities such as menstruation, hibernation, and seasonal mating behavior.

Important Endocrine Glands and Hormones

One major endocrine gland is the anterior pituitary. It secretes growth hormone as well as gonadotropins, which stimulate sex hormone production in the gonads, and prolactin, which is associated with lactation. Another important endocrine gland is the **posterior** pituitary. It secretes antidiuretic hormone, one of the key players involved in water balance, and oxytocin, which induces uterine contractions during childbirth.

Other significant endocrine glands can be cited. The thyroid is responsible for the thyroid hormones T3 and T4, which regulate growth, development, and metabolism. Of the adrenal glands, the adrenal medulla

produces epinephrine and norepinephrine, while the adrenal cortex produces steroid hormones including the mineralocorticoids and glucocorticoids. The pancreas secretes insulin and glucagon, two antagonistic hormones that together regulate blood glucose levels. Finally, there are the thymus, the pineal gland, and the ovaries and testes, which produce sex hormones. SEE ALSO BEHAVIOR; DOMINANCE HIERARCHY.

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Horse Trainer

The ancient Irish believed that certain people had the ability to whisper in the ears of horses and magically influence their behavior. Mary Twelve-ponies, John Lyons, Monty Roberts, and Buck Brannaman are all professional horse trainers who are sometimes described as horse whisperers. These trainers take wild, dangerous, or simply young horses into a round pen and in a matter of hours—without using force or fear—make friends with the horse, acquaint it with a saddle, and place a rider on its back. As Brannaman says, this is a phenomenal act of trust on the horse's part, as their historic enemies leaped on their backs to kill them.



This horse trainer leads her student through an exercise in an outdoor show ring.



The trainers describe what they do with phrases such as: seeing the world from the horse's point of view; turning frightened horses into friends using respect and trust rather than mastery or manhandling; thinking in harmony with the horses; trusting the horse; and treating it with love and understanding.

Though a horse trainer might work with wild mustangs or Olympic competitors, dressage horses or draft horses, cutting horses or jumpers, the basic approach remains the same. Respecting and working with the horse's nature is the most important step. Conveying calmness and deliberation with their movements, trainers allow the natural curiosity, cooperation, and playfulness of the horse to express itself. They teach one thing at a time, reinforcing learned behavior through constant repetition and approval, and remembering that, like any learner, the horse can grow tired and confused and need a break.

To begin a career in horse training, the novice can read books, watch videos, and get first-hand experience in an apprenticeship program or training clinic with a good teacher. It is also helpful to spend as much time as possible immersed in horses—observing them and enjoying their generous, affectionate personalities.

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Horses

One common misconception about evolution is that it occurs in a straight line, from an ancestor to a descendant. Although it is possible to trace the lineage, or history, of a certain species, the wider view shows that evolution is actually a very broad process. It may be helpful to visualize evolution as a tree from which many branches sprout, with each branch representative of a line of organisms evolving from the center of the tree. Many of these branches, or lineages, may die out. Other branches continue to grow and branch out further, resulting in the great diversity of life on Earth today. The history of the horse is an excellent example of this evolutionary “tree.” Horses did not evolve in a straight line from a common ancestor, through species after species, until the modern wild horse appeared. In fact, the evolution of the horse is a story of great divergence and extinctions that continued through time, until only one species remained.

Paleontologists have discovered a very good record of horse fossils in North America, where the horse first appeared, and have learned much about its early history. Other continents have been subsequently searched for fossils, and the migration and distribution of the horse is now well-known. From the remains of a few small **populations** of true wild horses in Europe and possibly central Asia, thriving communities of horses now exist in most regions on Earth.

populations groups of individuals of one species that live in the same geographic area



The Beginning

The ancestors of the horse were browsers who fed on the bushy and leafy types of vegetation found in forests. They ate leaves of trees and shrubs and occasionally fed on tender grasses. Scientists deduced what they ate from studying the fossil teeth of animals that had a similar bone structure to the modern horse, but that had bumpy teeth, instead of the flat, grinding teeth horses have today. These early ancestors were small animals, about the size of a fox or a medium-sized dog.

Evolutionary scientists recognize that environment often drives **natural selection**, and that natural selection leads to evolution. One force causing the transformation in horses was the constant alteration of **climate** that began about 60 million years ago and continues through the present. As the climate became hotter and drier, two important events occurred. First, the forests shrank and became patchy throughout North America. This reduced the **habitat** of the forest-dwelling members of the horse group. Second, different forms of grasses, called “C4 grasses,” evolved. These grasses were tougher than the fragile forest grasses and better able to withstand harsh conditions. They spread throughout the more arid regions and formed vast plains. These plains created a less nutritious but more stable food source for the animals. The formation of the grasslands provided a new habitat in which many forms of animals, like the camels and horses, thrived. C4 grasses contained a high concentration of a glassy mineral called silica. The horse species that survived this new diet developed stronger, flatter, and more complex teeth than their forest relatives. Most of the evolution of horses was identified and traced by studying these changes in tooth shape and structure.

The second major factor that affected the evolution of the horse was the emergence of more effective competitors, such as the artiodactyls (**herbivores** like camels, deer, and bison), and swifter predators, especially the cats with their saberlike canine teeth. These swift and efficient predators found the smaller, forest-dwelling horses to be easy prey, resulting in the swift extinction of the horses. This kind of selection pressure favored the swifter and more wary equids of the open grasslands. So as one horse lineage died out, another evolved quickly. This pattern continued until the end of the Pleistocene epoch about 11,000 years ago. Only one species of horse, *Equus equus*, remains from this once diverse group of animals.

The Story of the Bones

All information scientists know about ancient horses has been gathered from the fossil remains of their skeletons. The skull, and the teeth it contains, can be read almost like a book, revealing how and when physical changes occurred and in what order. While no real “trends” are apparent in the overall picture of horse evolution because so many different species are involved, there were some general changes. As horses evolved, their toes were continually reduced in number until the condition of standing on one toe, like the modern horse, was achieved. The teeth became larger, with a more complex surface. The face became longer. In addition, the overall body size increased, growing from the tiny size of the forest dwellers to the significantly larger modern horse size.

natural selection

process by which organisms best suited to their environment are most likely to survive and reproduce

climate

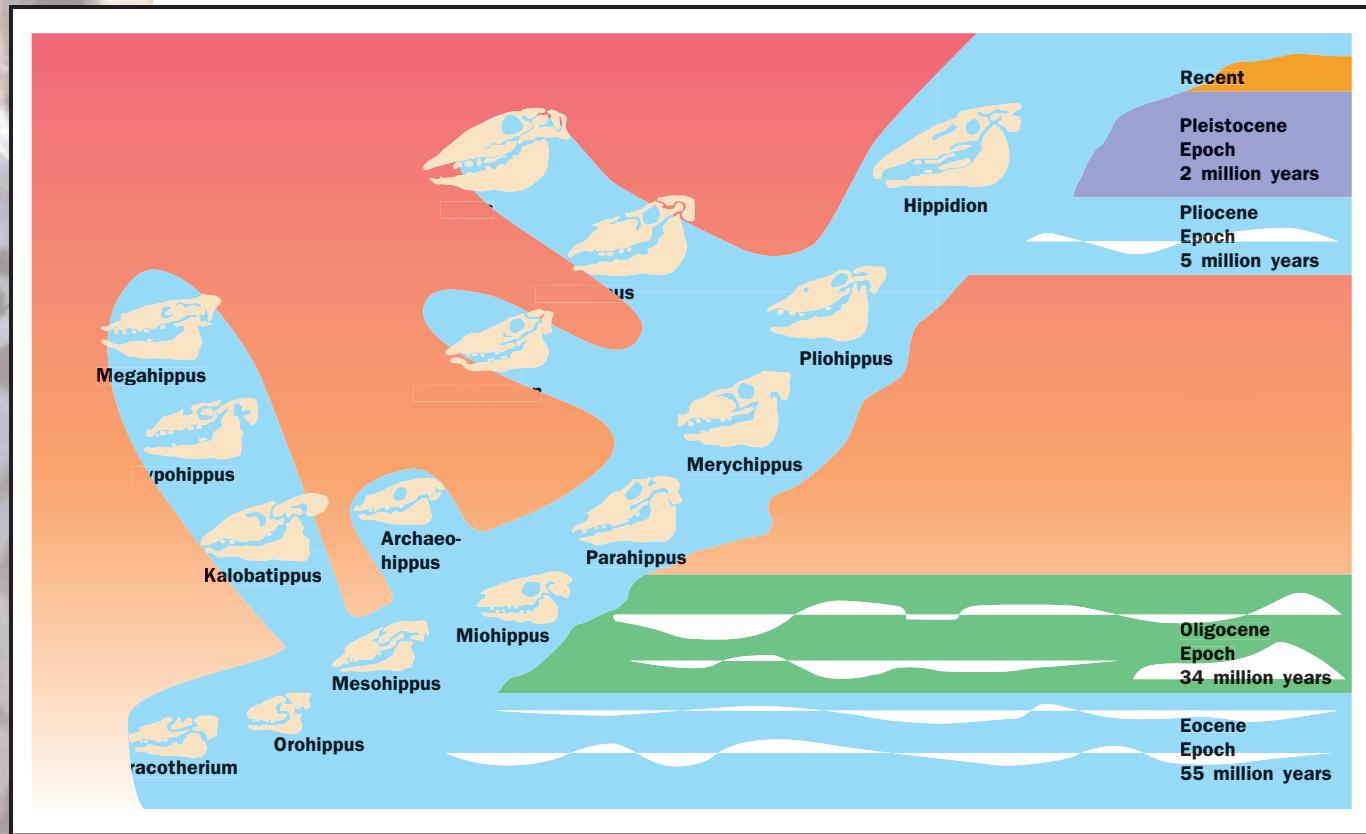
long-term weather patterns for a particular region

habitat

physical location where an organism lives in an ecosystem

herbivores

animals who eat plants only



Evolution of the horse charted by geologic time period. Redrawn from the Florida Museum of Natural History.

fossil record a collection of all known fossils

prehensile adapted for seizing, grasping, or holding on

An animal called *Eohippus* is often cited as the first identifiable horse ancestor. *Eohippus* lived about 60 million years ago and is nicknamed the “dawn horse.” It was a small, dog-sized animal with five toes on its front feet and three toes on its hind feet. The animal stood high on its toes, the tips of which were covered with strong little hooves. The teeth were the browsing type that had small bumps like those on human molars, but which more closely resembled those of a pig. Scientists estimate that this little horse was about 35 centimeters (14 inches) high and weighed a little over 5 kilograms (12 pounds).

The next candidate for selection in the **fossil record** is *Hyracotherium*, an animal that lived about 55 million years ago. *Hyracotherium* was more horse-like than *Eohippus*, with its skeleton showing the characteristics that became unique to horses. The skull was longer and larger, and had a shallow basin at the end of shortened nasal bones where the nose is. The lower jaw was bigger and stronger than its relatives. The top and bottom incisors, or front teeth, met squarely and formed a “nipping-type” set of teeth. The back of the head no longer sloped backward but was now straight up and down. The neck bones were shaped so that the neck not only was longer, but could be rotated upward. Eventually, this feature helped the descendants of *Hyracotherium* to reach downward for grasses. Scientists believe that *Hyracotherium* (and many other species of horses at this time) had a short, **prehensile** proboscis, or snout, that could pick tasty leaves from high up in trees and bushes.

The legs of *Hyracotherium* were longer than those of *Eohippus* and other horses. The front legs of its ancestors had been about 40 percent longer

than the hind legs, but the two sets of legs of *Hyracotherium* were more evenly lengthened. The feet began to change shape as their function for running became greater. The carpals and tarsals (wrist and ankle bones) became smaller and more square. The metacarpals and metatarsals (equivalent to the bones of a human palm) were longer and more slender. The wrist and ankle became more stabilized to prevent side-to-side motion and aid in more efficient running. One of the ankle bones, the astragalus, formed a unique notch where it met the lower leg bone, the tibia. This permitted greater force to be exerted on the foot when pushed against for running. In the wrist, the carpals interlocked with the lower row, providing a stronger pull stroke when running.

These trends continued in species named *Orohippus* and *Mesohippus*. The fossil record reveals a divergence of evolution around the time of *Mesohippus*, about 34 million years ago. One line contained the species *Kalobatippus* and *Hypohippus*, and died out with *Megabippus*. The other line, which leads to *Equus*, contained *Miohippus* and a tiny *Archaeohippus* and continued the skull and leg transformation. *Archaeohippus* was not highly successful, and its lineage died out relatively quickly. The ankle and wrist of *Miohippus* and its ancestors continued to strengthen, and the legs finally lengthened so that the animal stood higher in front than in the back. *Mesohippus* was the first ancestor of the horse to have one fewer front toe, although all the remaining horses eventually had three toes on each foot.

By the Oligocene (the end of the Tertiary epoch), major changes in the horses began to take place. The forest dwellers were no longer dominant, and horses who ate the newly rising C4 grasses began to spread into the great grasslands. These horses were larger, with increasingly long legs, and were able to explore new territory. The wrist and ankle bones continued to become more square and flat so that the force of running would not destabilize the foot. The side-to-side motion of the wrist and ankle was reduced to prevent wobbling, with the back-and-forth motion becoming stronger.

The trend toward an enlarged skull continued for the rest of horse history. The teeth, which were so important for grazing on tougher grasses, lost their roots and became hypsodont, or very high-crowned. One of the most identifiable characteristics of the horse is complex enamel, the tough outer coating of the tooth. Enamel resists the grinding actions of chewing. During the evolution of the horse, the enamel on the molars infolded from the sides, increasing the number of bumpy grinding surfaces. This trend continued for millions of years as horses ate more and more fibrous food. Many scientists believe that horses have the most complex and resistant teeth of almost all the large mammals. Some rodents have complex teeth, but like horses, they eat tough, fibrous foods, like seeds and silica-containing grasses.

The skeleton of the horse continued to grow from about 24 million years ago to the present. While the legs got longer and longer, the scapular (shoulder bone) and pelvis (hip bones) stayed relatively the same size. The neck and back elongated. This change resulted in two advantages for the horse. First, it allowed the horse's head to flex down to the ground to get the grasses. Second, the longer back gave greater flexure for a fast running pace. When an animal like a horse or cheetah runs, one of the important parts of the running pace is the springlike flexure of the back. Some species of horses that showed these changes were *Parahippus*, *Merychippus*,



Neohipparrison, *Pliohippus* (the first single-toed horse), *Dinohippus*, *Hippidion*, and *Equus*.

Hippidion and *Equus* lived at the same time, but *Hippidion* became extinct sometime in the Pleistocene. By this time, horses were gone from North America and it is believed that only a few populations continued in remote places. One population—a small, stocky, pony-type horse resistant to cold and wet—was discovered in northwest Europe. Another population—horses that were larger and resistant to heat—was found in central Asia. These central Asian horses were the ancestors of the desert horses of today.

The horse was reintroduced to North America by the Spanish during their explorations in the early sixteenth century. Many escaped or were let go and are the ancestors of the wild mustang. Horses now thrive all over the world. They are considered animals of beauty and grace and many cultures, such as the Native Americans of the North American plains and nomadic peoples in Mongolia, depend on the horse. SEE ALSO Biological EVOLUTION; PHYSIOLOGY.

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Human–Animal Conflicts

Conflicts and controversies involving interactions between human beings, their communities, and the environment have become defining issues of our time. There is a growing awareness of both the physical effects of people on the environment and the ways in which beliefs, cultural norms, and economic conditions shape the human response to these issues. Human beings are increasing in number worldwide. Many of our lifestyle choices now appear to have a measurable and harmful impact on biological and environmental systems in the United States as well as around the world. Continued growth in **population** and the resulting sprawl of people into previously unsettled land forces individuals, governments, and society as a whole to examine current and future priorities in regard to lifestyle and the natural world.

One of the serious environmental problems facing humankind today is the loss of biological diversity. **Biodiversity** is the vast and varied combi-

population a group of individuals of one species that live in the same geographic area

biodiversity the variety of organisms found in an ecosystem

nation of **habitats**, plants, and animals that thrive together to support life on Earth. Scientists feel that these losses are the direct result of the transformation of natural landscapes and **ecosystems** for farming, grazing, recreational, and residential uses.

Biodiversity is lost when farmers clear land to increase crop yield, when loggers clear forests to provide lumber for houses and furniture, and when city dwellers need more land for homes, schools, and industry. Cutting old-growth forests has encouraged erosion on slopes and mountains. Wetlands have been drained and rivers dammed and diverted to provide water for irrigation and drinking water. Overgrazing of grasslands and the use of fertilizers and **pesticides** have polluted lakes, rivers, and streams, creating fragmented habitats where native species have difficulty surviving.

Demographic shifts and population growth have encouraged people to live in areas once populated by wild animals. These habitats are increasingly affected by human-imposed changes including roads, new uses for private and public lands, and the environmental demands associated with agricultural and urban life. Species such as wolves, mountain lions, polar bears, and the northern spotted owl do not recognize these artificial restrictions on their habitats and have thus come into direct conflict with human beings and their way of life.

While government officials, environmentalists, developers, and industry representatives fashion regulations designed to protect, preserve, and safeguard both ecosystems and human beings, wild animals and people continue to come into conflict with one another. How these issues are resolved will depend on the ways in which conflicting priorities and questions are addressed. What are the ecological, sociological, aesthetic, and scientific benefits of preservation? What are the rights of animals? Do people have an obligation to preserve species? Can society balance economic interests and human needs with efforts to preserve and protect the natural world?

Spotted Owls vs. Loggers

For hundreds of years, the northern spotted owl has made its home in the lush old-growth forests of the Pacific Northwest. The owl feeds on the rich plant and invertebrate life created by decaying timber and nests in the cavities of old trunks. But the towering cedars, firs, hemlocks, and spruces have become a primary source of timber for a multibillion dollar logging industry. As a result of heavy logging since the mid-nineteenth century, only 10 percent of these ancient forests still exist, mostly on federally managed lands. As the forests have dwindled so have the number of spotted owls. Biologists estimated that fewer than 2,000 pairs were in existence in the early 1990s.

In 1986 the U.S. Fish and Wildlife Service was petitioned to list the spotted owl as an endangered species, a move that would bar the timber industry from cutting on these lands. In June 1990, after years of heated **controversy** among timber industry representatives, environmentalists, and government agencies, the northern spotted owl was declared a threatened species. Because of this, timber companies are required to leave 40 percent of the remaining old growth intact within a 2.1 kilometer (1.3-mile) radius of any spotted owl nest or site. This policy is opposed by the timber industry. Industry representatives claim that this requirement will leave thousands

habitats physical locations where an organism lives in an ecosystem

ecosystems self-sustaining collections of organisms and their environments

pesticides substances that control the spread of harmful or destructive organisms

controversy a discussion marked by the expression of opposing views





of loggers and mill workers jobless. They believe that this policy and others like it do not take into account the economic consequences of preservation. Environmentalists, on the other hand, argue that society has a fundamental obligation to preserve this rare species and the wilderness in which it lives.

The controversy over the spotted owl mirrors similar debates over dolphins, whales, and desert tortoises. In each situation, conflicting opinions exist concerning society's obligation to protect animals threatened by extinction. The question raised repeatedly is, "To what extent, if any, should preservation of endangered species and their habitats take precedence over economic considerations?"

Restoring Wolves in Yellowstone National Park

Wolves once ranged over most of the United States but were eliminated from the northern Rockies by the 1930s. From 1918 to 1935, government bounty hunters shot and killed predators including coyotes, wolves, and mountain lions. By 1926, the last wolf was eliminated from Yellowstone National Park. This was the result of an aggressive government-sponsored predator control program and public policy that was based on the assumption that wolves had no value.

This perception and policy continued until the 1970s, when many environmental protection provisions were implemented. In 1972 the U.S. Department of the Interior began an initiative to return native biodiversity to the national parks. As part of this effort, the Endangered Species Act required that the Fish and Wildlife Service have a recovery plan for threatened and endangered species.

In 1987 a Rocky Mountain Wolf Recovery plan was proposed to reintroduce grey wolves into the northern Rockies, including Yellowstone National Park. Local opposition was strong and vocal. Nearby residents worried that wolves would kill their domestic animals and perhaps cause injury to humans. Ranchers and hunters expressed concern that a top predator such as the wolf would reduce cattle, sheep, deer, and bison populations and travel outside the boundaries of the park.

Environmentalists countered that, as large predators, wolves were an essential part of the natural ecosystem that would help control the swelling populations of elk, deer, and bison and increase the numbers of eagles, pronghorn, foxes, and wolverines. An organization called the Defenders of Wildlife agreed to establish a \$100,000 fund to reimburse any rancher who lost livestock because of wolves.

In May 1994, the Interior Department and the Fish and Wildlife Service finally approved the plan for reintroducing wolves into Yellowstone National Park and central Idaho. This led to the successful reintroduction of sixty-six wolves in 1995 and 1996.

Monitoring suggests that the wolves are indeed having a positive effect by controlling the populations of elk, bison, and deer. Coyote numbers have dropped, allowing smaller predators such as foxes to regain strength. The reduction of elk, deer, and bison has allowed willow and aspen trees to regenerate and restore overgrazed areas.

In addition, the grey wolves have begun to recover. They are to be taken off the endangered species list when there are ten breeding pairs in Yel-

In the spring of 2001, the *Great Falls Tribune* (Great Falls, Montana) ran a front page story about the Interagency Annual Wolf Report. According to the report, the wolf population is reaching recovery level (30 breeding pairs). Removal of the wolf from the endangered species list, the report concluded, is probably only three years away.

lowstone, Idaho, and Montana. Ranchers are allowed to kill wolves that attack livestock. Some have also accepted reimbursement for livestock losses from the Compensation Trust set up by the Defenders of Wildlife.

Mountain Lions and Public Safety

Since the mid-1980s, encounters with mountain lions have become more frequent throughout the United States. Hikers, joggers, mountain bike riders, and suburban residents have unexpectedly found themselves in the company of these lions. Some encounters have led to the deaths of human beings.

Although unusual, these incidents have rekindled public debate about mountain lion management. Issues include the shrinking habitat of mountain lions, increased competition for space, the legalities of hunting the lions, and ways to increase public awareness and safety in areas where human beings are encroaching on the traditional habitat of mountain lions.

California has been at the forefront of this debate since the mid-1980s. The rising population of both humans and mountain lions in the state led to an intensive study of the problem by the Department of Game and Fish. Prior to 1986 there was very little concern for public safety from lions. Between 1986 and 1995, however, ten attacks were verified by state officials; a number of them resulted in deaths.

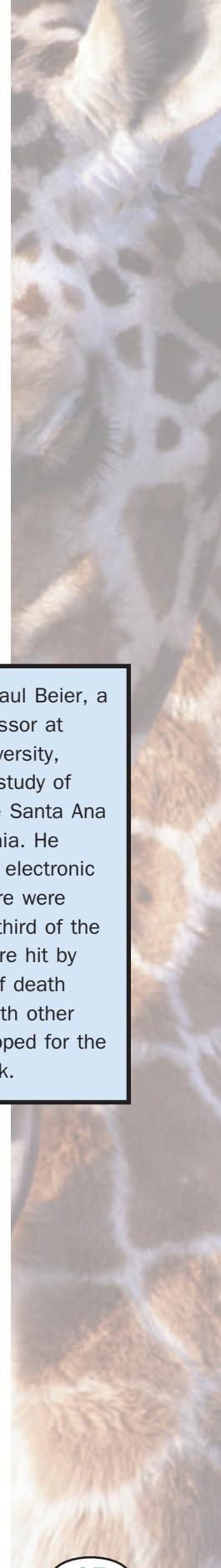
The study's findings concluded that an increase in the mountain lion population and its geographic range, combined with an increase in California's human population, had indeed resulted in increased encounters between animals and people. Research also revealed that the lions were expanding their range into new areas as competition for habitat increased. Since animals compete for food and space, some lions were being forced out of their ranges and ending up in residential or recreational areas where problems were more likely to occur. Wildlife officials recommended controversial safety precautions as well as habitat protection for the lions.

California voters approved a mountain lion initiative in 1990 that prohibited the hunting of lions. In 1996 the National Rifle Association filed a suit that resulted in the repeal of the 1990 initiative and once again allowed hunting and the use of steel-jawed traps, leghold traps, and poison, and decreased the amount of money to be used for habitat protection. Concern for public safety was given as the main reason for not giving any protection to the mountain lion.

Adventure Travel and Climate Change: Polar Bears in Canada

Churchill, Manitoba, is called the polar bear capital of the world. Nearly 15,000 tourists visit this northwestern Canadian town each winter to observe, film, and photograph the bears as they congregate near the mouth of the Churchill River, waiting for the Hudson Bay to freeze so that they can head out on the ice to hunt ringed seals, which are their primary food source.

During the tourist season, more than 500 people per day are allowed to go out on adventure expeditions to observe the polar bears. The sole means of observing the bears is from the "tundra buggy," which is best described as a large, roomy bus mounted on 1.8-meter (six-foot) high, all-terrain rubber tires. The vehicle is designed to transport tourists across the tundra look-



In 1993, professor Paul Beier, a wildlife ecology professor at Northern Arizona University, launched a five-year study of mountain lions in the Santa Ana Mountains of California. He fitted 32 animals with electronic collars. In 1998, there were only 25 survivors. A third of the animals that died were hit by cars. Other causes of death ranged from fights with other animals to being trapped for the protection of livestock.

These polar bears rifling through a garbage dump in Manitoba, Canada, illustrate concerns of human-animal conflict. Polar bears, naturally, do not adhere to human-devised artificial boundaries.



global warming a slow and steady increase in the global temperature

ing for bears. Many wildlife managers are concerned about the effect of this human encroachment on the fragile tundra. They are also concerned that the polar bears, who are at their weakest after months with limited food resources, are suffering from a lack of undisturbed time in their natural habitat at a critical point in their life cycle.

There is another concern about the human impact on the habitat of the polar bears in the Hudson Bay area, however. Researchers have been studying a group of 1,200 bears in the Churchill area for nearly thirty years. These bears are giving scientists glimpses of long-term changes in the climate that may be caused by **global warming**. The ice is melting earlier and earlier each year, causing the bears to come ashore sooner than they used to. These shorter feeding seasons have led to near starvation among the bears.

The combination of climate changes and increased tourism is putting stress on the population of polar bears and increasing the possibility that polar bears desperate for food will encounter people on a more regular basis, endangering human safety. Wildlife officials say that the bear population is declining. The adventure travel companies report that they are seeing fewer bears, and thinner bears. They are also reporting more encounters between humans and polar bears on the tundra.

In all of these conflicts involving human enterprise and wildlife habitats, there are few easy choices to be made. Environmentalists and animal rights activists raise reasonable questions about the preservation of wildlife for future generations and the right of wild animals to live peacefully in their native forests, deserts, tundras, or wetlands. Communities that are economically dependent on tourism, the harvesting of forests, the raising of livestock, or the expansion of their boundaries express reasonable concern about how to balance human needs with environmental protection measures. Meanwhile, both human beings and native wildlife continue to adapt to each

other's presence in environments they now share. SEE ALSO HABITAT LOSS; HABITAT RESTORATION.

Leslie Hutchinson

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Human Commensal and Mutual Organisms

From the moment of birth and throughout our entire lives, humans share their bodies with a surprising variety of microscopic organisms. Dust mites remove dead skin, amoeba live on their teeth and scavenge food particles, and eyebrow mites live on their eyebrows.

Scientists estimate that the human body has around 7.5×10^{13} cells. Many of these cells are not of human origin, but represent microscopic **commensal** and mutual organisms. In commensal interactions, one species of organism benefits and the other is unaffected. In mutual interactions, both organisms benefit.

The term "commensal" is derived from a Latin word *mensa*, meaning "table." Commensal organisms share their food from a common table. In the case of human commensals, the human host is the table. It is often difficult to identify a relationship between organisms as purely commensal, mutual, or parasitic, as the way in which one organism benefits or harms its host may not be obvious. A commensal or mutual organism may depend on its host for food, shelter, support, transport, or a combination of these factors. The host may receive a variety of benefits, including protection from infection, improved digestion, or cleaner skin.

While in the womb, humans live in a sterile environment, protected by the **placenta** and the amniotic sac. After birth, humans are introduced and subjected to an array of new organisms. If these organisms find themselves in a suitable ecological **niche**, whether on the internal or external parts of the human body, they will multiply and form complex communities, or colonies, with their host. The first step in this colonization process requires the microscopic organisms to adhere to their host. If the organisms find a suitable location, they will form long-term, stable, interdependent relation-

commensal symbiotic relationship in which one species benefits and the other is neither helped nor harmed

placenta structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

niche how an organism uses the biotic and abiotic resources of its environment





mutualism an ecological relationship beneficial to all involved organisms

populations groups of individuals of one species that live in the same geographic area

flora plants

fauna animals

ships with other organisms in the same location and the human that harbors them. Since the benefit to one or the other species may be subtle and hard to identify, it is often difficult to distinguish between true commensalism and **mutualism**. Humans certainly derive considerable benefit from many resident organisms.

A wide variety of microorganisms interact with humans, taking advantage of several microenvironments. Certain parts of the body, such as the solid organs, blood, cerebrospinal fluid, and urine, are normally sterile. However, established microbial **populations** may be found on the skin and in the lower respiratory tract, mouth, and lower gut. Throughout life, these resident organisms vary in type and number, and individuals can have significant differences in their resident populations. If for any reason the commensals gain access to inappropriate body sites, infections may occur.

Skin and Eyes

The skin is a highly complex organ that provides a variety of ecological niches for colonies of microscopic organisms. It is also the first line of defense against infection. The skin on the head, armpits, groin, hands, and feet has more microscopic organisms than on other places on the body. Bacteria, fungi, and mites form the commensal **flora** and **fauna** on the skin. The fungi *Malassezia furfur* and *Candida albicans* are found on the skin of some individuals. All humans can act as hosts to skin mites such as *Demodex folliculorum* and *Demonex brevis*. It is thought that a large majority of the human population acts as hosts to these mites. These microscopic animals survive on a diet of dead epithelial (skin) cells and sebum, an oil excreted by hair follicles and other skin glands.

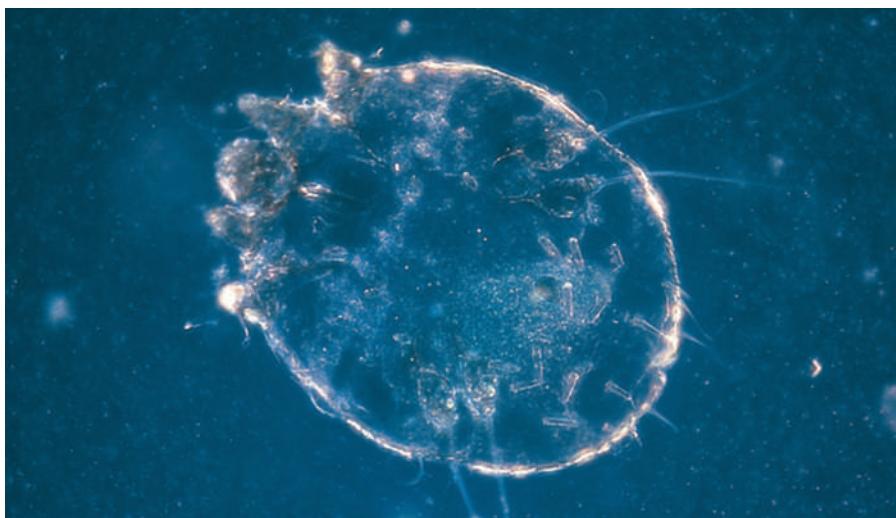
The commensal flora and fauna on the skin are dispersed into the environment when washed or sloughed off in some manner. This is important, because 10 to 40 percent of healthy individuals and up to 90 percent of hospital staff carry the bacteria *Staphylococcus aureus*. This bacteria is one of the most common causes of infection in wounds after surgery, and nearly all babies born in hospitals become colonized within a week.

Human eyes are covered with a specialized skin that is bathed in tears, and only a few microbes can survive these conditions. *Corynebacteria* such as *Corynebacterium xerosis* can establish themselves as resident commensals on human cornea.

Digestive Tract

The mouth provides a number of ecological niches where microscopic organisms can colonize. Dental caries (tooth decay) are caused by the interaction between commensal bacteria and sugar in the diet. *Streptococcus mutans* converts sugar into slime which sticks firmly to the enamel of the teeth, beginning the decay process. The crevices between the gum and teeth also harbor bacteria such as *Bacteroides* and *Fusobacterium* that can cause gum disease.

Commensal organisms usually do not colonize the stomach because it is highly acidic, although some acid-tolerant lactobacilli can live there. One bacteria, *Helicobacter pylori*, has recently been linked with ulcer formation in some people. The normal flora of the intestines, *Escherichia coli*, *Streptococcus*,



A microscopic image of a scabies mite.



and *Bacteroides* contribute to the normal functioning of the digestive system. The importance of the role of these organisms becomes more evident when the administration of antibiotics or laxatives kills them. Without these organisms, the digestive system may be colonized by pathogenic bacteria that are resistant to antibiotics.

Respiratory Tract

The respiratory tract is anatomically complex and constantly exposed to microorganisms in the air breathed in. The microflora of our nostrils resembles that of the skin, with colonies of commensal organisms such as micrococci, corynebacteria, staphlococci, and streptococci. *Streptococcus pyogenes* is part of the commensal flora of the nose in healthy individuals, but may cause tonsillitis and strep throat. The warm, moist environment of the upper respiratory tract provides a haven for commensal bacteria including *Streptococcus*, *Moraxella*, *Neisseria*, and *Haemophilus* species. The lower respiratory tract is generally free from microorganisms, mainly because of the efficient action of the **cilia** that line the tract.

cilia hairlike projections used for moving

Roles of Commensal and Mutual Organisms

Nineteenth-century French microbiologist Louis Pasteur believed that animals cannot exist without a population of commensal and mutual organisms, and early experiments to raise germ-free animals met with failure. All germ-free animals have weak, poorly developed immune systems. This suggests that the roles of normal microscopic organisms are very important.

Commensal organisms play a significant role in preventing infections. This may be simply because they deny the invading organism access to the target site, or because the benign organism actively produces substances that inhibit the growth of, or even kill, other organisms.

Commensal flora and fauna may also “switch roles” and become an important source of infection for the human host. Infections caused by microscopic organisms derived from commensal organisms are known as endogenous infections. These infections range from minor conditions, such as boils, to life-threatening infections. For example, streptococcal bacteria

equilibrium a state of balance

from the mouth or skin can gain access to the bloodstream and cause bacterial endocarditis, an infection of the interior of the heart.

Commensal and mutual organisms are in a constantly changing dynamic **equilibrium** with their human host. Strains, or groups of these organisms, are constantly being replaced and displaced by other strains. In this way, the commensal organism adapts to changes that occur in the host. SEE ALSO INTERSPECIES INTERACTIONS.

Leslie Hutchinson

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Human Evolution

Human evolution is the lengthy process of change by which people originated from apelike ancestors starting nearly five million years ago. The modern scientific study of human evolution is called paleoanthropology. A subfield of anthropology, this discipline searches for the roots of human physical traits, culture, and behavior. It attempts to answer questions: What makes us human? When and why did we begin to walk upright? How did our brains, language, art, music, and religion develop? By approaching these questions from a variety of directions, using information learned from other disciplines such as molecular biology, paleontology, archaeology, sociology, and biology, we continue to increase knowledge of our evolutionary origins.

Most cultures throughout human history have myths, stories, and ideas about how life and culture came into existence. Although the current theory of evolution, based on the ideas of Charles Darwin, is accepted by a majority of scientists in our time, it is important to remember that many earlier ideas were recognized as well.

Darwin's books, *On the Origins of the Species by Natural Selection* (1859) and *The Descent of Man* (1872), expressed his theory of evolution and revolutionized the study of life and human origins.

Darwin presented evidence showing that natural species including humans have changed, or evolved, over long spans of time. He also argued that radically new forms of life develop from existing species. He noted that all organisms compete with one another for food, space, mates, and other things needed for survival and reproduction. The most successful individuals in this competition have the greatest chance of reproducing and passing these characteristics on to offspring. Over hundreds of thousands of generations, one form of life can evolve into one or more other forms. Darwin called this process natural selection.

Darwin's theory of natural selection is commonly known as "survival of the fittest."

Modern science now understands that the mechanism for evolutionary change resides in **genes**, the basic building block of **heredity**. Genes determine how the body, and often the behavior, of an organism will develop over the course of its life. Certain information in genes can change, and over time this genetic change can actually alter a species' overall way of life.

In recent decades, biological and social scientists have made impressive strides in understanding our complex physical and cultural origins. Their research has revealed gradual alterations in our genetic structure, as well as shifts in culture and behavior, that have transformed humankind into the planet-dominant species.

Scientists estimate that our human ancestors began to diverge from the African primates between eight million and five million years ago. This figure is the result of studying the genetic makeup of humans and apes, and then calculating approximately how long it took for those differences to develop. Using similar methods of comparing genetic variation among human **populations** around the world, it is thought that all people living today share a common genetic ancestor.

Early Life in Africa

The human story begins in one of the most geologically fascinating areas on Earth, the Great Rift Valley of Africa. It is an enormous split torn into Earth's crust that runs from the forests in Tanzania to the deserts of Ethiopia. In some places the rift is thousands of feet deep and exposes the last fifteen million years of the earth's history. Here, fossil remains of our earliest ancestors can be found. Humankind appears to have first evolved in Africa, and the fossils of early humans, or **hominids**, who lived between five million and two million years ago, come entirely from Africa.

Starting with the modern human skull, it is possible to trace our ancestry back millions of years. As we travel back in time, our ancestors look less and less like us and begin to resemble our closest relatives, the African apes. Because our physical and genetic characteristics are similar, evolutionary theory offers evidence that ancestral humans had a very close relationship to a group of primates, the apes. Humans, chimpanzees, gorillas, and the large apes of Africa share a common ancestor that lived between eight million and five million years ago.

Humans, or hominids, belong to the scientific order named Primates, a group of more than 230 species of animals that includes the monkeys, lemurs, and apes. Modern humans have a number of physical characteristics resembling our ape ancestry. The social systems of humans also share similarities with the African apes and other primates, such as baboons, chimpanzees, and rhesus monkeys. Chimps live, groom, feed, and hunt together and form strong family bonds. Early humankind probably had a similar lifestyle.

Scientists now know that nearly 98 percent of the genes in humans and chimpanzees are identical, making chimps the closest living biological relative of humans. However, there are fundamental differences between modern humans and their primate relatives. The human brain is larger and more complex, giving humankind the ability to communicate through language, art, and symbols, to walk upright, and to develop a throat structure that makes speech possible.

genes segments of DNA located on chromosomes that direct protein production

heredity the passing on of characteristics from parents to offspring

populations groups of individuals of one species that live in the same geographic area

hominids belonging to the family of primates





One of the earliest defining human traits is bipedalism, the ability to walk upright on two legs. This characteristic evolved over four million years ago. Other important human characteristics, such as a large and complex brain, the ability to make and use tools, and the capacity for language and culture, developed more recently. Many of what we consider advanced traits, such as art, religion, and different expressions of cultural diversity, emerged during the past 100,000 years.

Most paleoanthropologists today recognize ten to fifteen different groups of early humans. They do not agree, however, about how they are related or which ones simply died out along the way. Researchers also disagree about how to describe, identify, and classify these early human species, and what factors influenced the evolution and extinction of each species.

Early Humans: Evolution of Australopithecines

bipedal walking on two legs

fossil record a collection of all known fossils

spinal cord a thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

Nearly five million years ago in Africa, an apelike species evolved with two important traits that distinguished it from the apes. This species had small canine teeth (next to the four front teeth), and it was **bipedal**, meaning it could walk on two legs instead of four. Scientists refer to these earliest human species as australopithecines, or australopith for short.

The **fossil record** shows that there is not an orderly sequence leading from one form to another. Several groups lived at the same time and characteristics developed at different rates; therefore the human family tree suggests a long and complex past.

Fossils from several early australopith species that lived between four million and two million years ago clearly demonstrate a variety of adaptations that mark the transition between ape to human. Prior to four million years ago, fossil remains are scarce and incomplete; where available, however, they do show a primitive combination of ape and human features.

Most of the key characteristics that stand out as distinctly human are related to their bipedal stance. The australopiths had an S-shaped spine that allowed for balance when standing. The opening through which the **spinal cord** attached to the brain was positioned more forward, allowing for the head to be balanced over the upright spine. The pelvic bone was shorter and broader than in apes, giving the pelvis a bowl shape that supported the internal organs when standing or walking upright. The upper legs angled inward allowing the knees to support the body while standing or walking. Shorter and less flexible toes functioned as rigid levers for pushing off the ground with each step.

Most early species had small canine teeth, a projecting face, and a small brain. They weighed between 22 and 37 kilograms (60 to 100 pounds), and were 0.9 to 1.5 meters (3 to 5 feet) tall. Males were generally larger than females. Both had curved fingers and long thumbs with a wide range of movement. The apes, in comparison, have longer, more curved, and stronger fingers that make them well adapted for hanging and swinging from branches. Apes also have short thumbs, which limits their ability to manipulate small objects.

There were at least two major groups of australopithecine, one with very large teeth and heavy jaw muscles referred to as robust, and another referred to as gracile. The main difference was in the size of the jaws and teeth. Beyond that, there was no appreciable difference in body size. The evidence

suggests that the large-toothed robust group ate primarily plant foods, whereas the gracile group concentrated on a more diverse diet that included meat. Details known about each group are delineated below.

Early Australopiths or Gracile Group

- *Ardipithecus ramidus*. Discovered in 1994 and estimated at 4.4 million years old. This ancient line suggests a close relationship with apes and chimps because of the enamel found on the teeth. Whether or not it walked upright is unknown.
- *Australopithecus anamensis*. Discovered in 1995 and estimated at four million years old. Jaws were apelike but the legs were humanlike; it may have walked upright.
- *Australopithecus afarensis*. Discovered in 1974 by Donald Johanson and known as “Lucy.” Estimated at 3.9 to 3.1 million years old. Thought to walk upright and bipedal, these may have left footprints in volcanic ash in Laetoli 3.7 million years ago. Fossils show sexual differences, and suggest that they were adept at climbing trees.
- *Australopithecus africanus*. First found in 1924 by Raymond Dart, this was the first known australopith. Dating from 3 to 2.4 million years ago, it had forelimbs longer than legs and walked upright. Many feel this is the best candidate as ancestor to early *Homo* species.

Later Australopiths or Robust Group

- *Australopithecus aethiopicus*. Found in 1985, this group dates from 2.7 million years ago. The skull, known as “the black skull,” shows a possible relationship with *A. afarensis*.
- *Australopithecus boisei*. This group lived over a long period of time, between 2.3 and 1.2 million years ago. This skull has the most specialized features of the robust group, with a massive, wide face capable of withstanding extreme chewing forces.
- *Australopithecus robustus*. This group lived between 1.8 and 1.3 million years ago in the same region as *A. africanus*. This group had jaws, teeth, and **habitat** similar to *A. boisei*, but the groups appear to not be related.



The skeletal remains of “Lucy.”

Evolution of Modern Humans

***Homo habilis*.** After researchers unearthed the australopithecines, the next major “missing link” to be found was *Homo habilis*, an early representative of modern humankind. Found by Louis and Mary Leakey at Olduvai Gorge in Tanzania, these fossils date to between 2.5 and 1.7 million years ago. This creature was bipedal, fully upright, and had the capacity to use forearms for handling tools and weapons.

These fossil specimens show an increased brain size of 600 cubic centimeters (37 cubic inches), and a jaw and tooth size more closely resembling modern humans. Any residual physical traits for climbing had also disappeared. Cut marks on bones suggest the use of tools to prepare meat. They probably retained some of the skeletal characteristics of the australopithecines that made them great climbers. They may have spent considerable

habitat physical location where an organism lives in an ecosystem





asymmetrical lacking symmetry, having an irregular shape

time in trees foraging, sleeping, and avoiding predators. They were the first of our relatives to have opposable thumbs, and the fossil skulls show physical traces of **asymmetrical** brain development, which is reflected in the way that stone tools were shaped.

Some researchers feel that *Homo habilis* had a large enough brain to have the rudimentary capacity for speech that may have encouraged cooperation and sharing amongst members of a group. That our distant *H. habilis* ancestors were able to produce such tools demonstrates that they had manual dexterity but also a capacity for planning, as well as knowledge about what kinds of stones to use and where to find them. The technology of these first toolmakers existed for more than 800,000 years.

***Homo ergaster* and *Homo erectus*.** Next in the story of human evolution, we find a group represented by *Homo ergaster*, a recently recognized African link between *Homo habilis* and *Homo erectus*. This group lived from about 1.8 million to 1 million years ago, when *Homo erectus* and other forms replaced it. *Homo erectus* fossils found in Java and the Republic of Georgia at 1.9 million years old and 1.6 million years old, respectively, indicate an early migration of *Homo ergaster* from Africa followed by *Homo erectus* evolving in Asia and spreading to other areas.

A fossil skeleton of *Homo ergaster* found in Kenya in 1984 became popularly known as Turkana Boy. This skull led researchers to believe this group may have been the first “naked ape.” This specimen suggested no body fur, a dark pigmented skin, and no evidence of living in trees. This species may have reached up to 1.8 meters (6 feet) in height; they appear to have had a near modern size brain and a striding gait. They may have been the first to make and wear clothing of some kind.

Homo ergaster made stone tools, including well-made hand axes and cleavers for the butchering and processing of hunted animals. This technology appeared in Africa and was later carried into western Asia and Europe by *Homo ergaster* or its descendants. This technology was widespread and used until the end of the Early Stone Age, only a few hundred thousand years ago.

It now appears certain that *Homo ergaster* was the direct ancestor to the first inhabitants of Eurasia, including *Homo erectus* in the Far East, as well as the predecessor of *Homo sapiens* and *Homo neanderthalensis* in Europe. *Homo ergaster* led to *Homo erectus*, the famous missing link, which is our first ancestor to occupy territory from what is now northern China in Asia, to southern Great Britain and Spain in Europe, and all of Africa.

Emergence of Modern Human Beings

Neanderthals and Modern *Homo sapiens*. The origin of modern humans is still controversial. The debate centers on whether modern humans have a direct relationship with *Homo erectus* or the Neanderthals, a well-known, more modern group of humans who evolved within the last 300,000 years. Some researchers feel that modern humans originated separately in Asia, Europe, and Africa. Others feel that modern humans originated in Africa and after migrating into Europe and Asia they replaced the Neanderthals or archaic *Homo sapiens* found there.

For many years, scientists believed that Neanderthals were the direct descendants of modern humankind. In the 1960s an interesting theory pro-

posed that different groups of *Homo ergaster* gave rise to numerous groups of *Homo sapiens*, including a group known as Neanderthals. This theory suggested that the Neanderthals had disappeared because of being outcompeted by and having interbred with *Homo sapiens sapiens*, sometimes referred to as Cro-Magnon people. However, more recent evidence suggests a different story.

In a landmark study conducted in 1997, scientists examined the **mitochondrial DNA** of a Neanderthal fossil and a modern human. This analysis done by molecular biologists provides evidence about when two populations of people last had a common ancestor. The results concluded that it is unlikely that Neanderthals were related to modern humans. Instead it is thought that Neanderthals were a distinct species that evolved side-by-side with early *Homo sapiens* for hundreds of thousands of years. In addition, the earliest version of *Homo sapiens*, one with the characteristics that would link it with a common ancestor for Neanderthals and modern humans, *Homo sapiens sapiens*, had evolved in Africa from *Homo ergaster* at least 600,000 years ago.

The scientists further calculated that, while Neanderthals and modern humans did indeed share a common ancestor, *Homo ergaster*, the two lineages had diverged sometime between 550,000 and 690,000 years ago. This established that the Neanderthals evolved in Europe and evolved from archaic *Homo sapiens* and go back perhaps nearly 300,000 years. It appears that the Neanderthals almost made it to the present, as they appear to have died out only 30,000–40,000 years ago, for reasons not fully understood at this time.

Compared with *Homo sapiens*, *Homo neanderthalensis* was barrel-chested with massive brow ridges, a nose that protruded forward, a low sloping forehead, a lower jaw without much of a chin, thick arm and leg bones, and heavier muscles in the shoulder and neck. The brain was actually larger than that of modern humans, possibly because of the additional capacity needed to control the extra musculature. Although the brain size of Neanderthals overlapped with early and modern *Homo sapiens*, the shape of the cranium was different, suggesting that perhaps the frontal cortex, which controls “higher thought,” was restricted.

The Neanderthals also appear to have been culturally quite advanced. While most lived in caves, it is possible that some may have begun to build house-like structures. They manufactured a variety of stone tools, including spear points, scrapers, and knives. They used and controlled fire, which probably helped in cooking frozen meat and in keeping warm. Evidence that they buried their dead with flowers and tools suggests that perhaps they had a form of religion.

It appears, then, that modern human beings are direct descendants of a group known as Cro-Magnon *Homo sapiens* that appeared in Europe and Asia 100,000 years ago. Although they overlapped with the Neanderthals, they were physically unrelated. They appeared thoroughly modern, with a high forehead and a well-defined chin. Artifacts and stone tools demonstrate that they had mastered the art of making tools and useful instruments from stone, bone, and ivory, and they may have used spears. A number of colored paintings left on cave walls suggest an evolving, rich, and complex cultural life. They hunted cooperatively and were perhaps the first to have a language.

mitochondrial DNA

DNA found within the mitochondria that control protein development in the mitochondria



Conclusion

In March 2001 a new fossil, known as *Kenyanthropus platyops*, was added to the family tree of early humans. Thought to be 3.5 million years old, it is considered a new genus and species of an early human ancestor that lived in the same area and time of Lucy. This recent find is an example of the ways in which our long and complex past slowly reveals itself to us as we come to recognize and understand more about our human ancestors, piece by piece and fossil by fossil. SEE ALSO Biological EVOLUTION; PRIMATES.

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Human Populations

bipedal walking on two legs

Modern humans (*Homo sapiens*) are grouped with the mammals (class Mammalia) in the subphylum Vertebrata. Within the mammals, humans are assigned by taxonomists to the primates (order Primates), along with lemurs, monkeys, and apes. Humans are grouped by most taxonomists together with the surviving species of Hominoidea, or great apes (the others include two species of gorilla, two species of chimpanzee, orangutans, and simangs). However, all members of the human family can stand upright with no difficulty and are naturally **bipedal**, whereas apes are naturally quadrupedal, only standing upright when necessary. Humans are also the only surviving members of the family Hominidae and genus *Homo*. Extinct members of the genus include *Homo habilis* and *Homo erectus*. The *Homo* sp. probably evolved from one of several species of australopithecines: *Australopithecus africanus*, *A. robustus*, *A. boisei*, and the recently discovered *A. garbi*. "Lucy" (*Australopithecus afarensis*) lived around 3.5 million years ago (abbreviated as mya) and may have been the ancestor of the evolutionary branch that led eventually to humans. It is not yet clear where the recently discovered *Kenyanthropus platyops* (who also lived around 3.5 mya) fits into the evolutionary sequence.

Evolution

About 2.5 mya, the first humans, genus *Homo*, first appeared in the fossil record. For the first half million years, early representatives of *Homo* lived in loose association with *australopithecines*, from whom they differed in two important ways. First, they were somewhat larger and had much larger brains

than australopithecines. Second, they used tools. Their tool use is the origin of the names for one species of these early humans, *Homo habilis*, or “handy” man. *H. habilis* lived in the dry savannas and forest edges, probably surviving for most of the year on roots, bulbs, and tubers. Although roots, bulbs, and tubers are very nutritious, digging them up from the hard, dry, savanna soils is difficult with only bare hands. Roots and tubers are also deficient in protein. So *H. habilis* would have needed to supplement the carbohydrate-rich diet of roots and tubers with high-quality protein, the best source of which is meat. *H. habilis* was a hunter and meat eater.

When you cannot run very fast and do not have big, sharp teeth, hunting large animals requires some form of social organization. So *H. habilis* individuals probably lived in small bands of closely related members. It is likely that some division of labor also existed, with the females doing most of the digging (something you could do while holding an infant) while the males hunted large game.

Fossils of another early member of our genus, *Homo erectus* (“upright” man) first appeared in Africa around 2 mya and spread rapidly into Asia. The fossils of *H. erectus* found in Asia were originally known as Java man or Peking man. *H. erectus* was as large as humans but had a heavier build. *H. erectus* also made another significant technological advancement, fire. They also had more sophisticated tools that were probably used for cleaning and cutting meat, for scraping hides, and as weapons. *H. erectus* survived in many parts of the world until around a quarter million years ago.

The same evolutionary patterns established by the transition from *Australopithecus* to *Homo erectus* were extended even further with the evolution of *Homo sapiens*. The earliest members of our species had larger brains and smaller teeth than did *H. erectus*. Several types of (probably competing) *H. sapiens* existed at the same time. All were skilled big-game hunters, suggesting a high degree of social organization and, probably, language. Another distinctly human trait also appeared with *H. sapiens*. They apparently had religious practices and some concept of an afterlife. This led to burial rituals and the inclusion of tools, clothing, weapons, and food in the burial, presumably to aid the deceased in the afterlife.

One type of early *Homo sapiens*, Neanderthal, was widespread in Europe and Asia between 75,000 and 30,000 years ago. Neanderthals were short, robustly built, and had brains that were somewhat larger than modern humans. They used a wide variety of tools and were skilled hunters. However, an even more modern human, Cro-Magnon, appeared around 100,000 years ago. Cro-Magnon peoples and Neanderthals lived at the same time, but Neanderthals abruptly vanished from their range. Some biologists think Cro-Magnons exterminated Neanderthals, whereas others propose that interbreeding may have obliterated the differences. Cro-Magnon humans had even more sophisticated tools, modern language capabilities, and made extraordinary cave paintings.

Language

Larger brains led inevitably to the evolution of human languages. Language, and the sophisticated social organization it makes possible, offers enormous evolutionary advantages. Not only were humans able to organize themselves into sophisticated hunting parties, they were also able to





population a group of individuals of one species that live in the same geographic area

habitats physical locations where an organism lives in an ecosystem

transmit information about other resources. Language also offers one other enormously important advantage. With language it is possible to transmit information from one generation to the next. The ability to pass along knowledge, traditions, rituals, and other information led to the development of culture. Cultural change can occur much more rapidly than genetic change. A cultural trait can spread through a **population** in less than one generation. The problem of cultural transmission is how to pass along cultural norms efficiently without being rigid and stifling the creativity necessary for a population to survive adverse changes in the environment.

Unique cultural traditions have been identified in the tools, weapons, and other implements found associated with human fossils. Along with cultural traditions, the domestication of plants and animals also spread rapidly. As a result most human societies eventually became sedentary. Agriculture and pastoralism (herding of domestic animals) replaced hunting and gathering. Agriculture and pastoralism led to cities, expanded food supplies, stratified societies, and the rapid growth of the human population.

Agriculture was independently invented three times at different places in the world. Agriculture was first discovered in the Middle East about 11,000 years ago and spread from there throughout Europe. From Middle Eastern agriculture we get cereal grains, grapes, and olives. European agriculture gave us rye, cabbage, celery, and carrots. Domesticated animals included cattle, sheep, goats, horses, pigs, dogs, cats, and chickens. Agriculture also developed in east Asia about the same time. From Asian agriculture we get rice, soybeans, citrus fruits, and mangoes.

When humans first entered the New World, they did not bring agriculture or domesticated animals with them, except for dogs. So agriculture developed a third time in the New World and gave us corn, tomatoes, kidney and lima beans, peanuts, potatoes, chili peppers, and squash. Domesticated animals were rare in the New World and included only llamas, alpacas, and turkeys.

Human Population Growth

Humans have successfully moved into every available nook and cranny on Earth. Our sophisticated technology allows us to survive comfortably where no other mammal or any complex organism could survive. Humans spend the winter at the South Pole. Humans live on mountaintops and in arid deserts. These are mere curiosities, but it is obvious that humans are able successfully to make a living in a wider variety of **habitats** and under a broader range of environmental conditions than can any other animal on Earth.

For the first few million years of our evolution, humans lived in small groups and survived by hunting and gathering. The invention of agriculture allowed human populations to grow rapidly. They are still growing. If the number of humans on Earth is plotted against time, the curve stays essentially horizontal until about 1000 C.E. At that time, there were less than 100 million people in the entire world. From 1000 C.E. to 2000 C.E., the population growth curve turned sharply upward and now appears almost vertical. It took 2 million years to reach the first billion people, 130 years to reach the second billion, 30 years to reach the third billion, 15 years to reach the fourth billion, and only 12 years to reach five billion.



Two private farms butt up against a development of homes and businesses upon land that once contained fields of corn in York County, Pennsylvania.

The population of the world passed six billion in September 1999 and in March 2001 was over 6,137,748,000. By 2010 the world's population will pass seven billion.

This rapid population growth and the spread of humans to every part of the globe have profoundly altered the environment. Obviously the population of Earth cannot grow indefinitely. At some point, resources will run out and population growth will be limited. Biologists wonder what the **carrying capacity** of Earth is and what the quality of life would be like if the human population were to be allowed to increase to that point.

carrying capacity the maximum population that can be supported by the resources

Carrying Capacity

Carrying capacity is the maximum population of a given species that an ecosystem can support for an extended period of time. Every habitat, ecosystem, or **biome** has a carrying capacity of any particular species. Humans have moved into every portion of Earth and inhabit a variety of different ecosystems. Discussions of carrying capacity for human population must include the whole Earth as an ecosystem. There is much debate and discussion of Earth's carrying capacity. Many feel that Earth is already overpopulated and that drastic measures must be taken immediately to reduce the population and to reduce resource consumption.

biome a major type of ecological community

Humans have already transformed or degraded 40 to 50 percent of Earth's land surface. Humans use 8 percent of the total productivity of oceans. The percentage is much higher in the areas of concentrated productivity, such as continental shelves. Humans have already increased atmospheric carbon dioxide by 30 percent. On many islands, over one-half of the species have been introduced by humans, often devastating native



populations. Over 20 percent of bird species have become extinct since 1800 as a result of human activity. Over 22 percent of marine fisheries are over-exploited and are now in decline. Another 44 percent are at the limit of exploitation.

The biggest problem humankind may have to face in the near future is the availability of clean, fresh water. Humans already use over one-half of the available fresh water. Some experts predict that in the twenty-first century competition for water resources will come to dominate local, national, and international politics. These experts predict that the competition for water resources will be much more severe and dangerous than the present competition for energy resources.

Land resources are also limited and cannot support unlimited population growth. Cropland, rangeland, pasture, and forests are all under pressure. Most land suitable for farming is already being farmed. Increases in agricultural productivity through higher yield crops and more efficient farming practices have allowed agricultural production to increase more rapidly than the population. Most experts think that this cannot continue indefinitely.

Human Impact on the Environment

Humans interact with both the living and nonliving factors in our environment. Environmental degradation occurs when a potentially renewable resource such as soil, grassland, forest, or wildlife is used at a rate faster than the resource can be replaced. The resource becomes depleted and environmental degradation occurs. If the rate of use of the resource remains high, the resource can become nonrenewable on a human timescale or it can even become nonexistent (extinct). Worldwide, species are disappearing at a rate greater than the rate of species loss during any of the mass extinctions Earth has undergone.

Not only are species being lost at an alarming rate, biodiversity is also being lost at the ecosystem level because of environmental degradation. Tropical forests are recognized as the most diverse ecosystems on Earth and are experiencing the highest rate of ecosystem loss, but temperate habitats are also suffering degradation. Because the temperate parts of the world were settled first, it is in these areas that the loss of **biodiversity** has been greatest.

Who is responsible for degrading the environment? We all are. Ordinary human activity from even the most responsible individuals inevitably pollutes and degrades the environment to some extent. We directly degrade the environment when we consume resources (burning wood in a fireplace, for example) and indirectly when resources are extracted and transformed into products we need or want. SEE ALSO BIODIVERSITY; POPULATION DYNAMICS; POPULATIONS.

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biodiversity the variety of organisms found in an ecosystem

Sustainable development is a form of social change that includes recognizing that maintenance of natural resources is a basic human need. The idea of resource sustainability emerged in the late nineteenth century with regard to renewable resources such as forests and fisheries. At the start of the twenty-first century, the concept encompasses many other ideas, including population control as one of the keys to maintaining Earth's biosphere.

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Hunter-Gatherers

"Hunter-gatherers" is a term generally used to describe people from ancient societies who survived exclusively by hunting, fishing, or gathering wild foods. There is controversy today among scientists, however, as to whether any societies in modern times can be considered to be true hunter-gatherer groups. Some scientists argue that no societies today dwell in isolation and that trade has existed between hunter-gatherers and neighboring societies for thousands of years. Others recognize the societal interaction but assert that the contact has done little to change the lifestyles of hunter-gatherers.

Despite varying opinions, one thing is clear: Until about 8,000 years ago, all people were foragers of wild foods. As recently as 3,000 years ago, the entire **population** of southern Africa depended on hunting game and gathering wild plants for their survival. Outsiders have given many names to the people in southern Africa who lived by hunting and gathering, including Bushmen, San, and Twa. Other notable hunter-gatherers, called the Soaqua, lived along the Western Cape coast of Africa, while others, known as Xam, thrived in the grassy plains of the semiarid Karoo region.

population a group of individuals of one species that live in the same geographic area

Basic Characteristics of Hunter-Gatherer Societies

While there is evidence that many differences existed among hunter-gatherer societies throughout the ancient world, there are also numerous uniting traits. The hunting and gathering lifestyle depended tremendously on large land areas where these ancient peoples could scout for adequate food. It has been estimated that people who depend on hunting and gathering must have approximately 20 to 1,500 square kilometers (10 to 700 square miles) of land per person, depending on the **climate**. Hunter-gatherer societies were generally very small. Large groups would have exhausted available food supplies rather quickly in any one area. These small groups were thought to be made up of individual family members or a number of related families collected together in a small band.

climate long-term weather patterns for a particular region

Hunter-gatherers usually moved in order to follow local food supplies. Possessions had to be carried from one camp to another. This suggests that permanent villages were rarely possible. Housing most likely consisted of crude lean-tos, huts, or primitive tents. A sedentary lifestyle may have been possible where food supplies were unusually abundant and reliable. Evidence suggests, for example, that the American Indians of the Pacific Northwest



A bushman in Namibia gathers magnetti nuts.

coast achieved high population densities and established permanent villages because resources were vast and reliable and food could be stored. Their main staples were dried salmon and flour made from acorns.

Ratio of Hunting to Gathering

Although hunting, fishing, or gathering of edible plants typically occurred together in hunter-gatherer societies, one activity sometimes prevailed. The Eskimos of Arctic Canada, Alaska, and Greenland, for example, traditionally relied on the hunting of whales and seals and on fishing for survival. By contrast, the San, or Bushmen, of modern-day South Africa tend to rely more on gathering than on hunting.

Varying Male and Female Roles

While hunting and gathering activities were usually performed together, different social roles were often associated with each function. For example, the !Kung people of Botswana are regarded by many scientists as living examples of early hunter-gatherers. Hunting was done by males, and females strictly gathered edible plants. This was the most important activity because up to 80 percent of this society's diet consisted of plant foods. Though plant foods were seasonal, they were more substantial and dependable as a food source than game.

The women, who had the knowledge of the location and seasonal availability of edible plants in their area, went out collecting every day or every few days, depending on the circumstances. The !Kung people were relatively lucky, compared to other groups in the region, because they lived in an area where there are mongongo trees, which bear nutritious nuts. The nuts could be eaten raw, but evidence shows that the !Kung liked to roast them in a fire. Among the !Kung, role distinctions were also made on the basis of age and degree of leadership within a group or society.

Other Kalahari hunter-gatherers also practiced roles where the men hunted and the women gathered. The importance of hunting lay in its significance as a source of prestige for the men of the group. Hunting also provided sought-after delicacies, thus allowing the sharing of social ties within the band. Hunting in very small groups of between two and six individuals, the men would often stay away from camp for two or three days while following wounded prey. Large animals were slaughtered and cut up at the kill site so the meat could conveniently be carried back to the campsite.

Farming versus Hunter-Gatherer and Primitive Agricultural Societies

Scientists consider hunting and gathering to be among the two oldest professions in existence. Most societies living this lifestyle eventually began practicing primitive agriculture by preparing simple garden areas to supplement their hunting and gathering efforts. In contrast to modern farming practices, primitive agriculture was typically practiced in forests where the loose soil was easily broken up with a twig or fallen branch rather than on grassy fields with heavy sod.

Additionally, primitive agriculture probably did not use extensive fertilizers or modern techniques such as crop rotation, irrigation, or terracing.

Primitive agriculture is, therefore, much less productive than farming. Also, the size of the societies remained small with most being no larger than the hunting-gathering societies. The overall population densities of the primitive agriculture societies were also very low compared with farming regions.

Primitive agriculture societies that lived in forest areas often practiced “slash-and-burn” techniques. After about two years of cropping a plot, the land was left fallow for a number of years and allowed to revert back to secondary forest or brush. The brush was then burned. The most highly evolved slash-and-burn societies were the Maya of Guatemala and Yucatan. SEE ALSO FARMING; HUNTING.

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Hunting

Hunting is the intentional act of tracking and killing wild animals for consumption or trophy. These animals are referred to as “game,” quarry, or prey. Fishing is a type of hunting restricted to catching fish. As omnivores, humans require proteins and vitamins that are most easily provided by consuming meat. This is why hunting was a necessity for our human ancestors and preceded agriculture as a means of food procurement. Through the use of tools, Paleolithic humans hunted to ensure an adequate food supply and to obtain skins for use as clothing. Although agriculture became widely developed in the Neolithic period, game hunting remained prevalent and may have acquired cultural as well as biological significance.

Archaeological evidence for hunting is investigated today by examining patterns in the location of animal carcasses; the degree to which the skeleton is disassociated; cut or teeth marks on the bones; and the type, location, and wear of discarded hunting tools. These clues reveal aspects of the societal structure of prehistoric humans, such as gender roles, migratory habits, and nutrition. In ancient Greece, the sequence and style of killing and preparing the meat of an animal were highly ritualized under the laws and customs of polytheistic religion. Similar rituals were preserved through the Middle Ages, when boar and stag hunting became popular throughout Europe.

Game hunting today is still a strong pastime and a necessity of life for indigenous peoples living in remote areas. The decrease and disappearance of many large predators because of **habitat loss** and inbreeding has made hunting a necessity for controlling the population size of certain prolific

habitat loss the destruction of habitats through natural or artificial means

Three goose hunters walk with their kills at Langford Creek in Kent County, Maryland.



poaching hunting game outside of hunting season or by using illegal means

falconry a sport where falcons are used for hunting

species, such as deer and geese. However, overhunting and **poaching**, the illegal slaughter and sale of rare animals, can lead to further extinctions.

Humans rely on trained animals and specialized tools and weapons to hunt. Hunting with trained dogs is called coursing. Sporting breeds of dog have been bred for size, temperament, and intelligence, to aid the human hunter. For example, the harrier is always used in rabbit hunting, the fox hound in fox hunting, the pointer and retriever in wild foul hunting, and the Rhodesian ridgeback in lion hunting. In some cases, such as with the terrier, the dog is expected to seek out and attack the prey, whereas in others, such as the fox hound, the dog's task is to startle, or flush, the prey from its hiding spot. Retrievers, pointers, and setters may be called upon to retrieve the fallen carcass of a killed game bird without damaging it. Horses, likewise, may be highly trained in the maneuvers and tactics a hunter uses when in pursuit of prey, and are conditioned to withstand the noise and ruckus of the hunt. **Falconry** is a term describing the use of falcons, hawks, or eagles as trained hunters. Falconry originated several thousand years ago in China and has since been adopted by other cultures. Wild raptors are caught as chicks and trained to fly on command after being released from the falconer's wrist. They will attack and kill prey, and then abandon the corpse to the falconer. Although an uncommon practice, southern Asians have been training cheetahs for thousands of years to kill antelope, deer, and other fast-moving prey for humans.

Aside from animal-assisted hunting, there are many accessories and tools unique to the time of year, environment, and type of game that will be hunted. Camouflage clothing is necessary for concealment, and some hunters use species-typical calls or decoys to lure the game into their immediate vicinity. Firearms, crossbows, and the sling are often used on sport hunting excursions, whereas poisoned darts, arrows, and spears are common in hunting by African and South American natives. Traps are designed to ensnare, hobble, or injure prey. They can be made of a pair of metal jaws

that snap shut when an animal's footstep depresses a switch or when bait is removed from a switch, a cage with a door that swings shut when the animal enters, or a pit that is thinly covered with debris so that animals fall through the debris to the bottom. Trapping is effective when covering large territories and for **nocturnal** prey. Unlike the use of weapons that leave holes in the coat, trapping preserves the integrity of the animal's hide because it affects primarily the lower limb. For this reason, the practice is popular with fur traders, who refer to it as fur harvesting. Whale hunting, or whaling, for blubber, meat, sperm, and bones and teeth, is an ancient practice common to many seaside civilizations. Harpoons are long barbed spears attached to ropes that are flung or shot at whales to injure and kill them. Australian aborigines rely on a unique hunting tool called the boomerang, which is thrown at game but returns to the hunter if it does not hit its mark.

Hunting is also characterized by the type of game being sought. Big game hunting includes large animals such as moose, caribou, bear, reindeer, wolf, tiger, leopard, elephant, and wild goat. It can be very dangerous because the hunted animal is capable of counterattacking the hunter, and because these excursions take hunting parties to remote wilderness where immediate medical attention is unavailable. However, big game are the preferred sport for trophy hunting. Small-game hunting, known as shooting in Great Britain, focuses on smaller animals such as wild fowl, hare, rabbit, woodchuck, raccoon, and squirrel. These animals are more often destined for food than for trophy.

Animal carcasses and skins, both mammals and birds, may be taken to a taxidermist, where they are formed into a three-dimensional, lifelike representation of the animal for permanent display. The skin of the animal is fitted around a hard framework, such as polyurethane, the eyes are replaced with large glass beads, and the ears and hairless regions are sculpted in clay, epoxy, or wax. Taxidermy originated in the 1800s, when hunters began bringing their skins to upholsterers, who would stitch them up with rags and cotton. This is why taxidermized animals are sometimes referred to as stuffed.

Because of the dangers of overhunting and thereby unwittingly bringing about the extinction of the quarry, all fifty of the United States and many other countries enforce laws restricting sport hunting to certain periods of the year. These **hunting seasons** cover different periods for different game, different hunting techniques, and different locales. They are determined based on the natural breeding and migration periods of the game, and on its **relative abundance**, a measure of the species' well-being based on population size. Hunters must register their firearms and report the number and kind of game they have killed. Hunting licenses must be purchased annually, to document and limit the number of lawful hunters, and the income from their sale is often allocated to animal conservation organizations. Further benefits from hunting include the prevention of diseases that can be spread from wild animals to humans or livestock, for example, the spread of rabies through raccoon populations and tuberculosis through wild bison. Several programs currently exist to increase hunting of overpopulated wild game, such as white-tailed deer, that are becoming a nuisance near cities. The surplus of meat resulting from the kills is inspected, packed, and donated to homeless shelter food pantries.

nocturnal active at night

hunting seasons a period of time during which hunting is permitted

relative abundance an estimate of population over an area





Hunting does have some benefits, but the risk of hunting to extinction is well-documented in human history. Beginning with the likely prehistoric slaughter of all mammoths, overexploitation has also eliminated large birds such as the moa and the dodo, smaller birds like the passenger pigeon and Carolina parakeet, large marsupials such as giant wombats and giant kangaroos, and marine mammals such as Steller's sea cow. Many animals are becoming locally extinct and universally endangered owing to a lack of regulations in certain areas of the world. Many others, such as the gray whale and the Indian elephant, are currently at a high rate of decline.

Even with the presence of adequate hunting regulations, poaching undermines the conservation effort. Poaching is the unlawful hunting of protected game either outside the allotted hunting season or against a hunting ban. It is strictly opposed by all sport hunting associations and should not be confused with lawful hunting. Unfortunately, because of the law of supply and demand, poaching becomes increasingly profitable as the number of game animals declines. This increases the risk of extinction at a time when animals most need to be protected. Tiger pelts, elephant and rhinoceros ivory, and sea turtle eggs are examples of luxury items that unnecessarily cause the endangerment of a species. Poaching is most easily counteracted by refusing to buy animal products without first researching the legality of the sale. The effects of hunting and poaching are becoming stronger with the decrease in animals' natural environments and the increased human demand for food and luxury products. Destitute peoples in developing countries may depend on poaching for money or on hunting protected animals for food. A global effort is needed to end extinctions caused by the overexploitation of game animals. **SEE ALSO** EXTINCTION; FARMING; HUNTER-GATHERERS.

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Ichthyology

Ichthyology is the science of animals that deals with fish. This field includes the study of fish growth, development, structure, characteristics, classification, geographical distribution, and the relationship of fish to their environment. The science of ichthyology was evolved in Europe during the eighteenth century. However, the Chinese were studying fish (with the intention to propagate them) at least ten centuries before the birth of Christ. There are also recorded observations on the varieties, habits, and qualities of various fish by the ancient Egyptians, Greeks, and Romans.

Today, ichthyologists strive to answer questions like, “How long can a fish live?” and “How big can a fish grow?” Although these questions may sound simple, the answers are based on a multitude of factors. And while it may be true that most fish live between sixteen and twenty years, it is much more difficult to predict size because fish growth never stops. Generally, fish get a little longer and a little thicker every year. One of the largest fish, a 13.7-meter (45-foot) whale shark caught off Florida’s Atlantic coast in 1912, was recorded at a weight of 20 tons.

One of the best places to study fish is the national fish collection, housed at the Smithsonian National Museum of Natural History. The collection is the largest in the world and contains approximately eight million species from all over the world. The collection continues to grow as specimens are added from parts of the world where the fish **fauna** is poorly recognized or understood. Zoologists from the National Marine Fisheries Service and the U.S. Department of Commerce are permanently stationed at the museum, and they work closely with the specimens, focusing primarily on commercially important species.

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Imprinting

Imprinting describes a process in which newborn animals rapidly develop a strong attachment to a particular individual, often the mother. It is associated particularly with precocious bird species (species that mature early) such as chickens, ducks, and geese, in which the young hatch fairly well-developed.

Imprinting is advantageous because once offspring imprint on their mother, they will try to remain close to her and follow her around, behaviors that are beneficial in terms of the offspring’s survival. The young also indicate distress when the mother is absent.

Imprinting was one of the first matters tackled by the field of **ethology**. Konrad Lorenz, one of the founders of ethology, studied imprinting to determine what controls and limits the behavior associated with imprinting. Lorenz showed that newly hatched birds imprint on practically any moving object to which they are close during their first day of life.

In natural conditions, of course, this object is almost certainly to be the mother. However, in a famous experiment, Lorenz was able to get birds to imprint on him. Interestingly, male birds that imprinted on Lorenz subsequently courted human beings when they tried to find mates, rather than courting members of their own species. This suggests that imprinting not only provides **behavioral** instructions to young birds soon after they hatch, but has important implications for future behavior as well.

Further work on imprinting in birds has revealed that species may respond preferentially to the appropriate stimulus. Although baby birds imprint on any moving object, they are also more likely to imprint on objects that have certain head and neck features corresponding to those it

ethology the study of animal behavior

behavioral relating to actions or a series of actions as a response to stimuli

These Canadian goslings follow their mother through the water. Imprinting is the process by which newborn animals develop a strong attachment to one or both of their parents.



expects to find in an adult of its own species. This makes it more likely that, in the wild, baby birds will imprint on the correct individual.

Two characteristics of imprinting are essential. First, imprinting describes an innate, preprogrammed response that is released by the appropriate stimuli. In the case of the baby birds, the presence of any mobile entity close to the chicks in the first hours or day of life is sufficient to release the response. In other species, different stimuli are required. Baby shrews also imprint on their mother, and will hold onto the fur of either the mother or another sibling when the mother wishes to move, so that the entire family is able to travel in caravan style. In shrews, the releasing stimulus for imprinting is suckling: Babies imprint on the odor of the female who suckles them.

A second feature of imprinting is that there is a very specific **critical period** when imprinting is possible. Goslings and other birds generally imprint in the first day of life and often within the first hours. For shrews, studies show that the critical period occurs between the fifth and fifteenth days of life. It is the female who nurses the babies during that time on whom they will imprint.

Imprinting is an example of a behavior that has both innate and learned components. **Innate behaviors** are preprogrammed, and appear fully developed in individuals. Innate behaviors tend to appear in situations in which the environment is fairly predictable. **Learned behaviors** are shaped by the environment. The advantage of **learning** is that it is flexible. Learned behaviors are suited to changing or uncertain environments.

Imprinting requires learning because young animals use cues from the environment in order to learn who is the parent. The behaviors that result, however, such as following behavior in precocious birds, is largely innate. The largely preprogrammed behavior that follows imprinting is believed to

critical period a limited time in which learning can occur

innate behaviors
behaviors that develop without influence from the environment

learned behaviors
behaviors that develop with influence from the environment

learning modifications to behavior from experience

have evolved because it is more efficient than learning, and because the flexibility that comes from learned behaviors is not advantageous in situations where imprinting occurs.

Some authors have extended the notion of imprinting to include other instances of preprogrammed behavior that require a releasing factor. **Parental imprinting**, for example, describes the imprinting of parents on their offspring. Parental imprinting is believed to be responsible for the success of **brood parasites**, bird species that lay their eggs in the nests of other species. The adoptive parents imprint on brood parasite young when they hatch, and then feed and raise them. Song imprinting has been studied in some bird species. In white-crowned sparrows, for example, young males imprint on the songs of adult conspecifics (members of the same species) that they hear sung around them, and sing similar songs when they mature and begin to look for mates. **SEE ALSO BEHAVIOR; BEHAVIORAL ECOLOGY.**

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parental imprinting a process by which a gene's expression in a child depends on which parent donated it before development

brood parasites birds who lay their eggs in another bird's nest so that the young will be raised by the other bird



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Instinct

An instinct is an innate, preprogrammed behavior that is genetically determined. Instinctive behaviors do not vary much within a species and are usually performed in similar, often stereotyped, ways. The acquisition of instinctive behaviors is not dependent on the environment in which an individual is raised, or on interactions with other members of its species. For example, individuals that are removed from their natural habitat and placed in isolation nevertheless develop the instincts typical to their species. Behaviors in which instinct often plays a significant role include mate recognition, courtship rituals, predator avoidance or defensive behavior, food-gathering behavior, parental care behaviors, and self-grooming.

Instinct is often contrasted with **learning**. Learned behaviors are shaped by experience and by the environment. Practically no behaviors, however, are purely the result of either instinct or learning. Most behaviors are the product of both, involving contributions from both **genes** and environment. Many behaviors that seem instinctive can be modified by experience, and many supposedly learned behaviors show biases that can be accounted for only by innate factors.

One type of instinctive behavior is called a **fixed action pattern**. A fixed action pattern describes a series of actions that is initially triggered by a stimulus, and then carried out to completion. Fixed action patterns are completed even though the behaviors are no longer necessary or no longer make sense.

learning modifications to behavior from experience

genes segments of DNA located on chromosomes that direct protein production

fixed action pattern behaviors that are common to all members of a species

An African lioness instinctively knows to carry her cub through the wilderness. This action helps to protect the cub from predators.



The classic example is the egg-retrieval instinct of the gray lag goose. If a gray lag goose suddenly notices that one of her eggs is outside the nest, she rolls it back to her nest with a series of highly stereotyped head and neck motions. Even if the egg is removed (by a researcher) while the goose is in the middle of this behavior, she follows the sequence to completion. The trigger for a fixed action pattern is also called a releaser.

The advantage of instinctive behaviors is that they are much less costly than behaviors acquired through learning. Learning takes more time and energy, and also requires extensive nervous system resources. Generally, species with small brains behave more instinctively, whereas those with larger brains rely more on learning. In addition, learning simply is not necessary or advantageous in many situations. It is helpful only where flexibility is important. In other circumstances, instinctive behaviors are highly adaptive and sufficient.

Instinctive behaviors are particularly suited to predictable aspects of the environment. An instinct of baby gull chicks, for example, is to peck at the red spot on the beak of adult gulls. This elicits feeding behavior from the parent. For the baby gull, there is no advantage to having to learn such a tactic.

Similarly, the fear of poisonous snakes in certain species of birds is instinctive. The motmot preys on small snakes, and young birds are attracted to these as potential food items. However, they also have an instinct to avoid snakes with a red and yellow banded coloration, which characterizes the highly poisonous coral snake. This highlights another big advantage of instinctive behaviors: Individuals know how to respond even if they are encountering a given stimulus for the first time. It is not surprising, then, that instinctive behaviors are often more prevalent in newborn or young individuals than in older ones.

Instinctive behaviors often weaken over time. In gull chicks, for example, it has been shown that newly hatched young are fairly undiscriminating. Food-begging behavior is triggered by any object that is long and narrow and that has a colored spot at the end. This object does not have to be a gull beak or even be attached to something that resembles an adult gull head. In older chicks, however, greater resemblance to an adult gull is required to elicit begging behavior.

Because of their relative simplicity, cues that trigger instincts can be taken advantage of by other species. **Brood parasites** are bird species that lay their eggs in the nests of other species, thereby sparing themselves the time and energy that would be required to raise those offspring. Examples of brood parasites include the cowbird and the cuckoo. The host parents feed the intruders because the baby cowbirds or cuckoos are able to produce the necessary triggers to elicit the parent's feeding instinct. These include making noisy hunger calls, stretching their necks high up out of the nest, and opening their beaks wide. In many cases, brood parasite offspring have evolved to produce triggers that are much more extreme and dramatic than those of the host's own young. As a consequence, the young brood parasites get fed preferentially in the nest.

brood parasites birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

Mating instincts are another category of innate behaviors that are frequent targets of the deceptive machinations of other species. In fireflies, for example, courtship typically consists of species-specific flashing by male fireflies followed by flashing replies from interested females. However, there is a certain species of predatory firefly that mimics the female reply of a different species in order to attract males as prey items.

In another species, the bolas spider, individuals release scents that resemble the **pheromones** (molecules that are used in chemical communication between members of a species) of female moths. Males who respond instinctively to this scent are caught as prey. Finally, certain flower species, including some tropical orchids, release female bee pheromones in order to attract male bees for pollination. This is one example in which learning can modify an instinctive behavior: Male bees that have encountered deceptive orchids repeatedly learn to avoid them. **SEE ALSO BEHAVIOR; BEHAVIORAL ECOLOGY.**

pheromones small, volatile chemicals that act as signals between animals that influence physiology or behavior

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populations groups of individuals of one species that live in the same geographic area

mutualistic relationship symbiotic relationship where both organisms benefit

obligative mutualism an animal that must exist as part of a mutually beneficial relationship

Interspecies Interactions

Populations of animals exist in cooperative and competitive relationships with each other. For any species to thrive it must find access to food resources and be able to successfully reproduce. Ecologists have identified many methods for survival among the species of animals and have, consequently, described many of the survival techniques. Three fascinating relationships exist that intrigue both the scientist and the layperson. They are mutualism, parasitism, and commensalism.

Mutualism

Mutualistic relationships may be the most fascinating because of the cooperation that exists between species. Competitive relationships in which two or more species compete for the same resource are quite common. However, when two species evolve a pattern of survival from which both benefit, it is an interesting scenario for biologists to consider.

In a **mutualistic relationship** two organisms from entirely different species behave in a way in which both benefit. Most often, the two organisms are from species with very different lifestyles and nutritional needs. Often the need is not even nutritional, but rather one in which the offspring are assured a better chance for survival. No matter the reason or outcome, the dependency of the two organisms continues to grow with each passing generation until the two life cycles are dependent on each other for survival.

Complete and total dependency is termed **obligative mutualism**. Obligative mutualists are found in the association between termites and their intestinal bacteria. The termites cannot digest the tough plant material cellulose. The bacteria can. Consequently the termite gut is full of these cellulose-digesting bacteria. The bacteria benefit by having a relatively safe place to live and reproduce, and the termite benefits by gaining access to the nutrition of the plant after the cellulose has been digested.

Another example of mutualism is the relationship between some large grazing animals like the rhinoceros and the small tick birds. The birds feed on the insects that cling to the skin of the rhinoceros. In turn, the size and reaction of the rhinoceros to predators helps the tick birds to remain safe and live a longer life.

Parasitism

Another interesting relationship between species is that of parasitism. In a parasitic relationship one species lives at the expense of another. There is a clear distinction between predation and parasitism. A predator will kill the prey outright and receive its benefit directly. A parasite will not kill its host (the organism on which it lives) outright. It is better for the parasite to have its host live as long as possible to ensure continued survival and reproduction for the parasite.

One of the most familiar parasitic relationships is that of a tapeworm. The tapeworm has no digestive or sensory (eyes, ears, nose) system. In fact, it does not even have a circulatory system (heart and blood vessels). The fact that tapeworms live in the digestive system of a host means they do not need to digest their own food. It is already done for them. They do not need



A cape buffalo grazes in a field while an oxpecker bird rests on the buffalo's back. Oxpeckers have developed broad, flattened beaks to better help them to pick their meals (ticks and embedded larvae) out of the skin of the buffalo.

to sense their environment because they are protected in the gut of the host. They are small, so nutrients are passed from one cell to another by simple **diffusion**. Unfortunately for the host, the nutrients it ingests are being absorbed instead by the tapeworm. Over a long enough period, the host will become malnourished, lose weight, and eventually die.

Another example of parasitism is less deadly on the host, but may eventually affect populations. Interspecific (between species) and **intraspecific** (within the species) brood parasitism is often seen in birds. One female will lay her eggs in the nest of another. The unsuspecting nesting parents may not recognize the odd egg and will continue to sit and hatch all the eggs in the nest. After the eggs hatch, the parents will spend more resources feeding and caring for the unrelated offspring, sometimes at the expense of their own.

Cuckoo birds have been known to lay their eggs and leave their young for others to care for. Often the baby cuckoo is larger and more demanding than the other babies. More food will go to raising the cuckoo than to the other nestlings. Sometimes the larger cuckoo will even kick the competing young out of the nest, duping the parents into raising the one single chick.

Purple martins are another species of birds in which brood parasitism occurs. The main difference is that the parasitism occurs within the species. This may not be as harmful a situation for the nestlings as it is with the cuckoo. In fact, some researchers suggest that this form of parasitism may even promote colonization and population growth.

Commensalism

Commensalism is a newer and more inclusive term for an older concept called **symbiosis**. The term "symbiosis" now more broadly describes the three types of relationships discussed in this article. Commensalism is a re-

diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

intraspecific involving members of the same species

symbiosis any prolonged association or living together of two or more organisms of different species





commensal symbiotic relationship where in which one species benefits and the other is neither helped nor harmed

lationship in which one organism benefits and the other is unaffected. There is a very fine line in identifying a relationship as **commensal**. Some relationships may actually be long-term parasitism. Much study is needed before a relationship can be truly described as commensal.

In one such relationship between a small crab and an oyster, the crab enters the oyster as a small larva. The inside of the shell provides a safe place for the crab to grow and develop. Once the crab has reached maturity, however, it is too large to leave through the oyster's narrow valve opening. It remains inside the oyster, feeding off floating particles of food that are siphoned by the oyster from the surrounding water. Neither animal is harmed, and the crab has a safe place to live and receive food.

Another commensal relationship exists between some species of ants and aphids, the sucking parasites of plants. The aphids secrete a sweet liquid substance that is consumed by the ants for food. The ants tend the aphids as a farmer would tend livestock. The aphids are not harmed and the constant attention by the ants keeps the aphid colonies fairly clean.

Scientists still do not completely understand why and how mutualism, parasitism, and commensalism evolved. Each of these types of relationships are distinct and specialized. They have evolved over time, and the survival of individual species is dependent on these highly evolved relationships. There is a great deal to be learned about each of them. **SEE ALSO** ENDOSYMBIOSIS; PARASITISM.

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Iteroparity and Semelparity

Success for an animal species does not only mean that it survives, but that it survives to reproduce. When a species or population of organisms is unable to reproduce enough offspring to keep the population numbers high, extinction is the result. However, reproduction is probably one of the most energy-depleting events a single organism may endure. Both plants and animals have a wide range of reproductive methods that result in repeated matings, **fertilization**, production of offspring, and survival of the next generation. However, for many groups, including some plants, all of the energy produced by the organism is directed to successful reproduction.

Within the animal group, **invertebrates** have a wide variety of reproductive strategies that insure their survival. Many produce so many eggs and sperm that the sheer numbers of offspring make success of a few likely.

fertilization the fusion of male and female gametes

invertebrates animals without a backbone

Feature	Texas	South Carolina	Ohio
Growth	rapid	intermed.	slow
Adult mortality	high	intermed.	low
Ave. size female	57	63	75
Ave. clutch size	9.5	7.4	11.8
Broods per year	3-4	3	2
Total offspring produced per year	33	22	24
Egg mass per egg	0.22	0.33	0.35

Proportions of births by age of female	Texas	South Carolina	Ohio
1	82	48	0
2	18	30	57
3	0	15	22
4	0	7	21

Vertebrates, however, tend to be more specialized in their reproductive habits. As a consequence, a great deal of energy is spent in assuring the most optimal conditions for survival of the young. Environmental pressures such as bad weather conditions or high predation rates call for species with the highest assurance of success. Two of the most successful types of reproductive styles are called iteroparity and semelparity.

Iteroparity occurs when a parent breeds year after year. This means that the success of the parent's genetic material surviving to another generation is increased with every brood. For most plants and animals this works quite well. If for some reason conditions do not favor the survival of the young one year, there is a repeat chance the next year.

Sea turtles are an example of iteroparity. After mating, the females come out of the water, dig a large nest with their flippers, and deposit several dozen eggs. Should a predator uncover the nest and eat the young, it is not a disaster for the parent since she will return the next year to repeat the egg-laying cycle.

Semelparity is a type of reproduction that occurs less frequently, but is no less driven by the need for reproductive success. A common example of semelparity is found in salmon, a meaty and delicious food source for many animals, including humans, bears, and other water-living predators. Salmon eggs are a nutritious and desirable food source for marine-dwelling organisms. In the face of these facts, natural selection has driven salmon to a very ingenious but costly reproductive strategy.

Juvenile salmon begin the oceanic phase of their lives in massive schools that migrate around the world's major oceans. When they become adults and are ready for breeding, instead of laying their large nutritious eggs in the marine environment, where they are likely to be eaten, the salmon change their entire **physiology** to survive in freshwater. The breeding adults smell the river in which they were born and begin to swim up to their spawning grounds.

Many films show the intense and difficult trek adult salmon take to get to those grounds. They leap up and over waterfalls and swim against swift and strong currents. Many species actually change their color and the shape of their mouths. They do not feed during this time. Their body tissues are

This chart demonstrates the results when there occurs an optimization of the tradeoff between growth and reproduction. The number of babies born yearly shows that an animal with a higher rate of mortality would benefit from a semelparous reproduction strategy since it may not survive until the next breeding season. Redrawn from the Association for Tropical Biology web site.

vertebrates animals with a backbone

physiology the study of the normal function of living things or their parts



Semelparous sockeye salmon bodies turn various shades of red, and their heads green, several days after reaching their fresh water spawning grounds.



gametes reproductive cells that only have one set of chromosomes

aquatic living in water

iteroparous animals with several or many reproductive events in their lives

converted to eggs or sperm. At the end of these breeding migrations, salmon look terrible. Their skin is peeling. They are wounded and damaged by accidentally hitting themselves against rocks and they are exhausted. Many fishermen do not eat breeding salmon because the conversion of body tissue to **gametes** makes the salmon meat soft and undesirable.

Before bear populations decreased, the annual migration of salmon was a source of feasting for them. Many salmon simply died before reaching their breeding grounds or were eaten by predators, including some large birds of prey such as eagles. The survival of adult salmon traveling to individual breeding grounds was often very low. This low adult survivorship is another reason, in addition to the dangers of the marine environment, why semelparity is an advantage to the fish.

The large burst of energy that completely disables the fish ends with the laying and fertilization of the eggs. Afterward, the adult fish all die. However, the adults have provided the next generation a safe place to grow and hatch. When the offspring emerge from the eggs, they have an abundant food supply from **aquatic** insects and, eventually, minnows. The young have time to grow and develop to a larger size free from most predators. The sacrifice of the parent provides safety to the next generation.

Many spiders, some anguillid lizards, and certain amphibians also undergo semelparity. It is a type of reproduction found among animals whose environmental conditions may be too harsh for the young to survive. On the other hand, iteroparity favors repeated matings. **Iteroparous** plants and animals live for many years, breeding each season. Often their strategies are to produce high numbers of young. Another approach is found among mammals, who are iteroparous. Most of them give a great deal of adult protection to the young and ensure their survivorship in this manner.

Basically, if the parent is at low risk of death when it is young, its species will be iteroparous. If the mortality rate is high for the young, semelparity might be observed. Both strategies work well as evidenced by the continuation of both reproduction styles. **SEE ALSO EXPENDITURE PER PROGENY; REPRODUCTION; ASEXUAL AND SEXUAL.**

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Internet Resources

The Association for Tropical Biology. <<http://atb.botany.ufl.edu/atb>>.

Jawless Fishes *See* *Agnatha*.

Jellyfishes *See* *Cnidaria*.

Jurassic

The Jurassic period is the second of the three divisions of the Mesozoic era, “The Age of Reptiles.” The Jurassic lasted for 64 million years, from about 208 to 144 million years ago. The period is named for rock strata found in the Jura Mountains on the border between Switzerland and France.

During the Jurassic, the supercontinent Pangaea began to break apart. This created two landmasses, a northern mass called Laurasia (North America, Europe, and Asia) and a southern mass called Gondwanaland (South America, Africa, Australia, Antarctica, and India). During the early Jurassic, North America separated from Africa and South America and moved northward, but still remained connected to Europe. By the late Jurassic, the North Atlantic was just beginning to appear between Europe and North America.

Widespread deposits of sand in western North America indicate that the region experienced a desert **climate** during the early Jurassic. Coral reefs and the remains of temperate and subtropical forests around the world provide evidence that the climate became moister and milder later in the period. Europe was covered with shallow seas throughout the Jurassic.

Jurassic vegetation consisted mainly of seed ferns, cycads, horsetails, conifers, and gingkoes. The Jurassic is sometimes called the “Age of Cycads” because of the variety and diversity of these seed-bearing, palmlike plants. Some cycads grew to be tall as trees; other forms were short and squat.

In the marine world, the great success story was that of the **ammonites**—the coiled, shelled relatives of modern squid. At the end of the Triassic (the period just before the Jurassic), nearly 47 percent of marine species went extinct, indicating a drastic rapid deterioration of the environment that results in a crisis for certain species and is known as an extinction event. Extinction events allow some species to adapt to different environmental conditions and fill new niches. This is known as **adaptive radiation**. Although only one family of ammonites survived an extinction event at the end of the Triassic, this family radiated into an astonishing array of forms, some of which attained sizes of 2 meters (6 feet) or more.



climate long-term weather patterns for a particular region

ammonites an extinct group of cephalopods with a curled shell

adaptive radiation a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches



This reptile fossil from the Jurassic era was found in Solnhofen, Germany.



bipedal walking on two legs

carnivorous animals that eat other animals

quadrupeds animals with four legs

The Jurassic period is known for an increase in the numbers and diversity of dinosaurs. At the beginning of the period, dinosaurs such as the **bipedal** and **carnivorous** theropods were small and lightly boned, feeding on insects or other small dinosaurs. By the close of the period, massive predators like *Allosaurus* and *Ceratosaurus* had appeared. These dinosaurs had heavy bodies, powerful hind legs, front limbs used for grasping and holding prey, and long, sharp teeth for spearing and stabbing. The largest of all dinosaurs, the plant-eating sauropods, also developed during the Jurassic. The sauropods include *Apatosaurus* (formerly called *Brontosaurus*), *Brachiosaurus*, *Diplodocus*, *Seismosaurus*, and *Suprasaurus*. These animals were **quadrupeds**, with pillarlike legs (like the legs of an elephant) that supported their enormous body weight, which was often 18 metric tons (20 tons) or more. The large size of the sauropods may have helped them maintain a consistent body temperature. The *Stegosaurus* is known for a distinctive row of heavy, triangular, bony plates, known as scutes, which were arranged along its back. Paleontologists (scientists who study dinosaurs) believe these plates helped the *Stegosaurus* regulate its body temperature and protected it from being eaten. Several sharp, bony spikes on the end of the tail of *Stegosaurus* probably served as a weapon against attack.

The debate continues as to whether birds most likely evolved from small, bipedal dinosaurs or other ground-dwelling reptilian ancestors. *Archaeopteryx* is one of the earliest undisputed bird fossils. It exhibits features of both dinosaurs and birds, including a long, bony tail; small, sharp teeth; feathers; and a “wishbone” that allowed for the attachment of flight muscles.

Jurassic and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Mesozoic	Cretaceous		144
	Jurassic		208
	Triassic		245

Mammals continued to diversify during the Jurassic, but remained small and **nocturnal**, possibly to avoid competition with the dinosaurs. These early mammals were almost all **herbivores**, **insectivores**, and **frugivores** (fruit eaters). SEE ALSO GEOLOGICAL TIME SCALE.

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nocturnal active at night

herbivores animals who eat plants only

insectivores animals who eat insects

frugivores fruit-eating animals

K/T Boundary

Toward the end of the Cretaceous period, many species of marine organisms became extinct. Land dinosaurs completely disappeared, along with flying reptiles, sea reptiles, and ichthyosaurs. Other land reptiles were little affected. Most species of turtles, crocodilians, lizards, and snakes survived. Amphibians and mammals were only mildly affected.

Overall there was a major, worldwide decrease in the number of species of plants and animals. This drop in the number of species is one of the events that signaled the end of the Cretaceous period and the beginning of the Tertiary period. The transition between the two periods is known as the K/T boundary ("Cretaceous" in German is *die Kreidezeit*).

Determining whether all the species died out in a few years or over millions of years has proved to be a difficult problem for geologists and paleontologists. Attempts to pinpoint the time of the K/T boundary event result in a margin of error of at least one million years, which means that it could have taken place one million years earlier or one million years later. Although one million years is a very short time on the geologic time scale, such a margin of error indicates that all the species may not have died out at the same time. In any case, instantaneous events are very rare and usually do not affect more than a small region. For these reasons, most geologists assumed the K/T event resulted from a gradual process, such as global cooling.

An alternate to the hypothesis of extinction by a gradual process has been suggested. A group of paleontologists has proposed that the extinction may have been due to a single, catastrophic event. The American geologist Walter Alvarez first discovered evidence for this event. While conducting research near Gubbio, Italy, in the late 1970s, Alvarez discovered an abnormally high concentration of the rare element iridium in a layer of rock at the K/T boundary. The iridium anomaly, or spike, has been found all over the world in layers of rock dating to the same time. It is called an iridium spike because on a graph of iridium concentration versus time, the concentration near the time of the K/T boundary is sharply higher than in adjacent rock layers. The iridium concentration is at least twenty times more than normal and is even greater at some locations. The iridium spike seems to mark one of those rare, catastrophic events that took place worldwide.

Because meteorites often contain high concentrations of iridium, Alvarez and his father, American physicist Luis Alvarez, suggested an extraterrestrial origin for the iridium. If the iridium concentration at the K/T boundary resulted from a collision at that time between Earth and an





photosynthesis the conversion of sunlight to food

continental drift movement of the continents over geologic time

matrix the nonliving component of connective tissue

asteroid, the dust from the collision would have substantially reduced the amount of sunlight available for plants to carry out **photosynthesis**. The plants would eventually die, the large plant-eating dinosaurs would starve, and the meat-eating dinosaurs that preyed on the plant-eaters would also starve.

However, the fossil record does not show a sharp decrease in the number of large land dinosaurs, as would be expected after an impact large enough to produce global cooling. Instead, the fossil record indicates a gradual decrease in the number of species of large land dinosaurs over millions of years. There is also no marked decrease in the number of land plants. Therefore, the asteroid impact theory may be inadequate in explaining the decrease in large land dinosaurs.

The asteroid theory is generally accepted as the most likely explanation of the iridium spike and may be the best explanation for the extinction of marine organisms. The foraminifera, ammonites, coccolithophores, and other species did disappear suddenly at precisely the right time. However, there are several competing hypotheses and it is not certain that the asteroid impact alone can account for dinosaur extinction. A major difficulty of all hypotheses is the selectivity of the extinctions. Why were dinosaurs wiped out while other land reptiles were little affected?

It is possible that the mass extinctions at the K/T boundary may be due to a combination of asteroid impact and other factors. The land animals may have died out as a result of seafloor spreading, **continental drift**, and volcanism occurring around the same time; while the marine organisms were affected by the impact. Shifting oceanic circulation patterns due to continental drift may have caused climatic changes and changes in sea level. SEE ALSO CRETACEOUS; GEOLOGICAL TIME SCALE; TERTIARY.

Elliot Richmond

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Keratin

Keratin is a highly durable protein that provides structure to several types of living tissues. It is a major component of mammalian hair and hooves, mammalian and reptilian nails and horns, reptile and fish scales, bird feathers, bird beaks, and the outermost layer of skin in most animals. Keratin provides a tough, fibrous **matrix** to these tissues. An important quality of keratin is its ability to flex in multiple directions without tearing.

Keratin's microscopic structure is the key to its durability and flexibility. The molecules of this protein twist into coils called alpha helices and



The beak of a bald eagle contains keratin.



contain many disulfide bonds (bonds between pairs of sulfur ions). Disulfide bonds are particularly stable and can resist the action of proteolytic enzymes, which specialize in breaking apart proteins. Keratin is also insoluble in water. When human hair is straightened or curled in a beauty salon, special chemicals must be used to break the disulfide bonds. The breaking and subsequent reconfiguration of these bonds allows the hair to change shape. The final shape depends on the relative positions of the sulfur ions in the new bonds.

The protective structures containing keratin form through a process called keratinization. In keratinization, precursor cells to the specific tissue types first migrate from the germinal layer to their target location. Then fibers of keratin gradually invade the precursor cells, displacing cell **organelles** such as the nucleus and **mitochondria**. These organelles are **resorbed** and are not present in the mature tissue type. The differentiated, mature keratinized tissue is nonliving and incapable of sensory perception. Keratinized structures grow through the additional migration of differentiating **germ cells**, not through the division of the existing tissue cells.

Keratinized tissues can form onto a base of skin or bone. Keratinized structures such as hairs and fingernails are embedded in the skin. Calluses on hands or feet are mounds of keratin which have been created in response to repeated stress on a particular region of skin. Other structures, such as the horns of a bull, are rooted onto a bony core.

Keratinized structures take on a wide range of characteristics depending on the thickness of the protein layers. Hair is thin and flexible, whereas scales are often tough and inpenetrable. Keratin is also present in sharp structures such as spines and porcupine quills. SEE ALSO BONE; CHITIN.

Judy P. Sheen

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Keystone Species

ecosystems self-sustaining collections of organisms and their environments

equilibrium a state of balance

population a group of individuals of one species that live in the same geographic area

habitat physical location where an organism lives in an ecosystem

All **ecosystems** on Earth are formed of a delicate balance of species. When an ecosystem is at **equilibrium**, the relative numbers of organisms within each species remain stable. A food web is a graphical representation of the trophic (food-based) interactions between species. Arrows are drawn between every species and its prey, and the sum of these interconnections forms a complicated tangle of lines. In 1966 Robert Paine, an American ecologist, conceived of the idea that not every interaction in the food web is equally important in maintaining the equilibrium of the ecosystem.

Some species can dramatically increase or decrease in **population** and have little effect on the gradual return of a static-state ecosystem. This means that if this species propagates or dies off in large numbers, the relative population sizes of other species in the community will be skewed, but the community will eventually return to its original state.

Alternatively, some species have much greater importance to the community. A sizable change in the population of this type of species causes a cascade of direct and indirect effects leading to the collapse of the food web and possible loss of **habitat**. The few web links that hold such a critical importance are called strong interactions, and the species responsible for this effect are keystone species.

For example, one species of shore crab in the tropical dry forest of Costa Rica feeds primarily on tree saplings. The saplings that are distasteful to crabs grow into mature trees and eventually dominate the landscape. The environment provided by a forest of these trees is relatively open compared to the denser off-coastal forest, and this environment attracts particular animal species that like open forests, such as howler monkeys, coatis, and tapirs.

If the crab colony were to suddenly become extinct, the forest would recover its dense heterogeneous character because the saplings of invasive trees would no longer be cut back. Those animals that depend on the open forest ecosystem would languish, and could undergo local extinction.

Keystone species were considered by Paine to be top predators. He based this definition on the observation of a tidal ecosystem at Mukkaw Bay on the coast of Washington, in which the diet of a particular species of starfish included several secondary predators (when a carnivore feeds on other carnivores, these prey are called secondary predators). In Paine's example, the secondary predators were in direct competition. Paine observed that removing the dominant starfish from an experimental plot increased competition among these secondary predators. Their populations increased because the top predator was no longer killing them off, and thus they were able to kill off more of their own prey, which were lower on the food chain.

As a result, the populations of the remaining species fluctuated rapidly. After two years, the species diversity, defined as the number of species per area of land, had decreased from fifteen to eight. This effect showed how the top predator's existence was keeping the other species in check. By feeding on the competing secondary predators, the keystone starfish had prevented them from devastating populations of species lower down the food chain.

When the starfish was removed, the food web was thrown into chaos. Note that the keystone species is not the dominant species—it does not have



the largest number of individuals in the ecosystem. By definition its influence must be far larger than its population can account for.

Since Paine's landmark study, species of other **trophic levels** have been described as keystone, and many of them are not top predators. Animals such as beavers are considered to be keystone because they engineer the environment. Beavers build dams in rivers and streams that create large bodies of still water. Pond-dwelling animals and plants may then colonize the new environment. If beavers were removed, the environment they created would collapse. The dam would eventually break apart and the entire pond food web would be disrupted.

Another type of keystone species is an exotic, or introduced, species. This is a foreign organism that enters a new habitat and disrupts the existing food web. One example of this is the spread of introduced kudzu in the Atlantic region of the United States. Kudzu is a vine native to desert habitats that is known to decrease erosion of sand dunes. After being imported into the United States in 1876 for ornamental gardens, kudzu was adapted to control erosion during the Great Depression of the 1930s. Kudzu quickly

trophic levels division of species in an ecosystem by their main source of nutrition



pathogens disease-causing agents such as bacteria, fungi, and viruses

adapted to the plentiful water and rich soil of the southern United States, in the process choking out native shrubs, flowers, and trees. Because trophic interactions with other plants and animals in the area were so greatly affected, kudzu is considered to be keystone.

Alternatively, some consider certain **pathogens** to have a keystone effect, such as the canine distemper virus's effect on lion populations in Serengeti National Park in Africa. This occurred in 1994, when the domesticated stray dogs living along the park boundaries in Tanzania and Kenya transmitted canine distemper virus to the wildlife. This resulted in thousands of deaths within the lion population. The disease also affects leopards, cheetahs, tigers, raccoons, coyotes, wolves, foxes, ferrets, skunks, weasels, mink, badgers, hyenas, and jackals.

Paine's narrow definition has since been broadened to include mutualists (animals that provide benefits for and receive benefits from another species), pathogens (disease-causing microorganisms), parasites, and many more feeding strategies than merely top predator. Also in the 1960s, researchers defined "functional group," a collection of many species that collectively perform the role of a keystone species.

Human beings cannot be called a keystone species because our influence on nature is not disproportionately large compared to our abundance (population size). Our cities, roads, and technologies, however, have altered nearly every ecosystem on Earth. Because species diversity is a strong signifier for a healthy habitat, it is important for humans to understand how to preserve the greatest species diversity within remaining natural habitats. This requires knowledge of how to stabilize a high species diversity in parklands and nature preserves.

The largest grouping of endangered species in the United States consists of primary predators, such as large predatory cats, bears, and eagles. If, as Paine suggested, many of these top predators are keystone, then their extinction will create turmoil in the relative numbers of remaining species. The overabundance of deer and raccoons in urban areas of the United States reflects this destructive trend. **SEE ALSO ECOYSTEM; INTERSPECIES INTERACTIONS.**

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Kingdoms of Life

Life on Earth originated between 3.5 and 4 billion years ago. Since then millions of different organisms have evolved (and most have gone extinct). Faced with such a multitude and diversity of organisms, biologists have

looked for ways to classify all these organisms into different groups to make it easier to study them. But what criteria should they use for grouping? And how big or small should the groups be?

The most meaningful way of grouping organisms is based on how they are related. In this way, group membership will reflect the organisms' common evolutionary history. This means that scientists want to group organisms that share a common ancestor. In addition, they want to show characteristics that unite all group members with each other but that also distinguish group members from nongroup members. For example, all mammals have hair and milk glands, characteristics unique to mammals. The number of groups and the number of organisms within a group depends on the grouping criteria and whether the emphasis is on how organisms are different or how they are the same (this is often referred to as the "splitters" vs. "lumpers" approach). There is really no incorrect way of grouping organisms as long as the grouping criteria are clearly stated and strictly followed.

Systematists (scientists that study the classification of organisms) have traditionally considered the kingdom to be the highest and most inclusive category. However, deciding exactly how many kingdoms to recognize had been a source of controversy until 1969, when Robert H. Whittaker of Cornell University introduced a five-kingdom system that became popular with most biologists. Whittaker's five kingdoms are Monera, Protista, Plantae, Fungi, and Animalia. One kingdom, Monera, contains all the **prokaryotes**, and the other kingdoms contain different groups of eukaryotes. However, work done in the 1980s by Carl R. Woese of the University of Illinois on the genetic makeup of cells seems to favor a six-kingdom system that divides Monera into two kingdoms, Bacteria (Eubacteria) and Archae (Archaeabacteria).

Bacteria and Archae are both prokaryotes, but when researchers compared their ribosomal RNA sequences, they found that Archae are more closely related to eukaryotes than they are to other prokaryotes. It appears that eukaryotes evolved from an Archae-like ancestor and subsequently took up **genes** from Bacteria (e.g., purple bacteria, cyanobacteria), thus acquiring **mitochondria** and chloroplasts.

Bacteria live in many different environments. This kingdom includes many **pathogens**, including *Salmonella*, which causes food poisoning, but also many economically important species such as *Lactobacillus*, which is used to make yogurt; *Rhizobium*, which "fixes" atmospheric nitrogen for plants to use; and *Streptomyces*, which is a source of many antibiotics. In contrast, Archae, including the methanogens, halophils, and thermophiles, live in extreme environments that are hot, salty, or **acidic** such as hot springs or deep sea vents. One Archae, a thermophil, is the source of a heat-resistant **enzyme** that is widely used in molecular biology.

The eukaryotic Plantae, Fungi, and Animalia kingdoms contain mostly multicellular eukaryotes that differ in their structures, modes of nutrition, and life cycles (before reproduction). For example, Plantae (mosses, ferns, conifers, flowering plants) have cell walls containing cellulose and are **autotrophs**, which means they make their own food from carbon dioxide and an energy source such as sunlight. In contrast, both Fungi (yeasts, mushrooms, truffles, bread molds) and Animalia (jellyfishes, sponges, worms,

prokaryotes single-celled organisms that lack a true cell nucleus

genes segments of DNA located on chromosomes that direct protein production

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

pathogens disease-causing agents such as bacteria, fungi, and viruses

acidic having the properties of an acid

enzyme a protein that acts as a catalyst to start a biochemical reaction

autotrophs organisms that make their own food



Kingdom	Type of Organism	Characteristics
Monera	Bacteria	Spherical, rodlike, or spiral forms
	Blue green algae	Photosynthetic
Protista	Diatoms	Single-celled; photosynthetic
	Silicoflagellates	
	Coccoliths	
	Dinoflagellates	
	Animal flagellates	Similar to euglenoids but lack chlorophyll
Fungi	Ciliated protozoan	Multinucleated organisms; parasitic; heterotrophic; have cell walls
	Slime molds	
	<i>Schizomycophyta</i> bacteria	
Plantae	Mosses	Have cell walls containing cellulose; autotrophic
	Ferns	
	Conifers	
	Flowering plants	
Animalia	Jellyfishes	Heterotrophic; no cell walls
	Sponges	
	Worms	
	Snails	
	Insects	
	Fishes	
	Amphibians	
	Reptiles	
	Birds	
	Mammals	

Five-kingdom classification system.

heterotrophs organisms that do not make their own food

snails, insects, fishes, amphibians, reptiles, birds, mammals) are **heterotrophs**, which means they get their energy by eating other organisms. Fungi and Animalia differ in that Fungi secrete digestive enzymes and then absorb the digestive juices, while Animalia ingest other organisms. In addition, Fungi have cell walls, Animalia do not.

The kingdom Protista contains a wide variety of organisms, ranging from single-celled autotrophs (diatoms, dinoflagellates) and heterotrophs (amoebas, ciliates) to colonially living heterotrophs (slime molds) and large multicellular autotrophs (algae such as kelp and seaweed). Protists were the first eukaryotes to evolve, and members of this group gave rise to the other eukaryotic kingdoms. The diversity that we find among the organisms in the kingdom Protista stems partly from the fact that Protista is what systematists call a “wastebasket” kingdom. This means that any organism the systematists cannot assign to one of the other kingdoms (using the above grouping criteria) is assigned to the Protista. This also means that with further work and the establishment of new grouping criteria, we may see a further division of the Protista into several new kingdoms in the not-too-distant future. Science is an ongoing process! SEE ALSO **PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS**.

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Lamarck, Jean-Baptiste

Botanist

1744–1829

Jean-Baptiste Lamarck was born on August 1, 1744, in Bazentin-le-Petit, France. He died on December 18, 1829. He is best known for his theory on evolution, which stated that acquired traits can be inherited. Charles Darwin later challenged this theory. Lamarck also was the first scientist to define animals as either vertebrates (having backbones) or invertebrates (those without).

Lamarck came from a long line of military horsemen. At the age of nineteen he left a school run by Jesuits (a religious order) to join the army. While serving he became interested in the plants along the Mediterranean Sea. Resigning from the army after an injury, Lamarck began to study medicine, but then switched his interest to **botany**. He studied under the French botanist Bernard de Jussieu at the royal botanical gardens in Paris. After years of studying and collecting, he published a three-volume work on the plants of France in 1778. This gained him recognition, and in 1781 he was put in charge of the royal gardens in Paris.

In the 1790s Lamarck changed his interest from plants to animals and soon developed a system for classifying invertebrates. He appears to have been the first scientist to relate fossils to the living creatures to which they are most similar. When the Museum National d'Histoire Naturelle was founded in 1793, Lamarck was placed in charge of the invertebrates. Lamarck was one of the founders of the modern concept of the museum collection.

From his studies on plants and animals, Lamarck developed his theory of evolution. He believed that plants and animals change their forms to adapt to their environment, and that their young inherit these changes. He thus believed, for example, that the forelegs and necks of giraffes have become longer due to the way they eat. These acquired traits would be passed on to following generations. Lamarck presented his ideas in the famous *Philosophie Zoologique* (1809). His theory, not unreasonable for its time, was later disproved by discoveries in **genetics** in the early 1900s and rejected by most scientists. However, the Soviet Union embraced Lamarck's theory in the Stalin era. This set that nation back in genetics until the 1960s.

Another area of interest for Lamarck was the weather. He was the first scientist to try to forecast it. He published an annual weather report from 1799 to 1810. He is believed to have named the various types of clouds: cirrus, stratus, cumulus, and nimbus. SEE ALSO ADAPTATION; BIOLOGICAL EVOLUTION.

Denise Prendergast



botany the scientific study of plants

genetics the branch of biology that studies heredity



Jean-Baptiste Lamarck's theory of evolution was later challenged by Charles Darwin.



Internet Resources

Jean-Baptiste Lamarck (1774–1829). Museum of Paleontology, University of California, Berkeley. <<http://ucmp.berkeley.edu/history/lamarch.html>>.

Leakey, Louis and Mary

Anthropologists

Louis Leakey 1903–1969

Mary Leakey 1913–1996

Louis and Mary Leakey were a husband-and-wife anthropology team that contributed much to the modern understanding of human origins. Louis Seymour Bazett Leakey was born in 1903 outside Nairobi, Kenya. He was sufficiently integrated into the local life there that he was accepted as one of the tribe of the Kikuyu people and learned their language first. To fulfill the foreign-language requirement at Cambridge University, Leakey was permitted to test himself on Kikuyu, as nobody else was qualified. At Cambridge, he specialized in archaeology and anthropology, receiving a Ph.D. in 1930. He discovered what he considered to be the oldest known human fossils in 1931, but a combination of poor notes and a shoddy understanding of geology prevented him from reliably identifying them.

This error precipitated a series of strong criticisms of Leakey's methods from a number of sources. His former colleague Martin Pickford suggested Leakey "broke records in misreporting the discovery context of important fossils and stone tools" over the course of forty years. Nevertheless, Leakey conducted numerous significant digs at Olduvai Gorge and was the first to characterize *Homo habilis*, a human ancestor. Mary Leakey discovered "Zinjanthropus" (*Australopithecus boisei*), an extinct hominid species that brought them worldwide fame. Louis disdained what he perceived to

The Leakeys work at an excavation site in central Africa in 1961.



be unnecessary measuring and statistical analysis by his contemporaries; he was much more interested in experiments of an occasionally crackpot nature. Naked, he charged a pack of hyenas to steal their prey and chewed off a hunk of the carcass to see if a modern human could do so. He thought zebra fat could cure tuberculosis; he wanted to flood the Sahara and make an ocean.

By contrast, Mary, who never earned an advanced degree, was a much more meticulous scientist and eventually gained greater respect in the field. They had met while she was illustrating his *Adam's Ancestors*. As a couple they encouraged Jane Goodall and Dian Fossey in primate research. Together the Leakeys established that the upright posture of later protohumans led to free hands, and therefore to tool making. Louis began to travel more from Africa, lecturing and womanizing despite being in poor health, while Mary stayed behind in Olduvai Gorge and Nairobi. The pair grew distant. Louis died in 1969, and Mary died in 1996 at the age of 83.

Ian Quigley

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Learning

The need for experimental proof is a key part of the scientific definition of learning. As outside observers of animal behavior, humans are practically incapable of understanding which cognitive processes, if any, lead to the production of a certain animal behavior. For example, a pigeon may be trained to type the letters “f-o-o-d” on a typewriter when it is hungry.

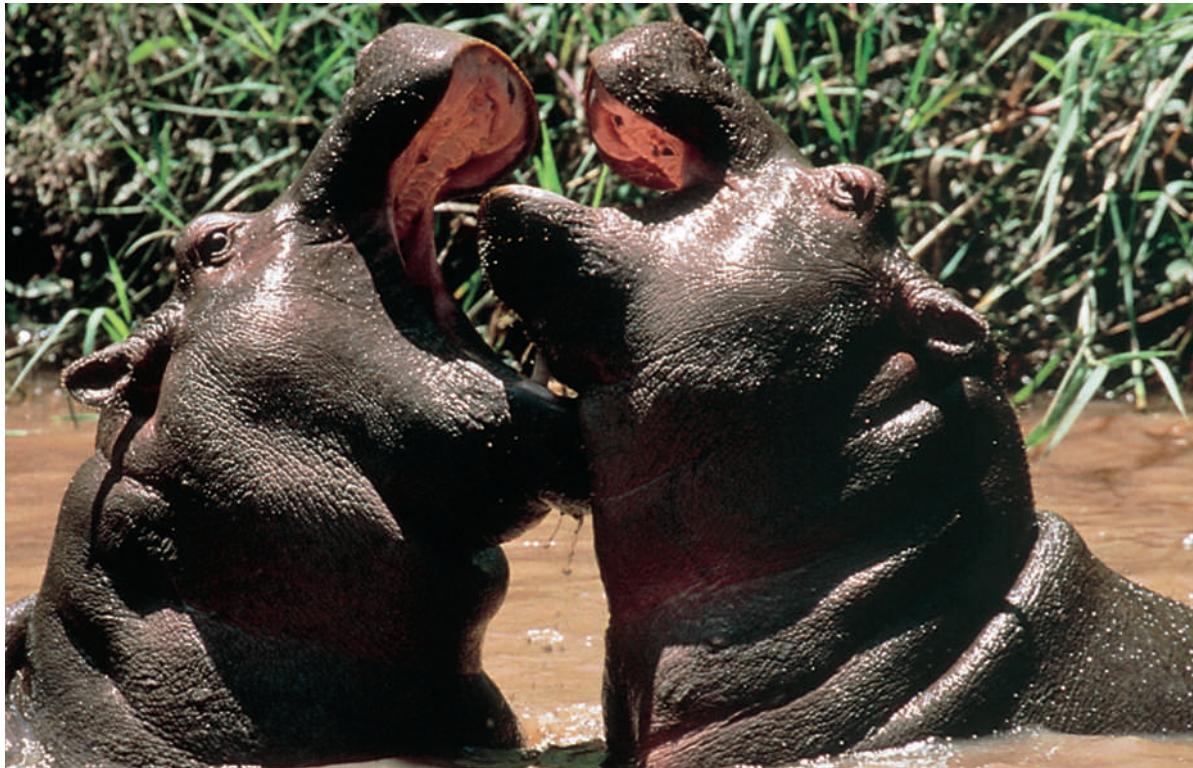
Although we may be tempted to conclude that the pigeon has learned a new word, this is unlikely. There may be many explanations for the pigeon’s behavior. Only with carefully designed experiments and a general learning theory, we can begin to dissect exactly what motives cause the animal to behave this way. Although we may observe animals performing complex tasks in the wild, we cannot conclude that the animal has learned without rigorous experimental tests in a controlled setting.

Even in a strictly monitored experiment, the results of a learning test can be inconclusive. The general model for such experiments was to train an animal to perform a task. This training was accomplished by choosing a natural behavior of an animal and modifying or encouraging that behavior with a treat and a signal. Eventually, the signal will cause the animal to perform that behavior in order to receive the treat.

In other words, the unconditioned **stimulus**, or natural behavior of the animal, is paired with a conditioned stimulus, the chosen signal. When the animal responds to the conditioned stimulus with the appropriate behavior, it is rewarded with a treat, which leads to an eating reward. Thus, a rat that displays the normal ratlike behavior of rearing on its hind legs is suddenly rewarded with a piece of fruit every time it performs the behavior. At the

stimulus anything that excites the body or part of the body to produce a specific response





Two young male hippopotamuses play fight. The lessons learned through play will benefit them in their adult lives.

same time that it rears, a red light flashes at the side of the cage. Eventually, flashing the red light will cause the rat to rear on its hind legs, supposedly because it expects to receive its treat. In this case, the rearing behavior is the unconditioned stimulus, the red light is the conditioned stimulus, and the fruit is the reward.

Psychologists and cognitive biologists have long argued over what exactly this hypothetical rat is learning. It is possible that the rat equates the conditioned stimulus, abbreviated as CS, with the treat reward, abbreviated as R. If this is true, then the rat learns that the flashing light means that treats are coming.

Alternatively, the rat may understand that rearing, which is the unconditioned stimulus (US), leads to a treat reward; in this case the light tells the rat when to rear, but has no real meaning with regards to the treat. Both of these examples assume that the rat is associating the stimulus, S, with the reward, R. This is called S-R learning. Another explanation is that the rat learned that one stimulus—rearing or the light—leads to another stimulus, the appearance of the treat.

The subtle difference between this interpretation and S-R learning is that in this case, appearance of the food is not the rat's reward. Instead, appearance of the treat is merely another stimulus that causes the rat to eat, and the actual consumption of the food is the rat's reward. Because the treat is considered another stimulus in this theory, it is referred to as S-S learning.

A class of scientists known as behaviorists believed that animals are defined solely by their behaviors, and that behaviors are determined entirely by environmental cues. Thus every animal is born with the ability to learn

any new task. Two of this field's main proponents were the psychologists B. F. Skinner and Ivan Pavlov. Pavlov discovered what was called classical conditioning, a method of pairing a conditioned and an unconditioned stimulus so that eventually the conditioned stimulus alone elicits the response.

His famous experiment tested a dog salivating when food is presented. If a bell is rung at the same time the food is presented, every time, eventually the dog will salivate to the sound of the bell even in the absence of food. Skinner used similar principles to describe the behavior of humans. He proposed the theory of operant conditioning. According to this theory, the animal performs a wide variety of activities in its daily life, and some of these activities are rewarded by a reinforcing stimulus. This reinforcement increases the effect of the operant, the behavior directly preceding the reinforcing stimulus. Operant conditioning is widely used to train animals, but it is also a theory on their methods of learning.

Ethologists such as Nikolaas Tinbergen disagreed with the behaviorists' opinion that the mechanisms of learning are the same for all animals. Ethologists believe that natural animal behaviors are innate, meaning that the animal is born with a neural system that promotes certain species-specific behavior. This is why animals tend to produce species-specific **vocalizations** and behaviors, even when they are raised in very foreign environments.

vocalizations sounds used for communication

Tool use is one example of an innate behavior for several organisms, such as the male satin bower bird of Australia and New Zealand, which constructs elaborate abstract designs out of twigs, leaves, and dirt to attract the female. He decorates these sculptures by crushing berries and fruits for their pigmented juice and then painting the structure using a wad of bark as a paintbrush. Elaboration of tool use is more easily taught to those species that have the innate tendency to use tools.

The combination of behaviorist and ethologist influences on the study of learning have shaped modern psychology. Animals are still used to test how humans learn, but unique species traits are now taken into consideration when interpreting the data. **SEE ALSO BEHAVIOR; TOOL USE.**

Rebecca M. Steinberg

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Levi-Montalcini, Rita

Italian-American neurologist
1909–

Rita Levi-Montalcini, born in Turin, Italy, is a prominent neurologist who discovered nerve-growth factor (NGF), a substance that controls how many



Rita Levi-Montalcini discovered nerve-growth factor.

regeneration regrowing body parts that are lost because of injury

cells make up the adult nervous system. This 1952 discovery has become an important clue to how life starts as a single embryonic cell and then marvelously differentiates into a complex organism made up of many different cell types. Levi-Montalcini's work has also contributed to the understanding of neurological diseases such as Alzheimer's and Parkinson's, tissue **regeneration**, and the mechanisms of cancer.

Before the discovery of NGF, little was known about how organs signal developing nerve cells to link up with them or how messenger chemicals tell nerve cells when to grow and when to stop growing. Scientists now know of several hundred signals that affect cells and organs, and growth factors can be used to speed up burn healing and to diminish the side effects of the chemotherapy and radiation therapy that are used to combat cancer.

Levi-Montalcini's discovery of NGF and her other scientific work are nothing short of remarkable considering her tumultuous life circumstances. Her childhood was dominated by an unreasonable father who refused to acknowledge her love of science. Rather than encouraging her to pursue science and math courses, he insisted Levi-Montalcini attend finishing school where, much to her disgust, she had to study childcare, etiquette, and marriage. After completing finishing school, and largely against her father's wishes, Levi-Montalcini hired a tutor to teach her math, science, Latin, and Greek for eighteen months until she was able to pass the entrance exam to the University of Turin medical school. In 1936 she completed medical school, specializing in neurology and psychiatry.

After graduation, Levi-Montalcini accepted a research position at the university. After only three short years, she was forced to leave when the fascist anti-Semitic laws that governed Italy at the time drove her away. Not to be deterred, Levi-Montalcini constructed a crude home laboratory using scrap materials and continued her research under secretive conditions. After World War II, she moved to the United States where she continued her research at Washington University in St. Louis, Missouri, from 1947 to 1981. In 1981 she returned to Italy, where she still lives.

In 1986 Levi-Montalcini was awarded the Nobel Prize for physiology or medicine, an award she shares with her American coworker at Washington University, the biochemist Stanley Cohen. She is also the founder of the Laboratory of Cellular Biology, one of the largest biological research centers in Italy.

Stephanie A. Lanoue

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Life History Strategies

Among biological organisms, there is a continuum in life history strategies between what are referred to as *r*-selected species and *k*-selected species. Life history strategy is correlated with many aspects of an organism's re-

productive strategy and life history, as well as with demographic variables such as generation time and life span, and **population parameters** such as **population density** and **population dynamics**. Where individual species fall on the *r*-*k* continuum is largely determined by the environment in which they live.

The variables *r* and *k* in *r*- and *k*-selection come from the logistic equation for population growth. This equation describes how population density changes over time. In the initial phase, population growth is very rapid and largely dependent on the variable *r*, which represents the intrinsic rate of natural increase of a species. Mathematically, *r* is the birth rate plus the immigration rate, minus the **death rate** and the emigration rate. A population grows rapidly in its initial phase because there are abundant resources, and consequently little or no competition between individuals. Thus, *r*-selected species exist in circumstances where they are often at this stage of rapid growth.

The *k* refers to the maximum density at which a population is able to exist in a given environment, and is called the carrying capacity of that environment. The value of *k* depends on the resources available. Once population densities are close to the **carrying capacity**, growth slows and population density levels off at or around *k*. Because resources are no longer in abundant supply in this saturated environment, there is significant competition between the individuals of a population. Species that are *k*-selected describe those for which the population density is usually close to the carrying capacity. Differences between *r*- and *k*-selected species exist over a wide variety of traits.

Those species that are *r*-selected exist well below the carrying capacity of their environment. This may be a consequence of either **biotic** or **abiotic** qualities of the environment. For example, many *r*-selected species are associated with unstable environments that alternate between periods of abundance and periods of high mortality. So long as resources are abundant, populations grow exponentially. Then, the population is decimated and the cycle begins again. On the other hand, population densities may remain well below the carrying capacity of an environment as a consequence of biological factors such as predation.

Because *r*-selected species exist well below the carrying capacity of the environment, there is generally little competition between individuals. In addition, mortality may depend largely on chance. Under these circumstances, the production of high-quality offspring may not necessarily pay off. It is more important to produce a large number of offspring as quickly as possible, thus increasing the probability that at least a few of them will survive long enough to contribute to the next generation. The emphasis is on the quantity of offspring produced rather than on their quality.

Features associated with *r*-selected species include small size, a short generation time, reproduction early in life, and the production of large numbers of offspring in which comparatively little investment is made. Some *r*-selected species are **semelparous**, meaning that individuals reproduce in one big reproductive bout and then die. This is sometimes referred to as big-bang reproduction.

In terms of life history, *r*-selected species exhibit what is called a Type III survivorship pattern, with very high mortality in the early stages of life,

population parameters a quantity that is constant for a particular distribution of a population but varies for the other distributions

population density the number of individuals of one species that live in an given area

population dynamics changes in a population brought about by changes in resources or other factors

death rate a ratio of the number of deaths in an area in a year to the total population of the area

carrying capacity the maximum population that can be supported by the resources

biotic pertaining to living organisms in an environment

abiotic nonliving parts of the environment

semelparous describes animals that breed only once and then die





exponential growth a population growing at the fastest possible rate under ideal conditions

iteroparous animals with several or many reproductive events in their lives

and only a very small proportion of individuals surviving into adulthood. The population patterns of *r*-selected species often show periods of rapid, **exponential growth**, followed by sudden crashes. Often, *r*-selected species are the first colonizers of a new habitat.

K-selected species, on the other hand, generally occupy comparatively stable environments. Because there are long periods of environmental stability, populations are able to increase in size until population densities are close to the carrying capacity k of the environment.

In these saturated environments, crucial resources are in short supply, and there is intense competition between individuals of the population. As a result, competitive ability becomes very important. The number of offspring produced becomes less important, while the quality matters more. (There is a necessary trade-off between the quality and quantity of offspring produced, because of the limited resources that a parent is able to acquire and process.)

In *k*-selected species, individuals produce fewer, high-quality offspring that will perform and survive better in a competitive world. This is associated with such traits as larger body size, longer generation time, slower development, and reproduction later in life. *K*-selected species also often exhibit parental care.

K-selected species are more likely to be **iteroparous**, that is, to reproduce in numerous bouts. They also tend to invest in survival more than *r*-selected species, and may generally be more intelligent. Unlike *r*-selected species, *k*-selected species have a Type I survivorship curve, where survival early in life is relatively high and most individuals live to a comparatively late age. Population sizes in *k*-selected species are relatively stable, at or near the carrying capacity of the environment. Unlike *r*-selected species, *k*-selected species are not effective colonizers. Instead, they tend to be found in climax communities (stable, long-established ecological communities).

It is important to remember that there is a continuum between *r* and *k* strategies among biological organisms, and that it sometimes does not make sense to try to pigeonhole species as one or the other. Mice, for example, seem to be *k*-strategists compared to clams, which are perpetually emitting tiny eggs. Mice are also characterized by parental care.

However, when compared to other species of mammals, mice are closer to the *r*-strategist extreme. Their generation time is shorter than that of most other mammals, as is their life span and time to reach reproductive maturity. In addition, mice have much larger litters than most mammals.

Small mammals such as rodents and rabbits are often closer to the *r*-selected extreme, while larger mammals such as humans and elephants are more *k*-selected. Among plants, weedy species are *r*-selected, while larger species with longer life spans, such as trees, are *k*-selected.

Jennifer Yeh

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Linnaeus, Carolus

Botanist

1707-1778

Carolus Linnaeus was born on May 23, 1707, in Råshult, Sweden. He died on January 10, 1778. Linnaeus was the founder of the modern scientific method of naming plants and animals. He was the first person to name each living thing with two names: the genus (group) and the species (kind). It was Linnaeus who first gave humans the scientific name *Homo sapiens*. Linnaeus, the son of the parish pastor, showed an early love of flowers. By the age of eight he was nicknamed "the little botanist." Linnaeus studied at the universities of Lund and Uppsala. He was appointed lecturer in botany at Uppsala in 1730. Two years later, with fifty dollars given to him by the Royal Society of Science, he explored Lapland, walking nearly 1,600 kilometers (1,000 miles) over a five-month period. From this experience, he wrote *Flora Lapponica* (1737), a book that firmly established his reputation. In 1735 he received his degree in medicine from Uppsala. While in medical school, he had a small botanical garden and wrote careful descriptions of its plants. These notes formed the basis for his later books. In Holland, he published his work on classifying and naming various plants in *Systema Naturae* (1735), *Fundamenta Botanica* (1736), *Genera Plantarum* (1737), and *Critica Botanica* (1737). Linnaeus created a revolutionary advance by introducing a Latin binomial (two-name) system: each species received a Latin name with two parts (the genus and the species). Linnaeus also recognized other, broader classification groups that are still used today: order, class, and kingdom. His system allowed plants to be placed rapidly in a named category, which was extremely useful during the eighteenth century, when new plants were being discovered at a very fast rate. Linnaeus classified not only plants and animals but also minerals and the kinds of diseases known in his day.

In 1738 Linnaeus returned to Sweden, settling in Stockholm, where he was very successful as a practicing physician. In 1739 he married Sara Moraea, the daughter of a physician. Two years later, he was appointed to the chair of medicine at Uppsala, but after a year he transferred to a chair of botany there. His later years were spent teaching and writing books. In 1761 he was knighted by the Swedish government in recognition of his work.
 SEE ALSO BINOMIAL (LINNAEAN SYSTEM).

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Livestock Manager

Livestock managers take care of livestock on farms and ranches. Livestock include animals such as beef cattle, swine (pigs and hogs), goats, and sheep. The animals are raised and sold for food, their hides, or breeding purposes. On farms and ranches, the animals may graze in open pastures and be housed in barns or pens.

Animals need to be taken care of every day. Unless they are grazing, they must be fed and watered daily. Livestock managers must be sure their herds are healthy. They routinely examine the animals and may give them vaccinations and medicines. Barns and pens must be repaired and kept clean, and fences around grazing areas must be maintained. The livestock manager may be involved in the planting, harvesting, and storage of different food crops for the livestock. Other activities include branding animals for identification purposes and rotating animals from one pasture to another. Sheep must be routinely sheared so that their wool can be sold.

Livestock managers may also breed animals. This involves picking the best livestock to be bred, artificially inseminating the animals, assisting with the births of the offspring, and feeding and caring for both the parents and offspring. Records must be kept regarding the animals' weights, diets, birth records, and pedigrees. Computers are important for managing this type of data.

Becoming a livestock manager does not necessarily involve formal training or education. A person may acquire the necessary practical knowledge by working under more experienced persons on a farm or ranch. In grade and high school, it is good training to participate in livestock programs run by organizations such as 4-H. A livestock manager would benefit from a university degree. A bachelor's degree in agricultural sciences (the study of farming, producing crops, and raising livestock) with an animal science major provides a thorough understanding of raising livestock. Courses include those in animal sciences (breeding, nutrition, **genetics**), agriculture (entomology, natural resources, veterinary science), and business (economics, accounting, marketing).

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genetics the branch of biology that studies heredity

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Living Fossils

The history of life on Earth is deciphered through the examination of fossils. Fossils are inorganic remains of plants and animals that reveal the structure of certain parts of the organism. By examining the way structures change in certain organisms over time, the natural history of a particular group can be reconstructed. Many organisms do not have structures suitable for fos-

silization, like the soft body of a snail. However, some portions of the snail's body (the shell) are easily turned into fossils over time. Snail shells, millions of years old, are discovered when they are exposed near the surface of Earth. By studying these fossils it is possible to partially deduce what snails, or any other fossilized lineage of organisms, looked like over millions of years of change. Living fossils are divided into two categories. The first includes organisms that are believed to have changed very little over time and that still retain a close resemblance to their older extinct relatives. Examples of these types of organisms are found all over the world. A familiar example of a living fossil of this type is the **horseshoe crab**. The structure and body of the horseshoe crab is very similar to ancient fossils of **arthropods**. Arthropods evolved to become several distinct and large groups of organisms. Insects, **crustaceans** (crabs, shrimp, and lobsters), and a wide variety of additional animals are all descendants of the early arthropods. Although the living arthropods share several features of the ancient arthropods, they are also quite different in major body structures and functions.

The horseshoe crab, however, is still very similar to the ancient forms of arthropods and helps us to understand how ancient arthropods looked and lived. This is why crabs are called living fossils. In the continental United States, the horseshoe crab is found only on the Atlantic seaboard.

Another example of this type of living fossil is the shark. Sharks do not appear to have changed very much over hundreds of millions of years. The rare fossils of sharks and their relatives show that they had bodies very similar to the species living today. Shark teeth are more commonly found as fossils since they are the only true bony part of the animal. By comparing the teeth of ancient and modern sharks it is possible to see that sharks also qualify as living fossils.

In the plant kingdom, the horsetail rush and the palmlike cycad are considered the last living relatives of their extremely ancient ancestors. The relatives of these plants are often found as fossils in regions where dinosaurs are discovered. They are believed to have been the food of some of these giant **herbivores**.

In the marginal areas of the sea that are adjacent to the land there is a single remnant of a once flourishing group of **bivalves** called the **brachiopods**. They once lived in the oceans by the millions. There were numerous species and they were distributed over the coastal regions of the entire planet. The brachiopods lived for many millions of years and were as common as clams are today. However, only one simple species has survived. It is a small brachiopod called Lingula.

The brachiopods appear initially to be similar to clams. In truth, however, they are quite different. Their soft tissues (internal organs) are nothing like those of a clam. In fact, brachiopods are so different from clams that they do not even belong in the same phylum, Molluska. If Lingula were not still living it is possible we would know very little about how the brachiopods lived, reproduced, or what their internal structure was like. This living fossil helps biologists to know a great deal about an ancient group that may have been a mystery.

The second category of living fossil is more exciting for researchers to discover. They are examples of species of plants or animals that were

horseshoe crab a "living fossil" in the class of arthropods

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

herbivores animals who eat plants only

bivalves mollusks that have two shells

brachiopods a phylum of marine bivalve mollusks



A coelacanth is an example of a living fossil.



believed to have been extinct, but have been rediscovered in modern times. They are truly living fossils in that they are species of ancient organisms that have survived extinction by living in small pockets of land or ocean in which conditions may have been marginal, but livable. They have lived and reproduced continuously for hundreds of millions of years, but managed to escape notice until the last century. These organisms may once have been found throughout the world, but live today in very specific, geographically small areas.

One of the most famous examples of this type of living fossil is the coelacanth. The coelacanth is a member of a group of fish called the Sarcopterygians, which are believed to be the ancestors of the land **vertebrates**. They are commonly referred to as the lobe-finned fish because their **pectoral** and pelvic (front and back) fins are very thick and sturdy and look more like heavy lobes than fins. These fish are long and round and often use these fins to rest the weight of their heavy bodies on the seafloor. The structure of the fins of the Sarcopterygians is very similar to that of the bones of all land vertebrates, including humans, leading researchers to believe that these ancient fish were the ancestors of the amphibians and all other tetrapods.

Until the early part of the 1900s, all that was known about the coelacanths was derived from the study of fossils. However, on a winter day in 1938, fishermen in a boat near the mouth of the Chalumna River, off the coast of South Africa in the Indian Ocean, found a strange fish tangled in their nets. As the story goes, a British woman living in the region recognized the fish as rare and unusual. The woman purchased the fish and sent it back to Britain where it was declared a marvel. A lineage of fish believed to have been extinct for over 65 million years was still alive! Examining this extraordinary fish was like looking into the past. It had all the characteristics of the fossil species, but was different enough to be given its own species name. The scientific name for this fish is now *Latimeria chalumnae*.

The excitement from the discovery of this fish has still not subsided. About 200 additional *Latimeria* have been discovered since the first one

vertebrates animals with a backbone

pectoral of, in, or on the chest

was caught. Scientists do not believe their **populations** are very large, and they apparently live in very deep water, which makes it difficult for researchers to study them. First, they are hard to find. Second, they are very difficult to keep in captivity for study because they require a high-pressure environment in order to remain alive. However, scientists are gradually **learning** more about this living fossil and are successfully keeping it alive in newly designed aquariums. In addition to this advance, another species, *Latimeria menardensis*, was recently discovered off North Sulawesi Island in Indonesia.

One of the important things scientists have learned by studying these living fossils is that they apparently hatch their young inside their bodies which is unusual for most fish. This piece of information has lead to speculation about how these early ancestors of amphibians may have reproduced. This may have led to the ability to possibly breed out of water without endangering or drying out their eggs. Unfortunately for the coelacanth today, this means that they cannot reproduce in large numbers and need all the help from conservationists they can get.

It is believed that there are only a few hundred of these fish alive at present. They are still in danger of extinction and in need of protection. However, if any animal qualifies for the title of “living fossil,” the coelacanth is probably the most famous.

Another living fossil was discovered during the last century. This fossil was of a plant believed to have been extinct since the demise of the dinosaurs. The plant belongs to a group called the gymnosperms, or naked seed plants. They are part of a group that includes plants that make seeds without a seed coat. The living fossil we are talking about is called *Ginkgo biloba*.

For hundreds of years this small tree was known only from fossil impressions in clay. Its **fossil record** extends back in time almost 200 million years and the tree was once common all over North America and Europe. The Ice Age is believed to have made environmental conditions too harsh for the plant’s survival. In more recent times, the gingko was considered a sacred tree in China, and a group of Buddhist monks cared for and nurtured the tree in a remote valley in China. This small group of trees was discovered by explorers and reintroduced to the world. Unlike the coelacanth, the gingko has flourished since being rediscovered and today gingkoes are found flourishing all over the world. They are a link to the days of the dinosaurs and can be found as ornamental trees in many communities. The gingko has become so popular it is even included in some botanical medicines.

Additional examples of living fossils exist in many groups of animals and plants. Some **mollusks**, such as the *Nautilus*, were another amazing discovery of a remnant species of an ancient group of cephalopods. Other modern relatives of the cephalopods include the octopus and squid. It too was discovered in deep ocean waters off the coast of Indonesia. One of the intriguing aspects of the nautilus is that it represents a very primitive form of the ancient cephalopods. Animals derived from this ancient group are called ammonites and have extremely complicated and beautiful shells. Some grow to extremely large size compared to the nautilus and measure several feet across. They are believed to be carnivores of the deep oceans and able to

population a group of individuals of one species that live in the same geographic area

learning modifications to behavior from experience

fossil record a collection of all known fossils

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses





swim up and down columns of water in the ocean feeding on fish they encounter.

Until the nautilus was discovered, the Nautiloids were considered extinct and people knew very little about the soft tissue structure of these amazing animals. Biologists have created special environmental aquariums, and the nautilus has been successfully kept and bred. These specimens are providing scientists with increasing information about the life history of this group of mostly extinct animals.

No matter what the type, living fossils provide scientists with a window to the past. They help us understand how life on Earth evolved and what kinds of plants and animals inhabited the planet before humans. It is hoped that we will continue to discover more living fossils and learn more about the inhabitants of this planet. SEE ALSO GEOLOGICAL TIME SCALE; MORPHOLOGICAL EVOLUTION IN WHALES.

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Locomotion

Animals have evolved an amazing variety of ways to get around. There are animals with no legs; animals with one appendage that serves as a “leg” (snails, clams); animals with two, four, six, or eight legs; animals with dozens of legs; even animals with hundreds of legs. There are animals that move constantly, and animals that stay in one place for their entire adult life. There are animals that swim purposefully and animals that drift wherever the currents take them. Animals slither, crawl, flap, glide, and swim. Some animals spend their entire life underground, whereas others spend almost their entire life in the air. All of these are different modes of animal locomotion.

Locomotion is not the same as movement. All animals move, but not all animals locomote. In **ethology**, or the study of animal behavior, locomotion is defined as movement that results in progression from one place to another. Animals that spend all or nearly all their entire adult life in one place are called **sessile**. Animals that move around are called **motile**.

Locomotion has evolved to enhance the animal’s success at finding food, reproducing, escaping predators, or escaping unsuitable habitats. Typically, the animal uses the same mode of locomotion for all these functions, but there are exceptions. For example, a squid normally swims forward or backward by undulating (rhythmically waving) finlike flaps on the sides of its body. However, when startled, the squid expels water through a nozzle and jets backward. Shrimp have a similar behavior. They normally swim using modified appendages called swimmerettes. When avoiding a predator, they contract their powerful tail muscles and rapidly move backward through the water. Even some normally sessile animals use crude forms of locomotion to escape predators. Scallops can clap their shells together to produce a sort

ethology animal behavior

sessile immobile, attached

of jet propulsion. Some **cnidarians** (such as sea anemones) can break free from their attachment point and then use an undulating motion to swim away from a slow-moving predator.

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

Principles of Locomotion

Locomotion can be passive or active. Each has its advantages and disadvantages. Passive locomotion is the simplest form of animal locomotion. This behavior is exhibited by jellyfish and a few other animals. In this form of locomotion, the environment provides the transportation. The advantage is that no muscular effort is required. The disadvantage of this type of locomotion is that the animal is at the whim of wind and wave. It goes where the current takes it. A somewhat different form of passive locomotion is exhibited by the remora (the name for various species of fish in the family *Echeneidae*). Remora attach themselves (harmlessly) to a larger fish or sea turtle and thus go wherever the larger animal goes. However, remora are perfectly capable of swimming on their own.

Most animals exhibit active locomotion at some stage of their life cycle. To move purposefully from place to place, animals must have a means of providing propulsion and a means of controlling their movement. In most cases animals use some sort of muscle tissue attached to a structure to contract and generate the force required to move. This muscle could be attached to a leg bone, causing the animal to jump, as in a frog, or it could contract a chamber, causing a jet of water to propel the animal, as in a squid. The amount, type, and location of contractions are controlled by a nervous system. The nervous system can be as simple as the nerve web in hydra or as complex as the elaborate and highly specialized human nervous system. Nervous system control produces rhythmic movements of the appendages or body that result in locomotion.

Active locomotion can be **appendicular** or axial. In appendicular locomotion, various appendages such as legs, wings, and flippers interact with the environment by pushing or flapping to produce the propulsive force. Axial locomotion occurs when the animal modifies its body shape to achieve motion. For example, squid contract their large body cavity and forcefully expel water through a nozzle, producing a form of jet propulsion. Eels produce rhythmic ripples down the lengths of their bodies. Leeches stretch out their bodies, extending their **anterior** ends forward. They then anchor and draw their **posterior** ends forward by shortening and thickening their bodies.

appendicular having to do with arms and legs

Whether passive or active locomotion is used, the physical environments occupied by animals fall into four broad categories, each requiring unique forms of locomotion. The four environments are fossorial (underground), terrestrial (on the ground), aerial (in the air, including **arboreal**, on tree-dwelling), and aquatic (in the water). Each environment has similar restraints on motion: mass or inertia, gravity, and drag. Drag is any force that tends to restrict movement.

anterior referring to the head end of an organism

posterior behind or the back

arboreal living in trees

In fossorial locomotion, drag is the most important factor restricting forward motion. If the soil is very loose, some animals (insects and lizards) can “swim” through. This form of locomotion is quite rare. Most fossorial animals must burrow or dig tunnels. Some dig as they go, pushing the soil behind them. However, most fossorial animals build permanent tunnels.





buoyancy the tendency of a body to float when submerged in a liquid

invertebrates animals without a backbone

Once the tunnel is constructed, the mode of locomotion in the tunnel is indistinguishable from terrestrial locomotion.

Animals that spend part of their time in the air (bats, birds, flying insects) need powerful muscles to maintain flight against the force of gravity. Animals that burrow underground or that move about on the surface also require strong muscles to balance the force of gravity. Thus animals that live in aerial, fossorial, or terrestrial environments have evolved strong skeletal systems. Muscles must also overcome inertia to propel the animal forward. The more massive the animal, the more inertia it has.

Many aquatic animals are weightless in water. The **buoyancy** of the water exactly balances their weight. So muscular effort is not required to maintain their position. However, these animals must still exert muscular effort to initiate motion. Because water has substantial drag, muscular effort is also required to maintain motion. Some animals have negative buoyancy. They sink to the bottom if they stop swimming. Animals with negative buoyancy must expend muscular energy to remain at a given level in the water. An animal with positive buoyancy floats to and rests on or near the surface and must expend muscular energy to remain submerged.

Because the amount of drag due to movement through water is substantial, animals that need to move quickly must have a very streamlined shape. Drag results mainly from the friction of the water as it flows over the surface of the animal. Drag is also caused by water sticking to the surface of the animal. Many fish have evolved a special mucous coating that protects the skin and also reduces friction. The flow of water over the skin of the animal is usually lamellar, which means different layers of the water flow at different speeds relative to the animal. The slowest layer of flow is the one next to the body surface. Moving away from the surface, each layer moves a little faster until the speed of the water flow over the animal is matched at the last layer. Turbulence reduces lamellar flow and increases drag, ultimately limiting the speed of the animal through the water. Dolphins have evolved a gel-like layer just under the skin that tends to absorb turbulence and restores lamellar flow, thus allowing them to swim at a higher speed.

The viscosity of air is much lower than that of water, producing much less drag. However, lamellar flow of air, especially across the wing surfaces, is even more critical. Lift is provided by the shape of the wing. Lift results from air flowing faster across the upper surface than across the lower surface of the wing. Turbulence eliminates lamellar flow and lift is reduced.

Fossorial Locomotion

Fossorial animals dig burrows, bore into the soil, or construct tunnels. Constructing tunnels or burrows requires that the material be compact and stick together. Semisolid mud or loose sand will not support a burrow. Lizards that “swim” through loose sand or amphibians that swim through mud do not leave tunnels or burrows. While these behaviors could be considered fossorial, they are not discussed here.

Fossorial invertebrates. Burrowing **invertebrates** have evolved a number of ways to dig through material. Some worms use the contract-anchor-extend method of locomotion. Contraction of the muscles in the rear half

of the body pushes the body forward and causes the proboscis to protrude. When the proboscis is fully extended, the worm anchors the proboscis in the soil and pulls the rest of its body forward. This process is repeated, producing a slow and erratic forward motion.

Clams and some other burrowing **mollusks** use a variation of the contract-anchor-extend method. They extend a muscular “foot” into the soil. Blood is pumped into the foot, causing it to swell and thus forming an anchor. Then the muscle contracts, pulling the clam down into the soil.

Many worms, such as earthworms, use peristaltic locomotion. This form of locomotion is generated by the alternation of longitudinal waves and circular-muscle-contraction waves flowing from the head to the tail. The movement is similar to the contract-anchor-extend method, but each peristaltic wave produces separate anchor points. So several segments of the worm may be moving forward at the same time.

Fossorial vertebrates. Fossorial vertebrates include amphibians, reptiles, and mammals. Locomotion of fossorial amphibians and reptiles is usually axial. Fossorial locomotion of mammals is appendicular. Moles are a good example of fossorial mammals. They have strong, flat forelegs with large, strong claws. Moles dig by extending a foreleg straight ahead in front of the snout and then sweeping it to each side. The loosened soil is pushed against the sidewalls of the burrow. Many rodents dig burrows for nesting but forage above ground. These animals dig by alternately extending their forelegs forward and downward. The loosened soil is pushed backward under the body. The animal may back up through the burrow, pushing the soil out to the surface.

Terrestrial Locomotion

This is the form of locomotion humans use to get around. However, few species use the pure **bipodal** locomotion of humans. Most animals use four or more legs. Only **arthropods** and vertebrates have evolved the ability to move rapidly on the ground using legs. Both groups of animals raise their bodies above the ground and use their legs to propel themselves forward. The legs provide both support and propulsion, so the animal must maintain balance as it moves. The sequence and patterns in which the various legs move is determined by the need to maintain balance. More legs create greater stability, but the fastest vertebrates and invertebrates use six or fewer legs.

Walking. Both arthropods and vertebrates use a similar pattern of walking or gait. A foot is planted on the ground and the body is pushed or pulled forward over the foot. The foot remains stationary as the body moves forward. Then the body remains stationary as the foot is lifted and the leg moves forward. For walking and slow running, gaits are generally **symmetrical**. The footfalls are regularly spaced in time. Fast-moving vertebrates, such as horses, have an **asymmetrical** but regularly repeating gait.

Insects tend to move their six legs in a simple pattern, lifting and replacing each leg in turn followed by the leg in front of it. Then the legs on the other side are moved. Forward motion always begins with the posterior legs. In slow walking, only one leg is lifted at a time. The limb movements of centipedes and millipedes are similar to those of insects, but with many

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

vertebrates animals with a backbone

bipodal walking on two legs

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

symmetrical a balance in body proportions

asymmetrical lacking symmetry, having an irregular shape





more legs and simultaneous waves of movement that progress from the posterior end to the anterior end on both sides of the animal.

Four-legged vertebrates must synchronize leg movements to maintain balance. The basic walking pattern of all four-legged vertebrates is left hind leg, left foreleg, right hind leg, and right foreleg. This cycle is then repeated. The faster symmetrical gaits of vertebrates are obtained by overlapping the leg-movement sequences of the left and right sides.

Running. Vertebrates that can run are known as cursorial. They have short, muscular upper legs and thin, elongated lower legs. This adaptation reduces the mass in the lower leg, allowing it to be brought forward more quickly. For slow, steady-running, cursorial vertebrates use a gait known as trotting. All-out running is known as galloping. The gallop is an asymmetrical gait. When galloping, the animal is never supported by more than two legs. Horses at full gallop have all four legs off the ground at the same time during part of the gait. This fact was first demonstrated by Eadweard Muybridge, the American photographer and motion picture pioneer, using high-speed photography involving multiple cameras. His groundbreaking, eleven-volume work, *Animal Locomotion*, was published in 1899.

Cursorial birds and some lizards use bipedal locomotion. These animals have evolved large feet to increase support. The axis of the body is held perpendicular to the ground. Cursorial birds and lizards have long tails for balance, so that the center of gravity of the animal always falls between its feet. The running gait is, of course, a simple alternation of left and right legs. Lizards begin with four-footed locomotion and switch to bipedal as speed increases.

Hopping. The locomotor pattern of hopping is found in both invertebrates and vertebrates. Invertebrates include a few insects, such as grasshoppers and fleas. Vertebrates include tailless amphibians, kangaroos, rabbits, and a few rodents. All hopping animals have hind legs that are approximately twice as long as the forelegs.

Frogs jump by first flexing their forelegs and tilting their bodies upward. The hind legs are swung out from the sides of the body. When the upper hind leg is perpendicular to the body, the hind leg is forcefully straightened out and the animal is launched upward at a 30° to 45° angle.

Rabbits, kangaroos, and all other mammals move their legs vertically when they jump, instead of horizontally. The hopping gait of rabbits is **quadrupedal**. A jumping rabbit stretches forward and lands on its forefeet. As the forefeet touch, the back flexes, and the hind end rotates forward and downward. The hind feet touch down next to the forefeet, and a new jump begins. Kangaroos take off and land on their hind feet. The back is not arched and the front legs are used only for balance. All of the muscular effort required for jumping is provided by the powerful hind legs.

Crawling. Invertebrates that crawl use either peristaltic or contract-anchor-extend locomotion. Limbless vertebrates use serpentine, rectilinear, concertina, or sidewinding locomotion. The most common pattern is serpentine locomotion, used by snakes, legless lizards, and a few other species. Rectilinear locomotion is used by most snakes, occasionally by large snakes all the time, and by fossorial limbless vertebrates when burrowing. Concertina and sidewinding locomotion are largely confined to snakes.

quadrupedal describes an animal with four legs



Serpentine. In serpentine (snakelike) locomotion, the body moves in a series of curves. In serpentine motion the entire body moves at the same speed. All parts of the body follow the same path as the head. Propulsion is by a lateral thrust in all segments of the body in contact with projections of the surface.

Concertina. Concertina locomotion is used when the surface is too slick for serpentine locomotion. The snake moves its body into a series of tight, wavy loops. These provide more friction on the slick surface. The snake then extends its head forward until the body is nearly straight or begins to slide backward. The snake then presses its head and upper body on the surface, forming a new frictional anchor, and pulls the posterior regions forward.

Sidewinding. Sidewinding locomotion is a specific adaptation for crawling over loose, sandy soils. It may also have the added advantage of reducing contact with hot desert soils. Like serpentine locomotion, the entire body of the snake moves forward continuously in a series of sinuous curves. These curves are sideways to the direction of motion of the snake. The track made by a sidewinding snake is a set of parallel curves roughly perpendicular to the direction of movement. The unique feature of sidewinding is that only two parts of the body touch the ground at any instant. The remainder of the body is held off the ground. To begin, the snake arches the front part of the body forward and forms a loop leaving only the head and the middle of the body in contact with the ground. The snake then moves in a sinuous loop, causing the contact point to move backward along the snake's body as each body segment loops forward. As soon as enough body length is available, the animal forms another loop and begins the next cycle. Each part of the body touches the ground only briefly before it begins to arch forward again.

Rectilinear Locomotion. In snakes, rectilinear motion is completely unlike the other forms of locomotion. The body is held relatively straight and glides forward in a manner similar to the motion of snails. The belly of the snake is covered by rows of wide, overlapping scales. Each scale is attached to two pairs of muscles, both of which are attached at an angle to ribs ahead of and behind the scale. Waves of contraction move from the front of the snake toward the back, lifting and moving each scale forward in turn. Then the scale is pulled rearward, but the edge of the scale digs into the surface, propelling the snake forward.

Aerial and Arboreal Locomotion

Animals have evolved many ways of moving without touching the ground. Aerial locomotion includes gliding, soaring, and true flight. Animals who move through trees are known as arboreal.

Climbing. Each group of arboreal animals has a unique adaptation for climbing. Arthropods weigh little so they show few specialized climbing adaptations. Most arthropods, especially insects, can climb. The heavier vertebrates have many climbing adaptations.

Arboreal frogs and lizards are slender-bodied animals whose climbing gait is essentially the same as their terrestrial gait. The tips of the toes on arboreal frogs are expanded into large, circular disks, which increase the contact area. The digits of arboreal lizards are spread out. On the bottom



Many different types of locomotion exist in nature. *Clockwise from upper left:* The flying squirrel glides, the cheetah uses its four legs to run over the earth, the centipede coordinates its multiple legs, and the mollusk pushes water through this body part to propel itself through the ocean.

of each of these spatula-shaped digits are claws and one or two rows of elongated scales. Chameleons have two more specialized adaptations. Their tails are able to grasp objects (prehensile), and their digits have fused into two groups of opposable digits. Chameleons can tightly grasp a thin limb.

Brachiation and leaping. Most arboreal animals must occasionally leap across a gap between trees or branches. The leaping motion is essentially the same as terrestrial leaping, although landing is trickier. Brachiation is using the arms to swing from limb to limb. A few primates have developed highly specialized adaptations for brachiation, although all monkeys brachiate to some extent. Primates that use this form of locomotion have extremely long, powerful arms or forelimbs.

Gliding. In gliding, the animal coasts from a high point to a low point, losing elevation constantly. Gliding animals include amphibians, reptiles, and mammals. The small animals known as flying squirrels demonstrate this behavior. A flying squirrel will climb to near the top of one tree and launch itself into space, gliding to a lower branch on the next tree, then climbing to the top and repeating the process as often as necessary. Gliders have adap-

tations that allow them to increase the width of their bodies. In the flying squirrels flaps of skin extend from the front limbs to the back. Frogs, snakes, and lizards are able to flatten their bodies. Some gliding lizards have elongated ribs that open like a fan.

Soaring. Soaring is a very different process. Birds who are able to soar are much better gliders than any of the gliding animals. They are able to soar because of their instinctive or learned ability to take advantage of columns of rising air to gain altitude. A vulture will soar in circles in a rising column of air to a high altitude, then glide to the next rising air column. In this way, vultures are able to stay aloft for hours with almost no muscular effort.

True flight. Three living groups of animals possess true flight: insects, birds, and mammals. They can propel themselves upward and forward by flapping their wings. Each of these groups evolved this ability independently of the others. A fourth group, the extinct winged reptiles known as pterosaurs, may have been capable of true flight or only of soaring and gliding. The aerodynamics of flight are basically the same for all flying animals. However, the mechanical details are quite different among the groups. While all three groups propel themselves forward by flapping their wings, many species of birds also include extensive gliding and soaring to conserve energy.

Aquatic Locomotion

Animals that live in aquatic environments exhibit many different forms of locomotion. Some animals crawl or burrow into the bottom of a body of water. Others swim through the water using a variety of different appendages. Still others float freely, following the currents wherever they go. Aquatic organisms range in size from microscopic to the blue whale, the largest animal that has ever lived.

Invertebrates. Aquatic invertebrates swim through the water, crawl along the bottom, or burrow into the bottom. In swimming, muscular activity propels the animal by pushing against the water. On the bottom, muscular activity moves the animal around by interacting with the bottom. Some bottom dwellers simply crawl around on the bottom in a manner exactly like terrestrial locomotion. Others take advantage of the weightless environment to move in ways unique to the water environment.

Aquatic invertebrates have developed two distinct modes of swimming. One mode uses hydraulic propulsion. Jellyfish are a good example of this type of locomotion. They have umbrella-shaped bodies, with the “handle” of the umbrella containing the digestive system. The outer margin of the top of the umbrella, or medusa, is a band of muscles that can contract rapidly. As the muscles contract (just like closing an umbrella) water is expelled forcefully and the jellyfish is propelled along. Scallops use a similar locomotion. They are the best swimmers among bivalves, but at its best, the motion is jerky and poorly controlled. It is used mostly to escape predators. Rapid clapping movements of the two shells create a water jet that propels the scallop.

Cephalopods, such as the squids and octopi, are also mollusks that use water-jet propulsion. Adult cephalopods have lost most of their heavy shell. Many squid are excellent swimmers and can swim forward or backward by undulating flaps along each side of their bodies. All cephalopods are much





mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

dorsal the back surface of an animal with bilateral symmetry

better swimmers than any other species of mollusk. The **mantle** of cephalopods encloses a cavity that contains the gills and other internal organs. It also includes, on its bottom surface, a narrow opening called a siphon. When the circular muscles surrounding the cavity simultaneously contract, water is forced through the siphon. This propels the cephalopod in a direction opposite to the direction of the siphon. Thus the siphon also provides directional control.

Fishes. Some fishlike animals use a purely undulatory motion to move themselves. Almost all fish use undulatory movement to some extent and supplement that motion with muscular effort by fins.

An eel swims by undulating its entire body in a series of waves passing from head to tail. This type of movement is called anguilliform (eel-like) locomotion. During steady swimming, several waves simultaneously pass down the body from head to tail. The waves move faster as they approach the animal's tail.

While eels have a body with a fairly blunt anterior and constant diameter for the rest of the length of the body, most fish have a body that tapers at both anterior and posterior ends. For these fish, undulatory motion is not the most efficient. So most fish exhibit carangiform locomotion, in which only the rear half of the body moves back and forth. The fastest swimming fish use this method of locomotion, so it is apparently the most efficient one. In contrast, ostraciiform locomotion uses only the tail fin to sweep back and forth. This is slower and apparently less efficient.

Whales and other cetaceans use undulatory body waves, but the waves move the whale's body up and down instead of from side to side. The elongated tail region of whales produces a form of carangiform locomotion apparently as effective as that of the swiftest fish. Fish, whales, and other aquatic vertebrates have some arrangement of fins distributed around their bodies. They all have a caudal (tail) fin, vertical in fish and horizontal in cetaceans. Aquatic vertebrates also have a large **dorsal** fin and a pair of large fins (or flippers) on the sides of their bodies close to the front. The caudal fin is the primary means of locomotion. The lateral fins do most of the steering. The dorsal fin or fins provide stability.

Tetrapodal vertebrates. Tetrapodal vertebrates (four-legged vertebrates) that use undulatory locomotion include crocodilians, marine lizards, aquatic salamanders, and larval frogs. However, adult frogs and other tetrapods primarily use appendicular locomotion. Many aquatic tetrapods move primarily by using the hind legs. However, sea turtles, penguins, and fur seals have evolved short hind legs with webbed feet used primarily as rudders. These animals use their powerful forelegs, which have evolved into flippers.

Diving birds, such as cormorants and loons, are propelled by their webbed hind feet. Loons are the best adapted for diving. Their body, head, and neck are elongated and slender; the hind legs have moved far back to the posterior end of the body; the lower legs are short; and the feet are completely webbed.

Frogs and some freshwater turtles have elongated rear legs with enlarged, webbed feet. Other aquatic turtles (such as snapping turtles) are relatively poor swimmers. These turtles walk on the bottom of the lake or

stream with limb movements very similar to those used on land except that they can move faster in water than they can on land.

Many mammals have swimming movements identical with their terrestrial limb movements. Most aquatic mammals—such as sea otters, hair seals, and nutria—use their hind legs and frequently their tails for swimming. The feet have some degree of webbing. Fur seals and polar bears swim mainly with forelimbs. **SEE ALSO** FLIGHT; SKELETONS.

Elliot Richmond

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Lorenz, Konrad

Zoologist and Ethologist

1903–1989

Austrian zoologist, ethologist, and Nobel Prize winner Konrad Zacharias Lorenz was born in Vienna in 1903, the son of a fabulously wealthy orthopedic surgeon. He spent his childhood roaming the forests and marshes of the family estate on the banks of the Danube in the company of the teeming wildlife of the area and a neighbor, Gretl Gebhardt. It was at play, splashing in the marshes pretending to be ducks, that the two seven-year-olds discovered what would become Lorenz's lifelong work. Newly hatched ducklings saw the children and followed them as though they were the ducklings' parents. This phenomenon, now called imprinting, is an example of a genetically programmed pattern of behavior that is innate in all members of a species but is dormant until triggered by some crucial experience. In the case of the ducks, imprinting stimulated them to follow and mimic the first thing they saw upon hatching. Lorenz went on to establish that birds and mammals imprint upon birth, by sight, sound, touch, or smell.

Lorenz obtained a medical degree in 1928 from the University of Vienna, where he reunited and married his childhood friend Gebhardt, who had become a gynecologist. He then immersed himself in his lifelong passion: observation of animals in their natural **habitat**.

After World War II (1939–1945) Lorenz moved his family to his childhood estate, Altenberg, and surrounded by animals both domestic and wild, he began a series of popular books. *King Solomon's Ring*, published in 1949,



Konrad Lorenz shared the 1973 Nobel Prize in physiology.

habitat physical location where an organism lives in an ecosystem



consisted of lively stories about his pets and their behavior as well as about Lorenz's relationships with a number of wild birds. *Man Meets Dog*, published in 1950, discussed the ancient and intimate bonds between human beings and dogs.

That same year, Lorenz and Erich von Holst established the Max Planck Institute for Behavioral Physiology at Altenberg. For the next twenty years Lorenz concentrated on the study of waterfowl, particularly investigating the process of instinct: how and why animals behave in appropriate and complex ways without human reasoning.

Lorenz dramatically shaped the way in which scientists approached the study of animal minds and behavior. In the mid-twentieth century, scientists tended to observe animals isolated in cages and to believe that all behavior was learned. Lorenz popularized **ethology**, the more difficult study of animal behavior in the field under natural conditions. His years of observations along with colleagues Nikolas Tinbergen and Karl von Frisch established the existence of many genetically inherited behavior patterns in animals, all subject to **natural selection**. Their work led to a shared Nobel Prize in 1973 in the field of **physiology**. Konrad Lorenz was also awarded the Gold Medal of the New York Zoological Society, was elected to the Royal Society of London and the American National Academy of Sciences, and received numerous honorary degrees worldwide.

Toward the end of his life in 1989, Lorenz said of his duckling discoveries with Gebhardt, "What we didn't notice is that I got imprinted on ducks in the process. I still am, you know. And I contend that a lifelong endeavor is fixed by one decisive experience in early youth. And that after all, is the essence of imprinting." (Wolf 1983, p. 32–34). SEE ALSO ETHOLOGY; IMPRINTING.

Nancy Weaver

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M

MacArthur, Robert Helmer

**Canadian-Born American Biologist
1930–1972**

Robert Helmer MacArthur was born in Toronto, Canada. MacArthur was an important scientist in the field of ecology, the study of the relation between living creatures and their natural environment. When MacArthur started his studies in ecology, it was a merely descriptive science. Under his influence, ecology developed into a science based on quantitative, or measurable, data.

MacArthur moved to the United States at the age of seventeen to study at Marlboro College in Vermont, where his father was a professor of **genetics**. In 1951 he earned a bachelor's degree, in the field of mathematics, from Marlboro. Two years later, in 1953, he achieved his master's degree in mathematics from Brown University. While pursuing a Ph.D. at Yale,

genetics the branch of biology that studies heredity

MacArthur switched from mathematics to zoology, with a concentration on ecology. After receiving his Ph.D. in 1957, MacArthur spent a year in England studying birds. In 1958 he was appointed as an assistant professor of biology at the University of Pennsylvania. In 1965 he became a professor of biology at Princeton. He held this position until his death from cancer at the age of forty-two.

MacArthur's first studies were on five similar species of birds called warblers that were living together in a spruce forest in New England. Some scientists believed that these birds might be an exception to the generally accepted **competitive exclusion principle**, which states that in stable environments, no two species occupy the same **niche** (the specialized role of an animal in its environment). However, MacArthur's studies showed that the birds occupied different parts of the trees, and thus did indeed follow the principle. This work earned for MacArthur the Mercer Award of the Ecological Society of America (1959).

MacArthur used his background in mathematics to focus on **population** biology. He studied how the population sizes of bird species varied with the size of their **habitats**. MacArthur and biologist Edward O. Wilson studied populations of birds living on islands. Their findings were published in 1967 in the book *The Theory of Island Biogeography*.

MacArthur and Wilson also developed the idea of life history strategies. They noted that some species have short lives characterized by very fast growth and high reproductive rates, then a sudden and drastic decline in numbers. An example of this type of species—called **r-selected species**—is the lemming. MacArthur and Wilson compared these animals to species that have slow growth and stable populations. An example of this type of species—called a **k-selected species**—is the elephant.

In 1971, when MacArthur learned that he had cancer and might live only a few more years, he decided to compile his many ideas into a single book. This book, *Geographic Ecology: Patterns in the Distributions of Species*, was published in 1972 shortly before his death. SEE ALSO LIFE HISTORY STRATEGIES; WILSON, E. O.

Denise Prendergast

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Malaria

Malaria is one of the oldest known infections. It is also the world's most deadly tropical parasitic disease. It kills more people than any other communicable disease except tuberculosis. The disease was first described in ancient Sanskrit and Chinese documents. **Hippocrates** also described the

competitive exclusion principle the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

niche how an organism uses the biotic and abiotic resources of its environment

biogeography the study of the distribution of animals over an area

population a group of individuals of one species that live in the same geographic area

habitats physical locations where an organism lives in an ecosystem

r-selected species a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

k-selected species a species that natural selection has favored at the carrying capacity

Hippocrates a central figure in medicine in ancient Greece, he is considered the father of modern medicine





anemia a condition that results from a decreased number of red blood cells

sporozoa a group of parasitic protozoa

sporozoite an infective stage in the life cycle of sporozoans

disease in his writings. It is believed that the army of Alexander the Great was wiped out by the disease during its march across India.

Malaria is thought to have been introduced into the United States by European colonists and African slaves in the sixteenth and seventeenth centuries. It is now endemic in ninety-two countries worldwide. With approximately 41 percent of the world's population at risk, the disease poses a serious health threat globally. As many as two million people die annually; half of the deaths occur in children under five years of age. According to the World Health Organization, this amounts to one child dying every thirty seconds.

Malaria is characterized by both acute and relapsing infection in humans. Hallmark symptoms include periodic episodes of chills and fever, spleen enlargement, and **anemia**. The disease is caused by microscopic one-celled organisms called **sporozoa**, which belong to the genus *Plasmodium*. These parasites are transmitted to humans by several species of anopheles mosquitoes. Malaria is also found in apes, monkeys, birds, bats, reptiles, and rodents. While humans can be infected only by Anopheles mosquitoes, birds and other animals are known to have become ill after being bitten by mosquitoes from the genus *Culex*.

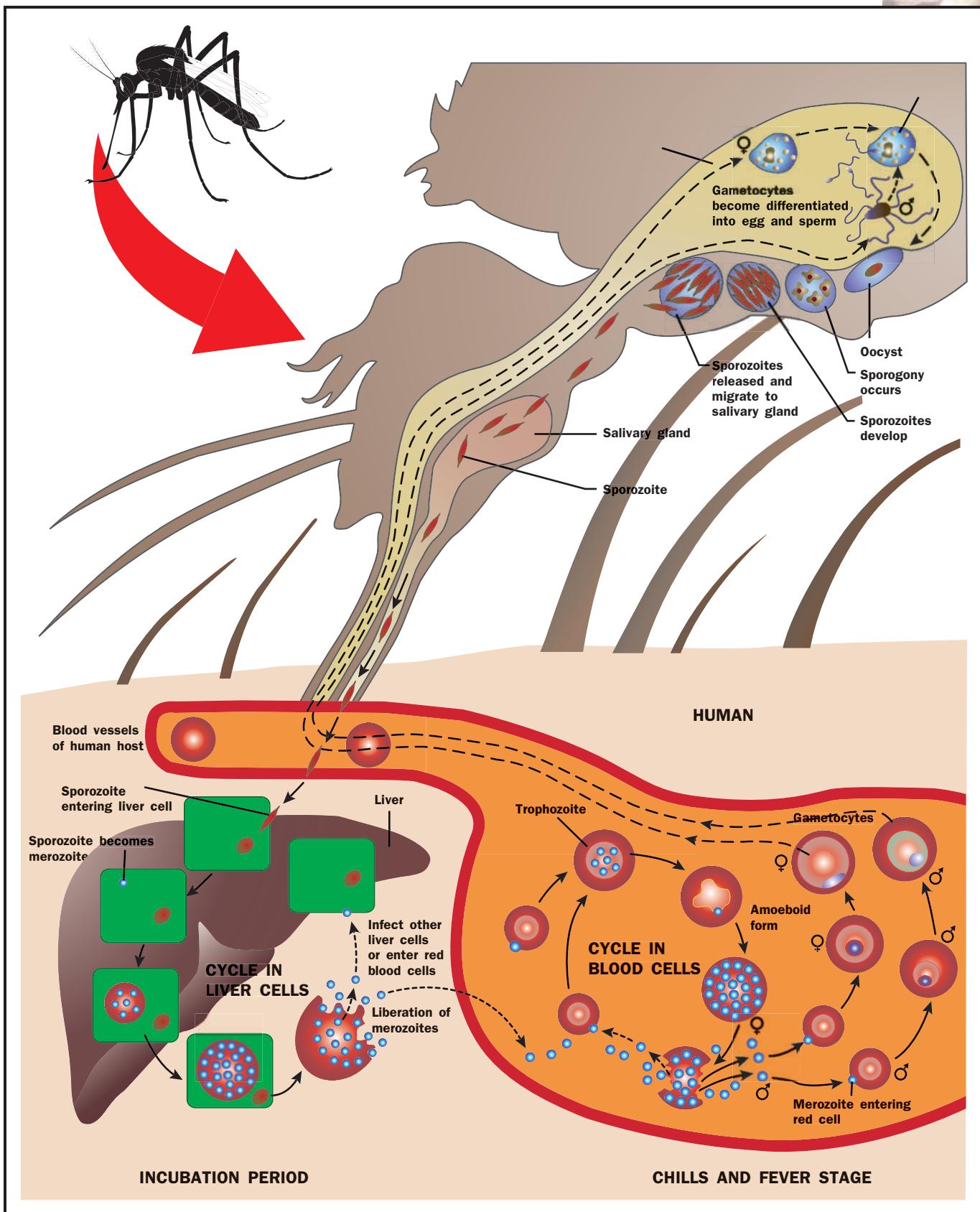
Four species of *Plasmodium* are known to cause human malaria: *P. falciparum*, *P. vivax*, *P. malariae*, and *P. ovale*. Diagnosis can be determined by a blood smear. The most common type, *P. falciparum*, requires relatively high environmental temperatures for development and is usually found in tropical areas such as western Africa. *P. vivax* malaria accounts for 43 percent of all cases and is widespread globally. It is known to occur even in cold-winter areas of Korea, Manchuria, and south Russia. The less common *P. malariae* malaria occurs in about 7 percent of all cases and is confined to the Mediterranean, while *P. ovale* malaria is rather rare and isolated within a small area of eastern Africa and the islands of the western Pacific.

Malarial attacks typically last four to ten hours during which a person experiences successive stages of chills, high fever, severe headache, and then profuse sweating. Between attacks, body temperature may be normal. The intervals between attacks are usually either forty-eight hours or seventy-two hours. The first attack typically occurs seven to nine days after a person is bitten by a disease-carrying mosquito.

Mosquito Transmission

Though malaria can occur in temperate regions, it is most common in the tropics and subtropics, where climatic conditions favor mosquito development. Mosquitoes lay their eggs in water where larvae mature and hatch into flying adults. Newly hatched female mosquitoes are especially blood-thirsty and require a blood meal to produce fertile eggs. When these mosquitoes bite a human who is already infected, they ingest the malarial parasite and the disease transmission cycle begins.

The life cycle of the *Plasmodium* starts in the stomach of the female mosquito. The organism's double life cycle has two phases—a sexual reproductive cycle and an asexual reproductive cycle. While the parasite is in its asexual, free-swimming stage, it is known as a **sporozoite**. When an infected mosquito bites, the sporozoite is injected along with saliva into the human bloodstream.



The life cycle of the virus that causes malaria.



merozoites a motile stage in some parasitic protozoa

gametocytes cells that produce gametes through division

zygote a fertilized egg

oocyst a cyst in sporozoans that contains developing sporozoites

quinine a substance used to treat malaria

chloroquine a drug commonly used to treat malaria

habitat physical location where an organism lives in an ecosystem

Once inside the bloodstream, the sporozoite enters a red blood cell. Inside the red blood cell, it changes shape and divides into smaller forms called **merozoites**. The red blood cell containing these merozoites ruptures, releasing them into the blood. The merozoites infect other red blood cells, and the life cycle is repeated. The rupturing of red blood cells causes the symptoms of fever and chills.

A mosquito biting an infected host at this stage can ingest merozoites. If this happens, the merozoites enter the mosquito's stomach and become male and female **gametocytes**. This kicks off a sexual reproductive life cycle where the separate male and female gametocytes unite together to form a single-celled **zygote**. This zygote grows to become an **oocyst** or large egglike sac, which eventually divides, releasing a multitude of asexual, free-swimming sporozoites.

These sporozoites move to the mosquito's head and salivary glands from which they can be injected into a human during the mosquito's next bite. This asexual cycle is repeated. During the asexual life cycle, the parasites grow and divide synchronously. The resulting merozoites produce the regularly occurring fever and chill attacks that are typical of malaria.

Early Cases and Treatments

The first documented treatment of the disease occurred in 1630 when “Jesuit's bark,” from a cinchona tree, was used to ease the fever of a Spanish magistrate in Peru. Amazingly, the magistrate recovered and eventually the substance **quinine** was isolated from the bark and processed commercially as a treatment. The *Cinchona* genus includes about forty species of plants, mostly trees, native to the Andes of South America. Certain species are also known to grow in India and Sri Lanka.

In the 1940s, the antimalarial drug **chloroquine** was introduced as an effective additional treatment. Chloroquine is a member of an important series of chemically related antimalarial agents, the quinoline derivatives. A global eradication program was initiated in the 1950s and 1960s by the World Health Organization (WHO), in Geneva, Switzerland, which led to a significant decrease in malaria cases in Asia and South America.

Drug Resistant Strains and Reemergence of Disease

Drug resistant strains of malaria began to emerge in the 1970s, making the disease harder to control. During the 1990s the prevalence of malaria escalated at an alarming rate, especially in Africa where control efforts have typically been piecemeal and uncoordinated. Additionally, the phenomenon of “airport malaria,” or the importing of malaria by international travelers, is becoming commonplace. Persons who are not normally exposed to this mosquito in its natural **habitat** can acquire “airport malaria” through the bite of an infected mosquito that has traveled far from its home.

In one study, random searches of airplanes at Gatwick Airport in London found dozens of airplanes from tropical countries containing mosquitoes. After a mosquito leaves an aircraft, it may survive long enough to take a blood meal and transmit the disease, usually in the vicinity of the airport. Incidents of malaria transmitted this way are expected to become more common, since airport travel has increased by almost 7 percent a year since 1980.

and is predicted to increase by 5 percent a year for the first twenty years of the twenty-first century.

Resurgence and increased risk of the disease appears to be linked to several factors. Changes in land use, such as mining, logging, and agricultural projects, particularly in the Amazon and Southeast Asia frontier area, are providing new mosquito breeding sites. Other reasons for the disease's spread include global climatic changes, disintegration of health services, armed conflicts, and mass movements of refugees into areas of high malaria transmission.

Reemergence of malaria through mobility occurred in Brazil, for example. Malaria had been practically eradicated from most areas of the Amazon region until massive population movements began to colonize new territories. New highways were built, linking the Amazon to the rest of the country and attracting laborers to work on road construction. In 1970, prior to new road construction in these new areas, there were approximately 50,000 cases of malaria reported; by 1990, reports had increased to more than 500,000, representing 10 percent of the world's reported cases outside Africa.

As a result of the explosion of international travel, imported cases of malaria are now showing up more in developed countries such as the United States. Malaria is also reemerging in areas where it was previously under control or eradicated, such as in Korea. According to the WHO, **global warming** and other climatic events such as **El Niño** also play a role in increasing the disease. Malaria has now spread to highland areas of Africa, where El Niño effects such as increased rainfall have influenced mosquito breeding sites and hence the transmission of the disease. The emergence of multidrug-resistant strains of parasites is also exacerbating the situation.

Disease Prevention

Prevention of malaria encompasses a variety of measures. Some may protect against infection—these are directed against mosquitoes—whereas others focus on stopping the development of the disease in human beings. Although only a limited number of drugs are available, if these are used properly and targeted to those at greatest risk, malaria can be reduced.

Since the early 1990s, considerable progress has been made in the search for a malaria vaccine. More than a dozen candidate vaccines are currently in development; some of them are in clinical trials. An effective vaccine could be available within the first twenty years of the twenty-first century. In the meantime, there are a number of prescription drugs available on the market in developed countries that can help prevent malaria, especially in individuals traveling to high incidence areas. Some of the best-known preventatives include Mefloquine, Malarone, and Primaquine.

Medical researchers continue to discover new drug therapies. Most recently, Chinese scientists discovered a drug called artemether that is derived from the Chinese herb qinghaosu. The new drug appears to be as effective as quinine although much slower acting. It may even kill resistant strains of malaria. **SEE ALSO** INTERSPECIES INTERACTIONS; PARASITISM.

global warming a slow and steady increase in the global temperature

El Niño a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns



Stephanie A. Lanoue



Economist Thomas Robert Malthus advocated controlling population growth to avoid food shortages.

population a group of individuals of one species that live in the same geographic area

habitat physical location where an organism lives in an ecosystem

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

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Malthus, Thomas Robert

Economist

1766–1834

Thomas Robert Malthus, English economist and demographer, proposed a theory suggesting that **population** growth generally tends to outrun the food supply and that therefore population growth should be curbed. Although most of his work was centered on social conditions and economics, Malthus had a significant impact on the theory of evolution.

Born February 13, 1766, in Surrey, England, Malthus was the sixth child of seven born to Daniel Malthus and Catherine Graham. The young Malthus was educated primarily at home until his admission to Jesus College in Cambridge, England, in 1784. He was graduated with a degree in mathematics, but was well read in French and English history, English literature, and Newtonian physics. A master of arts degree followed in 1791, and in 1797 he was ordained a minister in the Anglican Church. In 1804 the East India Company founded a new college to provide general education to staff members before they went on service overseas. Malthus was asked to join the faculty as professor of history and political science.

The Industrial Revolution encouraged rapid population growth in part to provide an accessible pool of cheap labor for the emerging spinning and textile industries. Public policy during Malthus's time supported the notion that population growth was desirable and that assistance should be given to poor people. Malthus, on the other hand, suggested in *An Essay on the Principle of Population, As It Effects the Future Improvement of Society* (1798) that overpopulation tends to be a drain on resources and that state welfare should be curtailed so that the population would level off. He argued that if it was not possible to maintain the production of food to satisfy the population, then the population must be kept down to the level of available food. He felt that individuals should marry late and practice "natural restraint" so as to have few or no children.

In addition to its relevance for the social policy of the times, Malthus's work made an important contribution to the development of ideas and theories concerning the evolution of plants, animals, humans, and Earth. In 1859 Charles Darwin published his theory of evolution in a book entitled *On the Origin of Species*. In this book, he agreed with Malthus's speculation that competition for resources such as food, **habitat**, and mates would have a cumulative effect on the evolution of different species of plants and animals. This principle became known as **natural selection** and was considered a primary factor in the evolution of new species. Alfred Russel Wallace, a geologist and contemporary of Darwin, also constructed and published a theory of evolution. He, too, acknowledged that

he was influenced by Malthus's work on population and competition for resources.

Malthus was elected to the Royal Society in 1819, the Political Economy Club in 1821, and the Royal Society of Literature in 1824. He was also admitted to the Statistical Society of London in 1834, the French Academy of Sciences in 1833, and the Royal Academy of Berlin the same year. Malthus died on December 23, 1834. **SEE ALSO** BIOLOGICAL EVOLUTION; DARWIN, CHARLES; WALLACE, ALFRED RUSSEL.

Leslie Hutchinson

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Mammalia

Mammals are a group of animals (of the class Mammalia) found throughout the world. Even in regions where the most extreme climatic conditions exist, there are likely to be mammals. Seals, walruses, and whales survive in the cold Arctic and Antarctic. Small pikas live near the tops of high mountain ranges. Arid deserts are home to a wide variety of rodents and their coyote predators. Camels and their amazing ability to survive for long periods without drinking water are an almost universal symbol of the desert. Mammals have successfully survived in so many environments that it is no wonder scientists call this the Age of Mammals.

Mammals, however, did not always exist over such a wide geographical range. They have an evolutionary history going back to the dinosaurs. The history of mammals may surprise people, because mammal fossils have been found in rock deposits similar in age to the fossils of dinosaurs. Fossils identified as belonging to mammals have been found in rocks of the Late Triassic, about 200 million years ago. Early mammal fossils have been discovered in Europe, Great Britain, southern Africa, the Turkestan Range of southern Russia, China, North America, and South America.

Although widespread, the fossils of early mammals are actually rare. Many of the fossils are incomplete skeletons and isolated teeth. By the Middle Jurassic era (208 to 144 million years ago), however, mammals were flourishing, and the numbers of various species and groups had increased dramatically. At the end of the Cretaceous era (144 to 66 million years ago), when the large dinosaurs faced their final extinction, mammals survived to become the group that would produce the largest animals remaining on Earth.

Characteristics of Mammals

What is a mammal? How is it recognized from other **vertebrate** animals? Some body shapes and features of mammals are shared with other groups of animals that have backbones. These shared characteristics are vertebrae, an internal skeleton, and a four-chambered heart.

vertebrate animal with a backbone





On the other hand, several characteristics of mammals are unique and help distinguish a mammal from something else. The most familiar of the unique mammal characteristics is that their bodies are covered with hair or fur. Hair is a form of scales and indicates a shared ancestry with reptiles. In fact, scales are still found on some mammals, as on the tails of rats. In some mammals, such as whales, the amount of hair is greatly reduced. This is a secondary characteristic and is considered an evolutionary loss from an ancestor who had hair.

The skin of mammals is unique in that it contains sweat, scent, sebaceous oil, and mammary glands. The skin of all vertebrates is an important aspect of their health and survival, but few have developed such an elaborate variety of specialized glands as the mammals. Sweat glands help to cool the animals. Scent glands help species to recognize one another. Sebaceous glands provide a special type of oily substance for the maintenance of healthy hair and the prevention of bacterial infection. Mammary glands are unique to mammals and are, in fact, the characteristic for which the group is named. The mammary glands in females secrete the nourishing milk that helps the young to grow. There are very few other groups of animals in which so much maternal care is given as is the case with mammals.

The skeletal features of mammals are similar to those of other vertebrates—fish, amphibians, reptiles, and birds—but are easily distinguishable as mammalian. Some of the more obviously distinctive features of mammals are found in the skull. It is difficult to indicate a skeletal feature completely unique to mammals, especially because there are a variety of modifications.

However, the general structural pattern of mammals is easily identified. Their teeth, which many consider to be part of the skeletal system, are what most scientists rely upon to identify mammals. Individual molar teeth have many cusps, or points. Reptiles, amphibians, and fish usually have simple cone-shaped teeth that are often replaceable throughout the life of the animal. Birds have no teeth at all. Mammals have only one set of replacement teeth, and when the second set is worn out, the animal may starve.

The heart of mammals is very efficient because it is four-chambered. Only birds and possibly dinosaurs share this characteristic. There are two atria and two ventricles for increased circulation. The great efficiency of this type of structure is important for high-energy animals, who need a great deal of oxygen to support their high rate of metabolism. Reptiles have a three-chambered heart and, consequently, have less efficient bodies because of the mixing of unoxygenated and oxygenated blood. This increased circulation pressure in mammals is the primary reason they are considered warm-blooded, or **homeothermic**.

Perhaps the most significant characteristic of mammals is the **placental** uterus. While many animals keep their eggs inside their bodies until the young hatch, the young are still living off a yolk inside an enclosed egg. The egg may hatch inside the parent, but it receives no nourishment from the parent throughout its development. Mammals, on the other hand, are often simply described as placental animals because of the remarkable temporary organ called the placenta.

homeothermic

describes animals able to maintain their body temperatures

placental having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

Once internal **fertilization** has occurred within the female, the egg attaches to the placenta, a blood-rich and nourishing lining of the uterus. The egg stays there and continues to develop into a fetus. The young mammal receives all its nourishment from the mother and is completely dependent on her even after it leaves the uterus.

Classifying Mammals

The classification of mammals is complicated and always changing. The natural world does not always fit neatly into schemes of classification. The **monotremes** are one example. The most famous monotreme is the duck-billed platypus. The spiny anteater, or echidna, is also a monotreme. The monotremes are the only group of mammals that are **oviparous**, which means they lay eggs that hatch outside the body. Their ancestry is not well-known and no monotreme fossils have been dated before the Pleistocene epoch (1.6 million years ago). Scientists continue to debate whether monotremes should be placed in the mammal group, but an agreement has not been reached.

Marsupials. Yet there are numerous agreements about classification. For example, one of the many agreed-upon criteria for deciding which groups of mammals are more primitive is based on placental care. The most primitive mammals that are fully accepted into the group are marsupials. Marsupials all have an abdominal pouch, the marsupium, in which they raise their young. The young are initially nourished in the uterus, but only for a short time, and a placenta-like organ is not very well developed.

Perhaps these mammals represent the first type of true mammal. It is believed that the early fossil mammals were marsupials. Fossils with marsupial-like skulls are found in rocks over 100 million years old. Many of today's marsupials are small, rodent-looking mammals like the brown four-eyed opossum or the ashy-mouse opossum. It is easy to imagine that mammals similar to these small creatures lived in the debris of forest floor alongside the mighty dinosaurs. They would have been hard to see and too quick for predators. Insects were in abundance and would, as they do today, compose the major diet of these tiny primitive mammals.

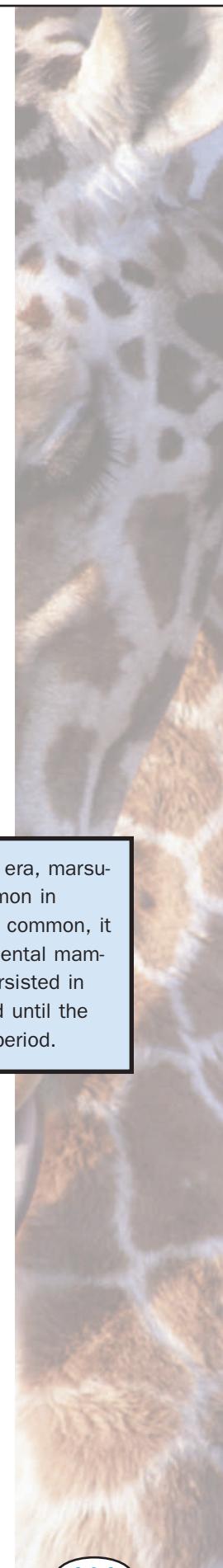
It is believed that marsupials reigned in the mammal world for many millions of years. Fossils of marsupials, and even filmed footage of now-extinct marsupials, like the Tasmanian devil, show that, without competition from the large dinosaurs and reptiles, they grew to very large sizes. Many became large **carnivorous** marsupials, like the saber-toothed *Thylacosmilus*. This mighty predator was the size of a jaguar and very dangerous in appearance.

Marsupial-type fossils are found over most of the planet, with the exception of the oceans. Fossil opossums have even been found on Antarctica. They are believed to have survived on this vast expanse of land when the **climate** there was more comfortable for life. When South America split from the large supercontinent of Pangea, it became a type of continental raft on which species of marsupials evolved in isolation from their cousins in Africa and Europe.

fertilization the fusion of male and female gametes

monotremes egg-laying mammals such as the platypus and echidna

oviparous having offspring that hatch from eggs external to the body



During the Mesozoic era, marsupials were very common in North America, more common, it is thought, than placental mammals. Marsupials persisted in this part of the world until the mid- to late-Tertiary period.

carnivorous animals that eat other animals

climate long-term weather patterns for a particular region



isthmus a narrow strip of land

herbivores animals who eat plants only

During the Ice Age, when tremendous amounts of water were tied up in ice sheets, the **Isthmus** of Panama was exposed, enabling marsupials to travel north into North America. Although many have since become extinct, it is still possible to see frequently the hardy opossum, *Didelphis*, in most regions of Mexico and the United States. In South America many marsupials still live in the forests, although their numbers are dwindling.

The last stronghold for marsupials is the continent of Australia. Because of its isolation from the other continents after the split-up of Pangea, the more evolved and efficient placental mammals never reached Australia. It is as though time was frozen for the marsupials in Australia. Delightful animals, like the kangaroo, koala, wombat, and numbat, still exist in this remote continent. However, as in the rest of the world, they are under threat from the placental mammals. True mammals, like house cats and rabbits, are making it hard for the small marsupials to survive. Rabbits and other grazers are competing for grasslands. The eucalyptus forests necessary for the survival of the koala are threatened. However, many human steps are being taken to help preserve these mammals in the wild and there are still many marsupials found in Australia.

Placental mammals. In every corner of the world, placental mammals thrive. They exist as two major types of animals, carnivores and herbivores. The story of the **herbivores** is as complicated as is that of the smaller groups of these mammals.

Rodents are often considered a nuisance, but their success at survival under the most extreme conditions is undisputed. They are hardy and reproduce quickly. Despite the efforts of many farmers, home dwellers, and urban developers, rodents have managed to live side by side with humans and even have secured an entire means of survival from the waste of humans, another highly successful placental mammal. Rodents are at the base of many food chains in the wild and in cities.

Around forty million years ago, an evolutionary adaptation of grasses provided the stimulus for a burst of evolution among the herbivores. Grasses developed a metabolic way to survive in more arid conditions. These new species are called the C4 grasses. These grasses, like crabgrass, are a type of grass that can survive in hostile environments. As these tougher species of grass became available in regions like flat plains and plateaus, the animals that ate the grass ventured into more open space. While this was good for herbivores because it expanded their food resources, it also became easier for predators to see them.

The animals that survived this evolutionary explosion were those with increased running ability. Grazing mammals evolved longer and narrower legs which they used to elude predators. Groups such as the gazelle, antelope, and horse became the fastest long-distance runners on Earth. They still exist and show no signs of slowing down.

In response, the predators also became faster. The large cats are unanimously considered the fleetest predator on land. The amazing speed of the cheetah has been recorded many times. It is heralded as the fastest land animal alive. Before their extermination by humans, many species of large cats roamed over most of the planet. The American lion and saber-toothed cats were only recently, in geologic terms, eliminated from Earth.



A ten-day-old grizzly bear cub attempts to nurse. The mammary glands that produce the milk for this cub characterize mammals alone.

Bears, many of whom are actually omnivores, are considered by most to be the mightiest land predator on the planet today. The strength of the grizzly, kodiak, and polar bear is legendary. They are surprisingly fast runners, and very few animals are prepared to withstand combat with them.

Mammals survive not only on land but in the ocean as well. Whales, dolphins, seals, walruses, otters, and other marine mammals are very successful in their ways of life. The killer whale may be the largest predator on Earth. They feed on other marine mammals and are especially fond of seals.

The largest animal on Earth is a mammal. The blue whale is estimated to weigh around 150 tons and is almost 27 meters (89 feet) long as an adult. It feeds on tiny **krill**, a shrimplike animal that it catches with the help of a **baleen**, a sievelike structure in its mouth.

Many species of whales had been hunted to extinction by the 1960s. Fortunately, an international ban was placed on the hunting of these magnificent mammals and many species are increasing in number.

It is surprising to read that the ancestors of whales were land dwellers, a group of mammals called creodonts. Fossil evidence indicates that these animals may have become increasingly adapted to a marine environment until they evolved to a completely water-based existence. They are still mammals, however, as evidenced by the formation of a placenta, live birth, and young that suckle for breast milk. Baby whales, although quite large, are completely dependent on their mothers for a long time.

One may find a mammal just about anywhere on Earth. They have evolved to fill almost every possible **niche** and continue to flourish despite harsh environmental and climatic changes. The current loss of mammals,

krill an order of crustaceans that serves a food source for many fish, whales, and birds

baleen fringed filter plates that hang from the roof of a whale's mouth

niche how an organism uses the biotic and abiotic resources of its environment





however, continues at an alarming rate and, over the last 20,000 years, the loss of mammal species, like the mammoth, is staggering. It is hoped this trend will not only halt but, in cases of endangered mammals, be reversed.

Ellen Brook Hall

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Marine Biologist

Marine biology is a field of study encompassing all oceanic life, including representatives from each of the taxonomic kingdoms (plants, animals, blue-green algae, fungus, and single-celled microorganisms called protists). **Taxonomy** is a system used to name organisms based on their evolutionary relationships. Specializations within this field include **ecology**, environmentalism, **parasitology**, reproduction, ocean farming, and anatomy. Many ocean-dwelling organisms have yet to be discovered and assigned a taxonomic nomenclature (scientific name). Other specializations are based on ocean regions, such as coastal, coral reef, deep-sea trench, arctic, and open ocean marine biology. This field is strongly rooted in international research and cooperation because ocean wildlife does not necessarily belong to any one government or country. It necessitates a love of the outdoors, and of the ocean in particular, a willingness to work independently at distant locations, good analytical skills, excellent writing skills, and environmental awareness. Strong swimming skills and certification in scuba (a word derived from the acronym for self-contained underwater breathing apparatus) are also mandatory. Marine biologists may seek employment as a teacher, researcher, resource manager for a governmental agency, field biologist in a consulting company, advocate in an environmental organization, or technician in an aquarium or zoo.

For those who have a strong interest in fishes, marine mammals, marine ecology, or any other related field, it is best to obtain a strong background in basic biology and oceanography. Look for colleges with large marine biology departments, preferably located along the coast of an ocean environment that interests you. Search the Internet for information on the field and make contacts with specialists at other institutions. It is extremely important that you join a research lab or intern at an aquarium or on a research boat during your undergraduate college education. Training marine mammals, for instance at a theme park or for biopsychology or communications research, requires knowledge of psychology and possibly of veterinary science. For a career in academics or college professorship, a doctoral degree from a high-level research institute is necessary. If you wish to work at a zoo or teach high school, a master's degree will suffice.

Rebecca M. Steinberg

taxonomy the science of classifying living organisms

ecology the study of how organisms interact with their environment

parasitology the study of parasites



Marine biologists diving in Bermuda use the quadrat—an ecological sampling unit that consists of a square frame of a known area—to help them count the number of a given species within a given area.



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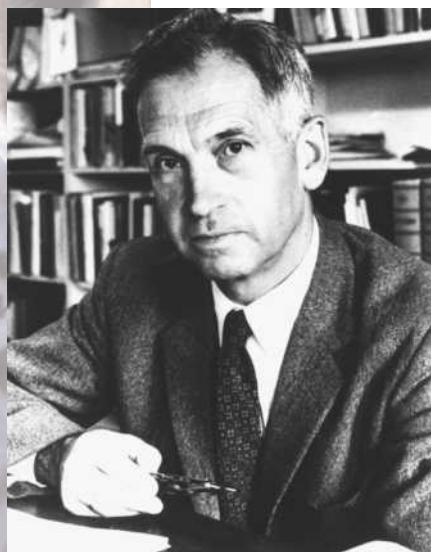
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Mayr, Ernst

American Biologist and Ornithologist

1904–

Ernst Mayr, one of the cofounders of the “Modern Synthesis” in evolutionary biology (along with Theodosius Dobzhansky, George Gaylord Simpson, and G. Ledyard Stebbins), is a naturalized American citizen born in Kempten, Germany. The Modern Synthesis sought to integrate Charles



Ernst Mayr attempted to synthesize the natural selection theory and population genetics.

natural selection a process by which organisms best suited to their environment are most likely to survive and reproduce

population a group of individuals of one species that live in the same geographic area

Darwin's theory of **natural selection** with the recent development of **population** genetics by R. A. Fisher, Sewall Wright, and J. B. S. Haldane.

Mayr showed an ardent interest in birds from an early age and took only eighteen months to complete his doctoral program in ornithology at the Berlin Natural History Museum (1926). In 1928 he began leading a series of ornithological expeditions to New Guinea, the Philippines, and the Solomon Islands. His field guides to the birds of these areas continue to be used by scholars of ornithology.

After his Pacific forays, Mayr joined the staff of the American Museum of Natural History (AMNH) in New York City in 1931 and was appointed curator of its ornithology collection in 1932, a position he would hold for over twenty years. During this time, he described twenty-six new bird species and 410 subspecies. In the style of Darwin, his intellectual hero, Mayr used his accumulated knowledge of natural history to gain insight into broad evolutionary questions. His work at AMNH focused on systematics: the classification, genealogy, and defining boundaries of species and populations. Mayr's classic "biological species concept" won wide acceptance among scientists in its time, and continues to structure many scientist's thinking about species: "species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups." This definition has led to the identification of many previously unknown species. Mayr's contribution to systematics is reflected in two seminal works: *Systematics and the Origin of Species* (1942), where the biological species concept was presented, and *Methods and Principles of Systematic Zoology* (1953).

Mayr left AMNH in 1953 to become the Alexander Agassiz Professor of Zoology at Harvard's Museum of Comparative Zoology, a position he still holds today as emeritus faculty; in 1961, he was appointed director of the museum. At Harvard, Mayr shifted his intellectual focus from systematics to speciation (how species are formed) and other general questions in evolutionary biology. He published *Animal Species and Evolution*, a major synthesis of evolutionary theory, in 1963. Mayr has been a leading advocate of population thinking—the notion that species are best understood by taking into account the fact that traits vary among individuals—in the classification and study of living things. According to Mayr, speciation typically occurs as a result of geographic separation, and therefore from a reduction of gene flow, between large parent populations and small founder populations.

Mayr is an eminent scholar in the history of evolutionary biology, and his recent career is marked by two major works on the subject, *The Growth of Biological Thought* (1982) and *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (1991).

Mayr's accomplishments have earned him numerous honors, including the National Medal of Science (1970), the U.S. government's highest award for scientific research, and the Royal Swedish Academy of Science's Crafoord Prize (1999).

Gil G. Rosenthal

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Medical Doctor

The long and sometimes bizarre history of Western medicine can be traced as far back as an Egyptian surgical papyrus of the seventeenth century B.C.E., which advises treating a head wound by “first softening the head with grease, then pouring milk into both ears” (Swierczynsky 2000, p. 115). Despite diagnoses and cures that might seem laughable or horrendous to us, doctors have always intended, as do medical students today, to “make a difference in people’s lives, to relieve pain and suffering.” From the bloodletting of the Middle Ages, where surgeons got their nickname “leeches,” to the miracle antibiotics and technological advances of the twentieth century, doctors have seen their job as the treatment of illness, injuries, and other adverse conditions.

Any degree holder can apply to medical school upon qualifying through the Medical Colleges Admission Test. The four-year graduate program includes two years of work in the areas of anatomy, biochemistry, biology of healthy organisms, pathology, immunology, writing skills, and clinical studies. The third year is a forty-hour hospital workweek divided into intensive sections of internal medicine, surgery, psychiatry, obstetrics and gynecology, and pediatrics. In the fourth year, the student takes electives focusing on an area of interest and applies for a residency with a hospital. Generalists, including family practice and internal medicine interns, take a three-year residency. Surgeons and specialists require up to five years.

The old catastrophic view of medicine is expanding to include preventive care. Diet, exercise, herbal remedies, healing touch, and techniques such as acupuncture are being added to the repertoire of tools for staying healthy as well as for recovering from serious illness. And doctors would probably still agree with Galen, the ancient Greek, concerning the patient’s participation: “confidence and hope do more than the physic.”

Nancy Weaver

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Mendel, Gregor

Botanist

1822–1884

Gregor Mendel, the father of **genetics**, was born on July 22, 1822, in Heinzendorf, Austria. He died on January 6, 1884. He was the first person to propose the idea of **genes** and to apply mathematics to genetics. Although his work was initially ignored by scientists, it proved to be the basis of modern genetics.

Mendel’s interest in natural science developed early. He studied at the Philosophical Institute at Olmütz for two years. In 1843 he entered the

genetics the branch of biology that studies heredity

genes segments of DNA located on chromosomes that direct protein production



Gregor Mendel was a pioneer in the field of genetics.

artificial pollination manual pollination methods

recessive hidden trait that is masked by a dominant trait

hybrid offspring resulting from the cross of two different species

monastery in Brünn, becoming a priest in 1847. Then he went to the University of Vienna, where he studied science from 1851 to 1853. In 1854 Mendel returned to Brünn and taught natural science in the technical high school there until 1868.

Seeking to learn how plants inherit different traits, Mendel began his experiments with garden peas in the small monastery garden in 1856. From 1856 to 1863 Mendel grew almost 30,000 specimens of garden peas. These plants had sharply contrasting characteristics (tall versus short, smooth seed versus wrinkled seed, and so on). He studied seven pairs of alternative characteristics, making hundreds of crosses by **artificial pollination**.

Mendel kept very careful records of the plants that he crossed and the resulting offspring. He noted that the occurrence of the alternative characteristics in the crossed varieties of plants followed simple statistical, mathematical laws. For example, Mendel crossed species that produced tall plants with those that produced short plants. Then, he counted the numbers of tall and short plants that appeared in subsequent generations. In the first generation, all of the plant offspring were tall. The next generation had some tall plants and some short plants in proportions of three (tall) to one (short). This showed that no blending of traits occurred (no medium-height plants). Further, if allowed to self-pollinate (fertilize themselves), the short plants always had short offspring. Mendel proposed that each plant received one character from each of its parents. Tallness was dominant and shortness was **recessive**, appearing only in later generations. Mendel also showed that when several pairs of alternative characteristics are observed, the several pairs enter into all possible combinations in the subsequent generations. In the pea plants he studied, he observed that the seven alternative characteristics recombined at random. He worked out the statistics of these combinations and confirmed his predictions by experiment.

Mendel developed three theories to explain the results of his experiments. His first law is the principle of segregation. It states that during the formation of sex cells (egg and sperm), paired factors are segregated (separated). Therefore, a sperm or egg may contain either a tallness factor or a shortness factor, but cannot contain both. The second law, the principle of independent assortment, states that characteristics are inherited independently of one another. Thus, the fact that the tallness factor is inherited does not determine which alternative of any other pair of characteristics is inherited. The law of dominance, which is the third theory, states that each inherited characteristic is determined by the interaction of two hereditary factors (now called genes). One factor always dominates the other (for example, tallness always dominates shortness). Mendel was the first to understand that trait units are physical particles passed from one generation to another by reproduction. This is remarkable, since at that time knowledge about cell structure was limited.

It is now known that Mendel's second principle applies only to genes that are transmitted in different linkage groups. Also, the appearance (or dominance) in **hybrid** offspring of one of the alternative characteristics has now been proven not to be true for all alternative characteristics. However, these limitations do not affect the fundamental truth of Mendel's findings. Mendel's system, called Mendelism, is one of the basic principles of biology.

Mendel presented his findings to his fellow scientists in 1865, but they failed to see the revolutionary nature of his work. When he was promoted to head of the monastery in Brünn in 1868, Mendel turned his focus away from science to concentrate on his duties at the monastery. He did, however, continue work in botany, bee culture, and the weather until his death.

Mendel was widely respected and loved, but went unrecognized as the great scientific thinker that he was. Fame and due credit came to Mendel only after his death. In 1900, three other European scientists independently obtained results similar to Mendel's. The researchers realized that he had already published both the experimental data laying out his results and a general theory explaining them nearly thirty-five years earlier. **SEE ALSO** BIOLOGICAL EVOLUTION; GENES; GENETICS.

Denise Prendergast

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Mesenchyme

Mesenchyme is a tissue found in organisms during development. It consists of many loosely packed, nonspecialized, mobile cells. Mesenchyme is derived primarily from the **mesoderm**, although there are also mesenchymal cells known as the neural crest cells, which derive from ectoderm. Mesenchyme gives rise to diverse structures of the developing organism, including **connective tissue**, bone, **cartilage**, teeth, blood and plasma cells, the endothelial lining of the vessels of the circulatory and lymphatic systems, and **smooth muscle**.

Mesenchymal cells are star-shaped in appearance, with an oval-shaped nucleus and comparatively little **cytoplasm**. They are widely spaced, with considerable extracellular space between cells. This space is filled with a dense intercellular **matrix**. An important characteristic of mesenchymal cells is that they are mobile, and move with a crawling, amoeboid motion.

Mesenchymal cells are undifferentiated and are therefore **pluripotent**—that is, they have the capacity to differentiate into any number of tissue types. A group of mesenchymal cells that will differentiate into another tissue type is called a **blastema**.

Mesenchymal cells are contrasted with the other major embryonic cell type: **epithelial cells**. Unlike mesenchymal cells, epithelial cells are not mobile. Epithelial cells form continuous sheets, with little extracellular space between cells. All epithelial cells have two definite ends, the basal end and

mesoderm the middle layer of cells in embryonic cells

connective tissue cells that make up bones, blood, ligaments, and tendon

cartilage a flexible connective tissue

smooth muscle muscle of internal organs that is not under conscious control

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

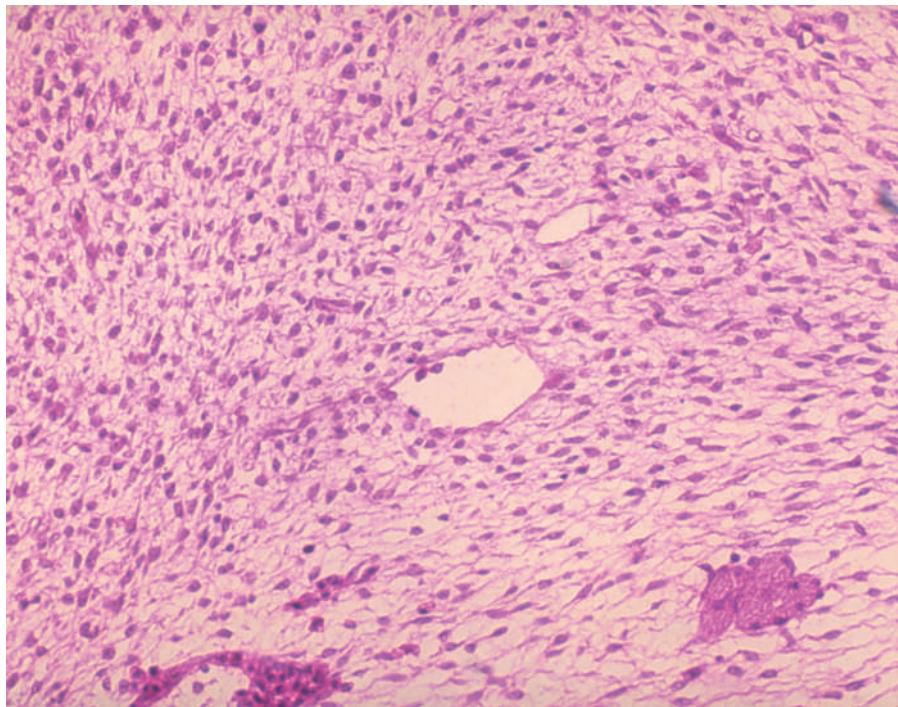
matrix the nonliving component of connective tissue

pluripotent a cell in bone marrow that gives rise to any other type of cell

epithelial cells cells that occur in tightly packed sheets that line organs and body cavities



Mesenchyme is the part of the embryonic mesoderm from which connective tissue and lymphatic and circulatory systems develop.



the apical end. Epithelial cells are attached to a structure known as basement membrane by their basal end.

Many important developmental events take place as a result of interactions between mesenchymal and epithelial cells. Often, epithelial cells are induced by adjacent mesenchymal cells, that is, they change in form or shape in response to signals from the mesenchyme. Induction occurs either via mechanical processes, in which the migrating mesenchymal cells cause changes in the arrangement of epithelial cells, or by molecular agents released by mesenchymal cells.

Epithelial-mesenchymal transitions, in which cells change from epithelial to mesenchymal morphology, are also frequent during development. These transitions take place through the loosening of the cell adhesion molecules that keep epithelial cells organized in tight sheets. The reverse transition (mesenchymal to epithelial) occurs during developmental processes as well.

Although mesenchymal cells are technically found only in embryonic tissue, some cells do remain undifferentiated in adults. These serve as stem cells, which retain the ability to differentiate into diverse types of connective tissue as they are needed by the body for regeneration or repair.

Mesenchyme initially gives rise to three types of cells—fibroblasts, which generate collagen; myoblasts, which form muscle cells; and **scleroblasts**, which form connective tissue. Scleroblasts later differentiate into **osteoblasts**, which generate bone; chondroblasts, which generate cartilage; odontoblasts, which generate dentin in teeth; and **ameloblasts**, which generate tooth enamel.

scleroblasts cells that give rise to mineralized connective tissue

osteoblasts potential bone forming cells found in cartilage

ameloblasts cells that form dental enamel

Jennifer Yeh

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Metamerism *See Serial Homology.*

Metamorphosis

Metamorphosis, or a change in form, in biology means the transition from a larval stage to an adult stage. In most animals, embryonic development leads to the formation of a larval stage with very different characteristics than the adult stage. Larval morphology, or form, may be specialized for some function such as growth (which requires feeding and associated structures) or dispersal. Some larval forms, called **exotrophic**, feed, while others, called **endotrophic**, are nonfeeding. Juvenile and adult forms often live in very different environments.

Cnidarians have varying types of metamorphosis. Some species have three distinct life history stages: the planula, medusa, and polyp. The planula stage is the free-living larval stage. The medusa stage involves a single individual or a colony of individuals that act as a single free-swimming organism (examples include jellyfish and man-o-war). The polyp stage is **sessile** (adhered to the substrate) and may involve a single individual or a colony of individuals (examples include sea anemones and corals). Some species lack the free-swimming medusa stage. In others, the medusa is the dominant life history stage and the polyp stage is lacking completely.

Molting and metamorphosis in **arthropods** is controlled by environment and **hormones**. Insects experience no size increase in the egg, pupal (the third stage in the life of an insect that undergoes complete metamorphosis), or adult stages. All growth occurs during the intermediate larval or nymphal stages. Anametabolous (without change) metamorphosis occurs in the primitive insect groups Colembola, Diplura, Protura, and Thysanura. Juveniles change little except in size and proportion from egg to adult. After reaching adulthood, defined as sexual maturity, they continue to molt, adding antennal segments.

Many insects (including dragonflies, grasshoppers, and cockroaches) and **crustaceans** (crawfish and crabs) develop through hemimetabolous (incomplete or gradual) metamorphosis. In hemimetabolous metamorphosis, the insect egg hatches into a nymph. The nymph is similar to the adult in general morphology, only smaller. The nymph is an actively feeding stage, and as it grows it must shed its **exoskeleton** and produce a new, larger one. This process is called molting. In insects with hemimetabolous metamorphosis, the gonads do not mature until after the final molt.

Some insects (including flies, butterflies, wasps, and bees) have holometabolous metamorphosis (they undergo a complete metamorphosis,

endotrophic deriving nourishment from within

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

sessile immobile, attached

molting the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

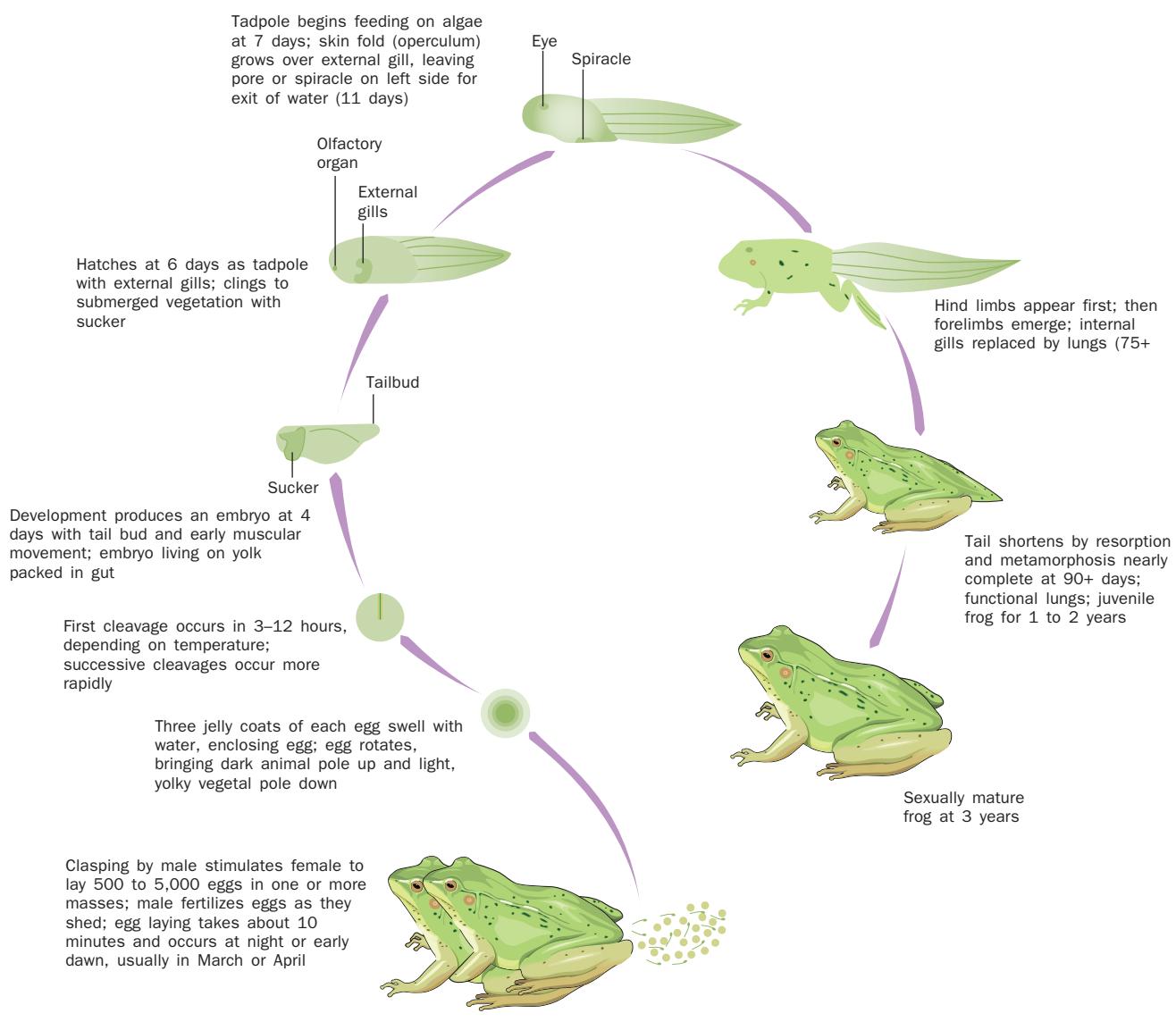
hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

exoskeleton hard outer protective covering common in invertebrates such as insects



LIFE CYCLE OF A FROG



The life cycle of the leopard frog (*Rana pipiens*). Metamorphosis occurs when the tadpole grows legs, and ends with the resorption of the tail.

instars the particular stage in an insect or arthropod between moltings

having distinct larval and pupal stages). There are four distinct stages in the life cycle of holometabolous insects: egg, larva, pupa, and imago (adult). The larva is segmented and wormlike. The larval stage is a feeding stage and consists of several subdivisions called **instars**. Each instar ends in molting, which allows the larva to grow.

The final instar ends with pupation. Prior to pupation, the animal stops feeding and the cuticle hardens and darkens to form the puparium (pupal chamber), where metamorphosis will take place. The pupa begins to darken just prior to the emergence of the imago. In the larvae of these organisms, imaginal disks (clusters of cells carried with a larva that will develop into different adult body parts) are formed. These disks will produce adult organs, but they remain quiescent, or inactive, in the embryo until the appropriate time.

Most, but not all, amphibians have a biphasic (two-phase) life history with an **aquatic** larval stage that **metamorphoses** to become an adult, a process known as indirect development. Many frogs have a free-living, aquatic larval stage as a tadpole. Near the end of the larval stage, many larval structures are reabsorbed or remodeled and adult structures begin to form.

During metamorphosis bones begin to ossify, the tail is reabsorbed, limbs form, and larval respiratory and feeding structures (including gills and a beak with keratinized—covered with a tough protein like our fingernails—mouth parts) are replaced by adult structures (including **lungs** and movable jaws). The digestive system is remodeled to accommodate a transition from a largely **herbivorous** diet to one that is strictly **carnivorous**.

In salamanders, the larval stage is more similar to the adult stage than is the case with frogs. Metamorphosis usually involves the replacement of larval gills with lungs; **ossification** of the skull, vertebral column, and limbs; and the remodeling of the tail and feeding apparatus to conform to the requirements of life on land.

Although this familiar mode of development is common among amphibians, some salamanders, caecilians, and frogs lack a free-living larval stage. In many species with a monophasic life history, a miniature version of the adult is hatched directly from the egg (direct development) in what is called **ovoviparity**, or birthed by the female, in what is known as **viviparity**.

The loss of a free-swimming larval stage has been hypothesized to release a major limit on morphological diversification in some groups of direct-developing frogs, because the pre-pattern established by larval structures is no longer present. Evidence of this morphological release can be seen in the great diversity of species and **morphologies** attained by some amphibian groups that have lost the free-living tadpole stage.

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aquatic living in water

metamorphoses

changes drastically from its larval form to its adult form

lungs sac-like, spongy organs where gas exchange takes place

herbivorous term describing animals that eat plants

carnivorous term describing animals that eat other animals

ossification the deposition of calcium salts to form hardened tissue such as bone

ovoviparity having offspring that hatch from eggs retained in the mother's uterus

viviparity having young born alive after being nourished by a placenta between the mother and offspring

morphologies the forms and structures of an animal

Metazoan

In the tenth edition of his book *Systema Naturae* (1758), Swedish botanist Carolus Linnaeus developed a biological classification system (now known as the Linnaean System) that placed all organisms into seven hierarchical groupings. He suggested that all organisms could be classified as belonging to two kingdoms, the Plantae (plants) and the Animalia (animals), and that members of these kingdoms could be distinguished by whether they have the ability to “sense” (both plants and animals grow and live, but only



prokaryotes single-celled organisms that lack a true cell nucleus

eukaryotes organisms containing a membrane bound-nucleus and membrane-bound organelles

autotrophs organisms that make their own food

absorption the movement of water and nutrients

photosynthesis converting sunlight to food

heterotrophs organisms that do not make their own food

protozoa a phylum of single-celled eukaryotes

flagella cellular tail that allow the cell to move

aquatic living in water

habitats physical locations where an organism lives in an ecosystem

niche how an organism uses the biotic and abiotic resources of its environment

consumers animals that do not make their own food but instead eat other organisms

animals sense). This two-kingdom classification system remained virtually unchallenged for over a century.

Today, most biologists group living things into five kingdoms: the Monera, the Protista, Fungi, Plants, and Animals. The Monera includes all **prokaryotes**. The monerans include the most ancient forms of life and were the only organisms on Earth from around 3.5 to 1.5 billion years ago. The Protista is a diverse group of single-celled **eukaryotes** that originally derived from the Monera. The protists gave rise to the other three kingdoms: the multicellular fungi, plants, and animals.

Plants are distinguished from fungi and animals because they are **autotrophs**, meaning that they gain all their nutrients and energy from inorganic materials and from the Sun. Plants take nutrients from the soil through **absorption**, the passing of molecules through pores in cells; they take energy from the Sun through **photosynthesis**. Fungi are different from plants and animals because they are **heterotrophs** (they require preformed organic material, that is, material made by other organisms), which obtain their nutrients through absorption. Animals, on the other hand, are heterotrophs that obtain their nutrients through ingestion, the active intake of other organisms or decomposing organic material. Today's Animalia, also called the Metazoa, differs from the Animalia of Linnaeus in that it does not include any of the animal-like unicellular eukaryotes, commonly termed the **Protozoa**, which are now grouped in the Protista.

Multicellularity evolved in the Protista a number of times. The commonly held view is that multicellularity derived from colonial unicellular ancestors, which formed loose collections of interconnected cells. The benefit of being part of a colony is that individual cells may become specialized for certain tasks, such as sensation, secretion, or gamete production, and thus raise the efficiency of the colony as a whole. As these colonial organisms become more intimately associated, some members may lose their **flagella** to become completely dependent on their neighbors. At the point when a colony transports nutrients from cell to cell, eliminating the necessity of all cells to feed individually, the colony becomes a true multicellular organism.

Multicellular eukaryotes arose approximately 700 million years ago in **aquatic habitats**. One of the first benefits that multicellularity allowed was an increase in organism size. Greater size and greater cell number allowed greater variation in organism shape and structure. Consequently, the diversity of multicellular life exploded and began occupying a variety of new **niches**. Around 400 million years ago, multicellular eukaryotes living at the edges of lakes and streams colonized land, giving rise to the enormous diversity of terrestrial multicellular life seen today.

The Metazoa contains more species than any other kingdom. While plants are relatively immobile and utilize simple molecules as a food source, animals have become specialized **consumers** of all types of organisms, including other animals.

Brief Survey of the Diversity of the Animal Kingdom

The sponges are a group of sedentary aquatic animals first classified as plants. Although sponges and other animals evolved from protists, sponges may



have arisen independently from the other animals. Sponges obtain their nutrients by drawing water into a central cavity and filtering the water for food. They are able to move water through their bodies through the coordinated beating of flagellated cells that line their pores. Sponges differ from other animals in that they lack distinct body tissues and body symmetry.

A second group of animals that may also have independently evolved from protists contains the **cnidarians** and the ctenophorans. These animals are **radially symmetrical**, meaning that their body parts are arranged symmetrically around one main axis. Examples include jellyfish, sea anemones, and corals. Cnidarians differ from ctenophorans in that their mouth and anus form a single opening, whereas ctenophorans have separate openings for the mouth and anus so that food moves in a single direction through the gut.

The remaining metazoans are more closely related to each other than to the other animals. They may be classified into three groups: the **acoelomates**, the **pseudocoelomates**, and the coelomates. All these animals are **bilaterally symmetrical**, meaning that their bodies can be divided into mirror images through only a single plane.

Acoelomates are animals that lack internal body cavities. The acoelomates include the flatworms and the ribbon worms. Flatworms have distinct organs but do not have a fully formed digestive tract or a means for transporting oxygen through the body. Thus all cells must undergo respiration individually, necessitating a flat body whereby all cells have access to oxygen at the body surface. Ribbon worms are similar to flatworms but have a complete digestive tract and a simple circulatory system.

Pseudocoelomates have a simple, fluid-filled body cavity in which many of the internal organs float. The body cavity protects the internal organs from external jarring and allows them to grow somewhat independently from the rest of the body. The pseudocoelomates include the rotifers and the nematodes. Nematodes are probably the most numerous of all animal species, inhabiting virtually every corner of Earth. One of the most well-studied organisms in the world is the nematode *Caenorhabditis elegans*, a roundworm that lives in soil.

The third group of bilaterally symmetrical metazoans, the coelomates, have a relatively complex body cavity inside which the organs are suspended from the body wall. Most coelomates can be further divided into two groups, the **protostomes** and the **deuterostomes**, which are distinguished by the way in which cells of their **zygotes** divide. Protostomes include **mollusks** such as snails, **annelids** such as earthworms, and **arthropods** such as insects. The deuterostomes include **echinoderms** such as starfishes and chordates such as humans. **SEE ALSO** BINOMIAL (LINNAEAN SYSTEM); PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

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cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

radially symmetrical an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

acoelomates animals without a body cavity

pseudocoelomates animals with a body cavity that is not entirely surrounded by mesoderm

bilaterally symmetrical describes an animal that can be separated into two identical mirror image halves

protostomes animals in which the initial depression that starts during gastrulation becomes the mouth

deuterostomes animals in which the first opening does not form the mouth, but becomes the anus

zygotes fertilized eggs

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

annelids segmented worms

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

echinoderms sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

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Migration

populations groups of individuals of one species that live in the same geographic area

Migration is defined as the regular, usually seasonal, movement of all or part of a **population** of animals. Many different animals migrate, including birds, hoofed animals, bats, whales, seals, and salmon. One-way movement of animals that do not return is called emigration. Emigration is due to different causes and is not considered migration. Also, the regular daily movements that many animals undertake are not considered migration.

Most birds and mammals that migrate follow an annual or seasonal pattern related to cyclic variations in temperature, vegetation, or precipitation. Salmon and some other fishes do not migrate annually. Instead, they return to their place of birth in order to reproduce. Some ethologists do not consider these movements migration but reserve the term for cyclic movements. In some parts of the world, animals will suddenly move into a new area temporarily. These sudden and temporary movements are called irruptions. Irregular movements, such as irruptions, are generally due to population growth during periods of abundant food followed by dispersal when food supplies diminish.

Most migrations involve horizontal movement. Animals move north and south with the seasons or move in a circular pattern to take advantage of cyclic rain patterns or new forage growth. Some animals, however, migrate by changing elevation. **Aquatic** animals may move from deeper water to the surface according to the season. Many birds, mammals, and insects migrate to higher or lower elevations in mountainous areas. This kind of migration produces the same kind of change in the environment as horizontal migration but involves only small horizontal displacements.

aquatic living in water

Invertebrate Migration

Some shrimp and crabs migrate for purposes of reproduction. Pregnant females move into shallow water to lay their eggs. The shallow water environment has fewer large predators, so the chances of the baby shrimp growing to maturity is increased. After they mature the shrimp move into deeper water to feed.

Probably the best known insect migrant is the monarch butterfly (*Danaus plexippus*). In the summer, these insects move northward as far as Canada's Hudson Bay, where they breed and reproduce. Adults from the last generation of the year migrate southward in autumn through Oklahoma and



Texas. Many move as far south as the mountains of central Mexico. After overwintering in the tall firs of these mountains, they follow spring northward, breeding and laying eggs on their preferred milkweed plants. Since a few of the returning butterflies are members of the first generation that developed from the overwintered insects, they can be considered true migrants. Most insects that arrive in the north, however, have been born in route. The longest distance recorded for the complete flight of an individual monarch butterfly is 3,010 kilometers (1,870 miles), truly a remarkable flight for this tiny insect.

Snow geese fly away from a grain field near Delta, Utah, a resting place for many migrating birds.

Vertebrate Migration

The three categories of migratory fishes are oceanodromous, **anadromous**, and **catadromous**. Oceanodromous fish live and migrate entirely in the ocean. The many species of herring with different migration patterns are typical of oceanodromous fish. Anadromous fish live in the sea and migrate to freshwater to breed. Pacific salmon are typical. They hatch from eggs in mountain streams or lakes. The young feed and grow in the freshwater, then migrate to the sea after a year. Adult fish usually remain in the sea for two or three winters, where they grow to full size. Then they undergo dramatic **physiological** changes and migrate back to the stream where they were born. There the females lay eggs that are fertilized by the males. Then both sexes die. Some Atlantic salmon breed two or three times.

anadromous moving from the ocean up a river to spawn

catadromous living in freshwater but moving to saltwater to spawn

physiological the basic activities that occur in the cells and tissues of an animal

Catadromous fish reverse the behavior pattern of anadromous fish. Catadromous fish spend most of their lives in freshwater, then they migrate to the sea to breed. Eels of the genus *Anguilla* are the best known. Both European eels and North American eels spawn in an area of the Atlantic Ocean known as the Sargasso Sea. The larval forms of the fish are carried by the Gulf Stream to the shallow waters of the continental shelves. After about two years, when the larval eels are about 8 centimeters (3 inches) long, a **metamorphosis** occurs. The nearly transparent free-swimming larval eels are transformed into bottom-dwelling, dark-colored, cylindrical fish. Their migration upstream is spectacular, as the young fish gather by millions, forming a dense mass several miles long. In freshwater, the eels grow to full size.

metamorphosis a drastic change from a larva to an adult



They live for several years in freshwater, then undergo a final metamorphosis before they swim back to the Sargasso Sea to spawn.

Terrestrial reptiles and amphibians do not migrate regularly enough to be significant, although some species migrate vertically. Reptiles and amphibians have evolved other strategies to deal with adverse environmental conditions, such as hibernation and estivation. Sea turtles are the exception. Most sea turtles migrate to beaches to lay their eggs. They then disperse back into the ocean. Green sea turtles (*Chelonia mydas*) lay their eggs on the coast of Costa Rica in Central America and then disperse through the Gulf of Mexico and the West Indies.

The taxonomic class Aves includes most of the best known migrating species. Most species of birds require a large input of food to maintain their body temperature and other behaviors. Many birds have evolved behaviors that allow them to move to areas where food is more abundant. Birds have evolved a highly efficient means for traveling swiftly over long distances with great economy of energy.

Migratory birds do not differ greatly in gross physiological characteristics from nonmigratory birds. There is a spectrum of birds from completely nonmigratory species to species that fly thousands of kilometers every year.

Since insect populations drop dramatically during the winter, insectivorous species of birds, such as warblers, flycatchers, and wagtails, are highly migratory and typically spend the winter in the tropics. The geographical arrangement of the North American continent determines migration routes for many species of North American birds. Principal routes are known as flyways. They include the Mississippi flyway, the central flyway, the Pacific flyway, and the Pacific oceanic route. Many birds spend the winter in the states that border the Gulf of Mexico, but the principal wintering areas are in Mexico and Central America. Panama has the greatest density of winter bird residents in the world.

Tropical regions do not have the four seasons of temperate regions, but they do have cyclic rainy and dry seasons. Birds of tropical regions migrate according to these wet and dry seasons.

Arctic terns (*Sterna paradisaea*) are the world champion migrators. These birds breed in the coastal regions of northern Europe, Asia, and North America. They then fly south and spend the winter in the extreme southern Pacific and Atlantic along Antarctic pack ice 17,600 kilometers (10,940 miles) from their breeding range. American populations of the Arctic tern cross the Atlantic to Europe, then fly south along the coast of western Europe. Arctic terns thus travel farther than any other bird species.

Most terrestrial mammals do not migrate. True migration among terrestrial mammals occurs mostly among large hooved animals living in **habitats** with wide fluctuations of climatic and **biotic** conditions. For example, before the central United States was largely fenced in, American bison (*Bison bison*) migrated regularly. Large herds containing millions of animals moved in circular routes to the southern part of their range in winter and back north when spring rains brought fresh grass to the northern part of their range.

habitats physical locations where an organism lives in an ecosystem

biotic pertaining to living organisms in an environment

In North American Arctic regions, caribou (*Rangifer tarandus*) regularly migrate between the open tundra, where they calve, and the forest, where they spend the winter months. In winter, each caribou herd moves independently of the other herds in response to local conditions. Then in the spring, the herds move back onto the tundra. These migrations follow the same routes from year to year.

In contrast to terrestrial mammals, marine and flying mammals typically do migrate because of their inherently greater mobility. The only true flying mammals are the many species of bats. Huge colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) spend the summer in Texas and adjoining states. The Congress Avenue Bridge in Austin, Texas, is home to the largest urban bat colony in the world, with around 1.5 million bats. It is a huge bat nursery containing females and nursing babies, called pups. Since they are insectivorous, these bats leave around the middle of November for their winter home in Mexico. They return in mid-March when the insect population in Texas increases dramatically. Most of the females in the Congress Avenue colony give birth to a single pup in early June.

Among mammals, the marine mammals are the distance record holders. Antarctic whales, such as humpback whales (*Megaptera novaeangliae*), migrate regularly to the tropics. Whales migrate to areas rich in food, particularly the northwestern coast of Africa, the Gulf of Aden, and the Bay of Bengal. Northern whales, such as blue whales (*Balaenoptera musculus*), have the same migratory habits as Antarctic whales. They migrate northward along the east coast of the United States, then through Davis Strait to Baffin Bay (north of Canada) or to waters off northern Scotland or the coast of Norway.

Migration Routes

Birds tend to follow well-defined migration routes called flyways. A population of birds may be scattered over thousands of square kilometers. As they begin their migration, the birds may be spread out over a migration front hundreds of kilometers wide. These routes are determined by geographical factors, ecological conditions, and meteorological conditions. Some routes cross oceans. American golden plover fly over open ocean from the Aleutian Islands southwest of Alaska to Hawaii, a distance of 3,300 kilometers (2,050 miles).

Many birds fly at relatively low altitudes. Hawks and other passerines, however, fly at altitudes as great as 4,000 meters (13,120 feet). The highest altitude ever recorded for migrating birds is 9,000 meters (29,520 feet) for geese near Dehra Dun in northwest India.

Some birds fly nonstop. Others are **diurnal**, flying during daylight hours and resting at night. Pelicans, storks, birds of prey, swifts, swallows, and finches migrate during daylight hours. Other birds reverse the pattern. Cuckoos, flycatchers, thrushes, warblers, orioles, and buntings fly at night and rest during the daylight hours.

Most birds abandon their instinctive territoriality during migration. Even unrelated birds with similar habits sometimes travel together. Some birds migrate in large flocks. Geese, ducks, pelicans, and cranes fly in well-known V-shaped formations that allow each bird to receive lift from the bird just in front.

Mexican free-tailed bats are among North America's most important animals, from both an ecological and agricultural standpoint. They consume phenomenal volumes of insects nightly, a large number of which are agricultural pests. Serious bat population decline has been observed, largely due to human activities (i.e., the destruction of old buildings or the use of pesticide) and vandalism of important roosting habitats

diurnal active in the daytime



Finding Their Way



Animals use several different techniques to navigate while migrating or to locate the place of their birth. Experiments have demonstrated the ability of animals to orient themselves geographically. Starlings have returned to their nests after being moved 800 kilometers (500 miles) away; swallows have found their way home from more than 1,800 kilometers (1,120 miles). A Manx shearwater (*Puffinus puffinus*) flew 4,900 kilometers (3,040 miles) across the Atlantic from Massachusetts to Britain in twelve days. Laysan albatrosses (*Diomedea immutabilis*) found their way back to Midway Island in the Pacific after being released at Whidbey Island, Washington. The journey covered 5,100 kilometers (3,170 miles) and took ten days. Experiments with fish and mammals have demonstrated similar homing ability.

Some homing animals use landmarks. The use of landmarks, however, cannot explain how migrants find their way along routes covering many hundreds or thousands of kilometers.

Birds apparently possess a compass sense. This sense is probably related to a sensitivity to Earth's magnetic field. When homing pigeons were released with tiny magnets attached to their necks, they were unable to navigate. Experiments have also shown that the orientation of birds is partly based on celestial bearings. In one well-known experiment, indigo buntings were placed in compartments in a planetarium and shown star patterns. Scratch marks on sensitive paper showed that the birds attempted to move "north" according to the star patterns displayed on the dome of the planetarium.

Experiments have shown that salmon and similar fish apparently use Sun orientation while at sea to find their way back to the general area of the stream in which they hatched. Once in the correct general area, salmon apparently use their sense of smell to locate their home waters.

What Triggers Migration?

Migration is part of the life cycle of animals. Metabolic patterns usually change prior to migration, and fats accumulate in the body tissues. Food consumption increases in the autumn reaching a peak at the beginning of the migration season. These fundamental physiological changes are apparently controlled indirectly by the pituitary gland. The pituitary acts as a sort of internal clock. Variations in temperature and hours of daylight are detected by the pituitary gland. The pituitary then influences the development of gonads and all other metabolic processes, including the thyroid gland. The thyroid gland excretes the chemical substances that cause the physiological changes that prepare the animal for migration. The pituitary serves only to prepare the animal for migration. Actual migration is triggered by appropriate environmental conditions, such as precipitation, availability of food, temperature, and weather conditions. A sudden period of cold weather during autumn may induce the immediate departure of many migrants.

Evolution and Ecology of Migration

Migration as a behavior among birds and mammals probably appeared gradually. Erratic dispersals were probably the precursors of true migration. Such erratic dispersal would have led to greater survival rates and reproductive success among animals that moved to the most favorable places.

These originally erratic movements gradually acquired stability through **natural selection**. In some cases, original habitats were in present-day wintering areas, and animals developed a tendency to leave in spring in order to breed in other territories. Seasonal changes of weather and food supply in these newly settled regions forced the animals to migrate in fall, and they thus retreated to their former range. Many birds now nesting in the Northern Hemisphere, such as hummingbirds, tyrant flycatchers, tanagers, orioles, and swifts, have distinct tropical characteristics. These birds may have gradually spread northward as glacial ice receded.

The evolution of migration must be related to the ecological significance of migration. Migration allows fast-moving animals to exploit variations in resources and to move into areas where they could not remain year-round without the ability to move rapidly. Exploitation of peaks of food production, such as the dramatic increase of insect populations in temperate regions in the springtime, would not be possible without migratory populations. **SEE ALSO** HABITAT.

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natural selection

process by which organisms best suited to their environment are most likely to survive and reproduce

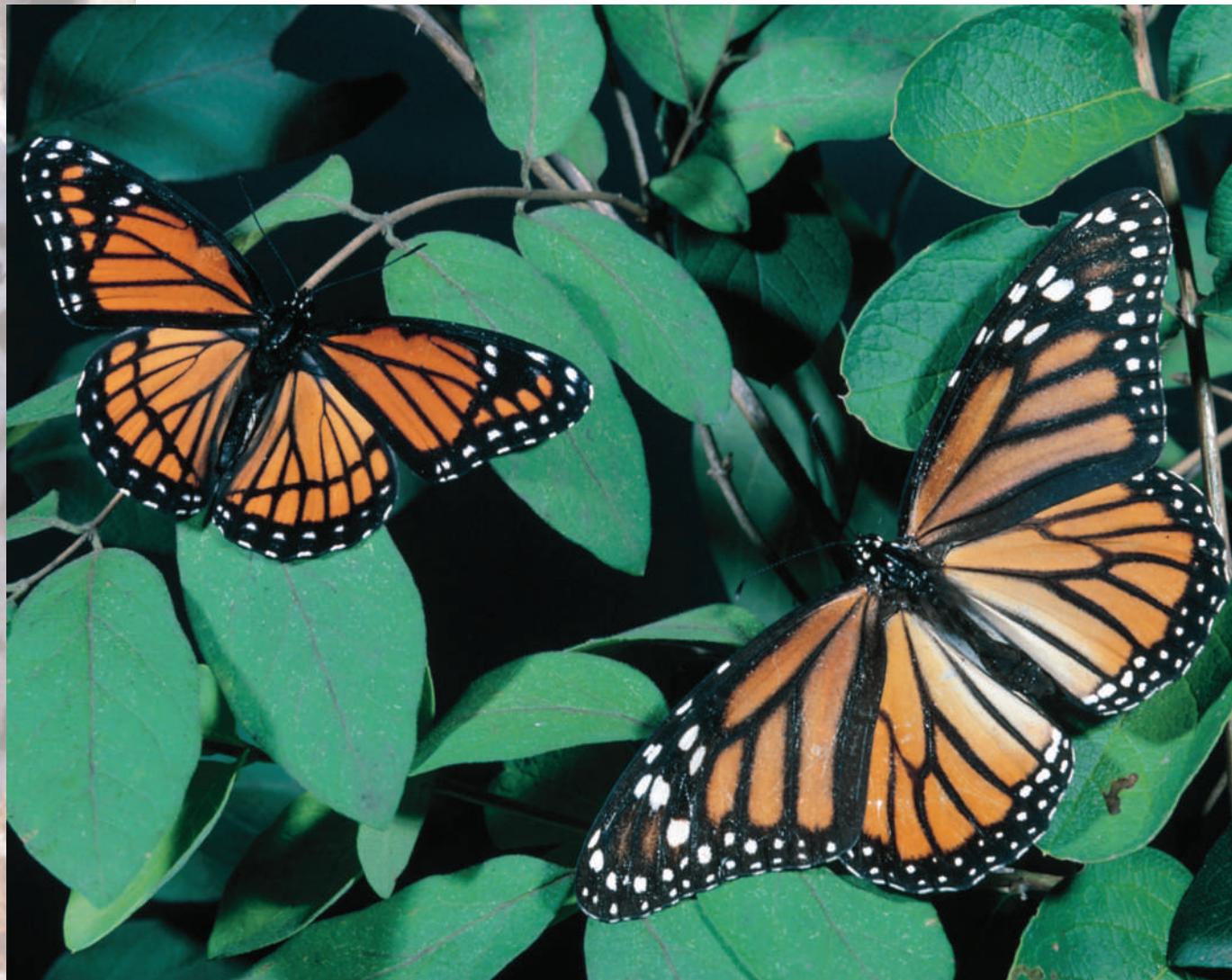


Mimicry

Animals that are toxic, armed with spines, or are otherwise unpalatable, or disagreeable, to predators often exhibit conspicuous colors or patterns. These superficial characteristics, called **aposematic** signals, are used to warn potential predators of the animal's physical or chemical defenses. The distinct colorations are highly conspicuous against certain backgrounds. This imposes a cost on the aposematic prey because the predators can more readily spot them. However, the predators will also be quick to learn and remember which prey to avoid because of the distinctiveness of the signals. Of course, if the prey is not sufficiently unpalatable, then the costs are greater than the benefits for the attacked animal.

aposematic a feature or signal that serves to warn

To evaluate whether the benefits outweigh the costs of any predator/prey strategy, the Evolutionary Stable Strategy (ESS) should be taken into



A monarch butterfly (left) and a viceroy butterfly. The viceroy evolved to look like the monarch as a defensive mechanism.

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

account. The ESS is a strategy that, when common among members of a particular role—such as aposematic coloration of prey—is not invaded or displaced over evolutionary time by any rare alternative. In addition, at evolutionary stability, each role has its own ESS.

An important aspect of aposematic signaling is the evolution of another defense, mimicry. A mimic is a predator or prey that bears a superficial resemblance to another species. The mimic resembles the model, which exhibits aposematic coloration. There are two forms of mimicry: **Batesian mimicry** and Mullerian mimicry.

In Batesian mimicry, a palatable species mimics an unpalatable model, thereby gaining protection through the traits of another species. For example, juveniles of the harmless lizard species *Helobolus lugubris*, inhabitants of the Kalahari Desert of southern Africa, mimic the color and posture of the ooglyster beetle, a species that sprays noxious fluids at predators. As the lizards mature and grow larger than the average beetle, they develop cryptic coloration as a line of defense.

Another example is the monarch butterfly. Monarch butterflies store **cardiac** poisons acquired from milkweed plants they eat as larvae and are therefore distasteful and potentially harmful to other species. Viceroy butterflies, by contrast, are harmless and palatable and so need a good defense to ward off predators. The viceroy is protected by having wings of the same coloration pattern as the monarch butterfly. Many innocuous snakes mimic the conspicuous red, white, and black markings of the poisonous coral snake in an attempt to protect themselves.

It is important to note that for Batesian mimicry to be effective, there must be a larger **population** of models than mimics so that predators are not clued in to the fact that they are being tricked.

Mullerian mimicry involves two or more unpalatable, aposematically colored species that resemble each other in appearance. This strategy evolved so that predators will learn more quickly to avoid animals with particular warning signs.

Some predators practice a reverse mimicry in order to trap their prey. Some species of snapping turtles, for example, have tongues that resemble wriggling worms. By sticking their tongues in the water, these turtles are able to lure small fish that are looking for a meal of worms.

Although mimicry seems a rather straightforward tactic, several conditions must be met in order for it to function as an ESS. The first condition for the strategy to be successful is that very conspicuous signals of aposematic coloration should be avoided so that it is somewhat difficult for predators to learn to avoid the aposematically patterned prey. Second, increasing prey unpalatability should increase the chances that any attacked prey will survive because the predator will quickly learn species avoidance after attacking the prey. It is important to note that the degrees of unpalatability and signal conspicuousness at ESS depend on the predators' patterns of **learning**.

Despite all the warning patterns and colors, predators do sample aposematic prey on occasion. And although Mullerian mimicry is found among quite a few species, Batesian mimicry is considered a rare defensive strategy. The balance between the employment of mimicry and its success rate supports the notion that these aposematic signals are a relevant ESS.

Danielle Schnur

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cardiac relating to the heart

population a group of individuals of one species that live in the same geographic area

learning modifications to behavior from experience



Modern Synthesis

The Modern Synthesis describes the **fusion** (merger) of Mendelian **genetics** with Darwinian evolution that resulted in a unified theory of evolution. It is sometimes referred to as the Neo-Darwinian theory. The

fusion coming together

genetics the branch of biology that studies heredity

Ernst Mayr, Theodosius Dobzhansky, Gaylord Simpson, and Ledyard Stebbins are considered the founders of Modern Synthesis.

allele one of two or more alternate forms of a gene

populations groups of individuals of one species that live in the same geographic area

mutation an abrupt change in the genes of an organism

natural selection process by which organisms best suited to their environment are most likely to survive and reproduce

phenotypic physical and physiological traits of an animal

allopatry populations separated by a barrier

Modern Synthesis was developed by a number of now-legendary evolutionary biologists in the 1930s and 1940s.

The Modern Synthesis introduced several changes in how evolution and evolutionary processes were conceived. It proposed a new definition of evolution as “changes in **allele** frequencies within **populations**,” thus emphasizing the genetic basis of evolution. (Alleles are alternate forms of the same gene, characterized by differences in DNA sequence that result in the construction of proteins that differ in amino acid composition.) Four forces of evolution were identified as contributing to changes in allele frequencies. These are random genetic drift, gene flow, **mutation** pressure, and **natural selection**. Of these, natural selection—by which the best-adapted organisms have the highest survival rate—is the only evolutionary force that makes organisms better adapted to their environments. Genetic drift describes random changes in allele frequencies in a population. It is particularly powerful in small populations. Gene flow describes allele frequency changes due to the immigration and emigration of individuals from a population. Mutation is a weak evolutionary force but is crucial because all genetic variation arises originally from mutation, alterations in the DNA sequences resulting from errors during replication or other factors. The Modern Synthesis recognized that the majority of mutations are deleterious (have a harmful effect), and that mutations that are advantageous usually have a small **phenotypic** effect. Advantageous mutations may be incorporated into the population through the process of natural selection. Changes in species therefore occur gradually through the accumulation of small changes. The large differences that are observed between species involve gradual change over extensive time periods. Speciation (the formation of new species) results from the evolution of reproductive isolation, often during a period of **allopatry**, in which two populations are isolated from one another.

There are several differences between the Modern Synthesis and the older Darwinian conception of evolution. First, mechanisms of evolution other than natural selection are recognized as playing important roles. Second, the Modern Synthesis succeeds in explaining the persistence of genetic variation, a problem that Charles Darwin struggled with. The dominant genetic theory of Darwin’s time was blending inheritance, in which offspring were thought to be the genetic intermediates (in-between versions) of their two parents. As Darwin correctly recognized, blending inheritance would result in the rapid end of genetic variation within a population, giving natural selection no material to work with. Incorporating Gregor Mendel’s particulate theory of inheritance, in which the alleles of a gene remain separate instead of merging, solves this problem.

There were several key players involved in the Modern Synthesis. The theory relied on the population genetics work of R. A. Fisher and Sewall Wright. Theodosius Dobzhansky made extensive studies of natural populations of the fruitfly *Drosophila* that supported many aspects of the theory. Ernst Mayr developed the biological species concept and created models concerning how speciation occurs. George Gaylord Simpson helped integrate paleontological observations into the theory behind the Modern Synthesis. G. Ledyard Stebbins contributed tenets (principles) based on his botanical work.

Since the 1990s it has been recognized that the Modern Synthesis omits some biological disciplines that are also relevant to evolution. In particular, much attention has focused on patterns of **ontogeny** and development. SEE ALSO BIOLOGICAL EVOLUTION; DARWIN, CHARLES; MAYR, ERNST; GENES; GENETICS; MENDEL, GREGOR; SIMPSON, GEORGE GAYLORD.

Jennifer Yeh

ontogeny the embryonic development of an organism

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Molecular Biologist

Molecular biology is a branch of biology that has been growing in importance since the 1940s. It developed out of the sciences of **genetics** and biochemistry. Genetics is the study of **heredity**, the process by which certain characteristics of an organism are handed down from parent to offspring. Biochemistry is the study of chemical compounds and processes in organisms. Molecular biologists seek to explain biological events by studying the molecules within cells. They are especially interested in the molecular basis of genetics and inheritance and the production of proteins. Proteins are large, complex molecules that are an essential part of all living cells.

genetics the branch of biology that studies heredity

heredity the passing on of characteristics from parents to offspring

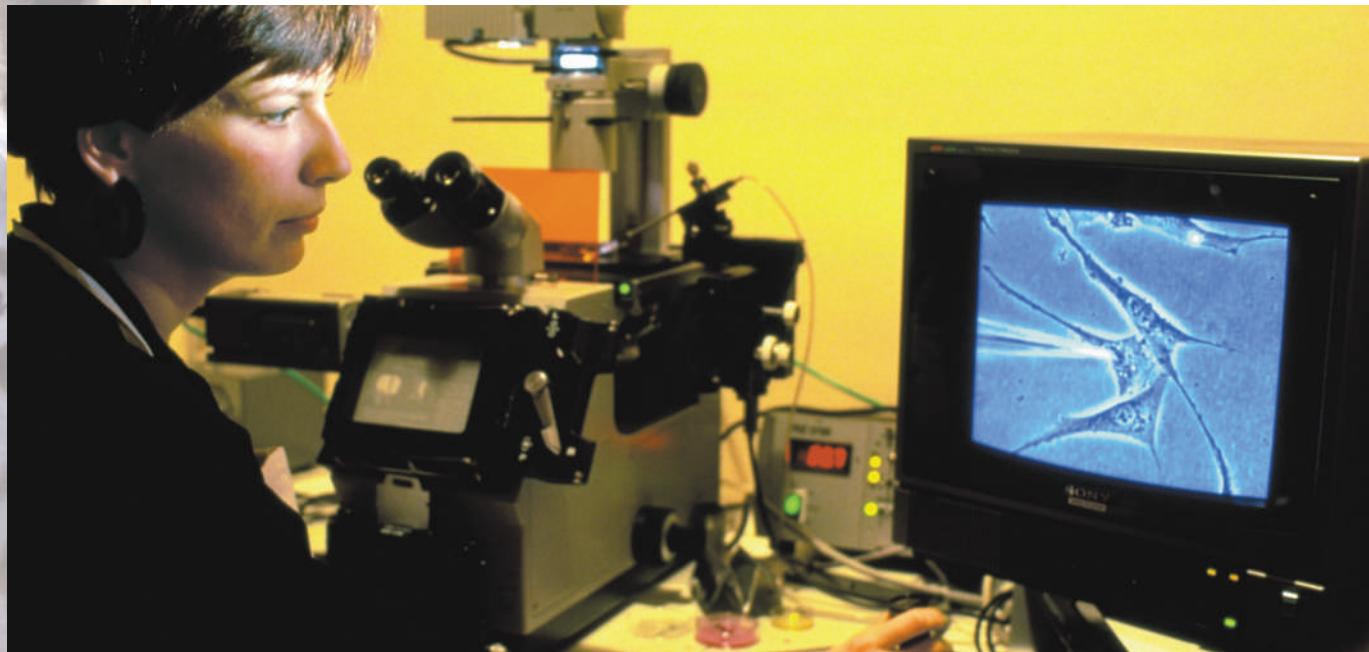
Most molecular biologists are involved in research and development. Some conduct basic research to expand knowledge without the direct aim of benefiting humans. Others may conduct applied research, which is used to benefit humans directly. Applied research generally focuses on issues important to the health, agricultural, and environmental sciences.

Human Genome Project
a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

At the turn of the twenty-first century, some molecular biologists are involved in a very important study, the **Human Genome Project**. This international research program aims to identify all of the approximately 30,000 **genes** of humans. Molecular biologists are also involved in related investigations of the genetic makeup of several nonhuman organisms. These include *Escherichia coli* (a microscopic organism found in the human gut), the fruit fly, and the laboratory mouse.

genes segments of DNA located on chromosomes that direct protein production

Many molecular biologists are employed by county, state, and federal agencies. Also, they may be employed by private industries such as a pharmaceutical corporation, an animal vaccine supply company, or a laboratory doing tests for doctors and health departments. At the beginning of the twenty-first century, emerging job opportunities for molecular biologists include environmental and pollution control companies and the biotechnology industry. The biotechnology industry uses molecular biology research to improve agricultural crops, develop new tests for disease screening, and develop new drugs. Also, some molecular biologists work at universities and colleges. They teach classes, train students in how to perform research, and



A molecular biologist executes a DNA microinjection technique.

ecology the study of how organisms interact with their environment

conduct their own research in their particular area of interest. An important part of the research is writing up the results for publication. Publication of research allows new information to be shared with the scientific community. Also, publication is important in obtaining grant funding for future research projects.

At the high school level, persons interested in becoming a molecular biologist should study math, chemistry, physics, biology, English, writing, and computer studies. Although there are career opportunities for molecular biologists with bachelor's degrees, most professionals have either a master's or doctoral (Ph.D.) degree. College-level course work generally includes biology (microbiology, genetics, **ecology**, and so on), chemistry, physics, and computer science. SEE ALSO GENES; GENETICS.

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Molecular Biology

Molecular biology is the study of life processes on a small scale. As a whole organism is composed of cells, so are these cells composed of tightly regu-

lated molecular machinery that keep them alive and functioning. Molecular biologists use chemical and biological tools to study DNA, RNA, proteins, and the interactions between them.

These tools have allowed scientists to have a far more detailed understanding of cellular processes than was imagined possible a century ago. One of the most groundbreaking developments in this field has been the **polymerase** chain reaction (PCR), first conceived by Kary B. Mullis in the 1970s. This technique, which uses DNA-copying polymerases derived from bacteria found in hot springs, can be used to isolate a tiny needle of DNA from a nucleic haystack and copy it many times over. Today, PCR is used in nearly every molecular biology lab to reproduce **genes** and obtain enough copies of them to study the genes efficiently. This allows scientists to put the genes in other cells, to activate them, or to match them to their protein products.

Molecular biologists also study proteins. They frequently do this through electrophoresis, in which proteins are separated by size as they drift through a thickened gel, propelled by electric current. Once the proteins are separated out by size, a scientist may “probe” the proteins with **antibodies** specific for only one protein shape and determine if that particular protein is present. The antibody will be radioactive or have some visual marker for easy detection. This technique is called a Western blot. One can also run DNA and RNA through electrophoretic gels and probe with complementary nucleic acids. The double-stranded DNA or RNA is split, and an exact negative copy of the gene is introduced to the gel. The negative copy will stick fast to the positive copy, so if the gene is on the gel, its presence is quickly identified.

With these techniques, and others, such as growing cells in culture and the purification and harvesting of **bioactive proteins**, molecular biologists are among the best researchers to examine health, disease, and development in animals and humans. While **ecology** and behavior are useful for large-scale understanding of long-ranging processes in biology, molecular biologists are able to study and manipulate organisms on an individual level and study the mechanisms by which they operate. As molecular biology improves, more and more life processes are seen as the product of biochemical interactions, and scientists are more and more able to paint a complete picture of the physical interactions that make life work. SEE ALSO CELLS; PCR.

Ian Quigley

polymerase an enzyme that links together nucleotides to form nucleic acid

genes segments of DNA located on chromosomes that direct protein production

antibodies proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

bioactive proteins proteins that take part in biological processes

ecology study of how organisms interact with their environment

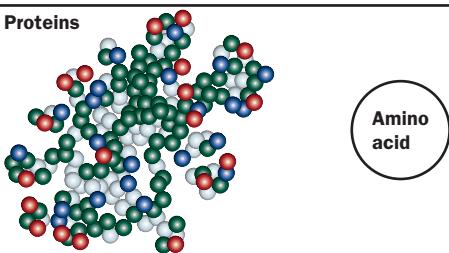
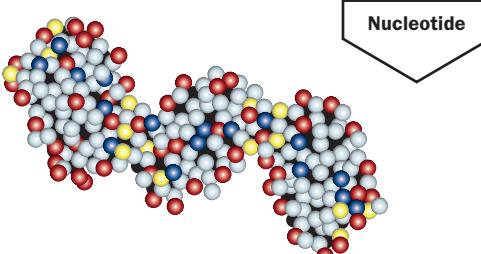
Molecular Systematics

Molecular systematics is the use of molecular **genetics** to study the evolution of relationships among individuals and species. The goal of systematic studies is to provide insight into the history of groups of organisms and the evolutionary processes that create diversity among species.

For thousands of years, **naturalists** have looked at the world and attempted to describe and explain biological diversity. This attempt to examine

genetics the branch of biology that studies heredity

naturalists scientists who study nature and the relationships among the organisms

Class	Typical subunit	Roles	Examples
Proteins		Serve as enzymes	Lactase
		Structural components	Hair, cartilage
		Peptide hormones	insulin
Nucleic Acids		Store genetic information	DNA
		Direct production of proteins	RNA

Classes of macromolecules. Redrawn from Johnson, 1998.

and classify is called systematics—a system for imposing order on the seeming chaos of nature. In 1758 Swedish naturalist Carolus Linnaeus devised a hierarchical classification system using two-part Latin names to categorize plants and animals. This system is still used today. Linnaeus was opposed to the theory of evolution, and his system was originally based on morphological features of structure and form. However, evolutionists rapidly adopted the Linnaean system and developed it into a classification based on phylogenetics, the evolutionary development of species. By 1866, German zoologist Ernst Haeckel had published a collection of detailed phylogenetic “trees” depicting what was then known about the evolutionary history of life.

physiology study of the normal function of living things or their parts

phylogenetic relating to the evolutionary history of species or group of related species

molecular clocks using the rate of mutation in DNA to determine when two genetic groups split off

genes segments of DNA located on chromosomes that direct protein production

Interest in phylogeny waned over much of the nineteenth century, replaced by an emphasis on genetics, **physiology**, and geographic variances. That began to change with the work of botanist Walter Zimmerman in the 1940s, and German zoologist Willi Hennig, in the 1950s and 1960s. These scientists pioneered the definition of objective criteria for determining the shared genetic attributes of living and fossil organisms. A revolution in molecular biology took place in the 1960s. Methods for determining the molecular structure of proteins and amino acids allowed biologists to begin to estimate **phylogenetic** relationships. The exponential growth of molecular systematics in the late twentieth century is due to a combination of increased sophistication in molecular biology techniques, and computer advances in hardware and software that allow scientists to model large and complex data sets.

Molecular systematists use a variety of techniques to derive phylogenetic trees. Polymerase chain reaction (PCR) is used to investigate variations of DNA on a large scale. Gene amplification is also fundamental to new approaches to DNA fingerprinting. Scientists can use “**molecular clocks**” to predict both past and future molecular divergences in **genes**.

This theory claims that molecular change is sufficiently constant to determine how current genetic lineages branch off from a common ancestor and to determine when the branching occurred. Genetic markers are used to make inferences about relationships between environment and morphology, as well as physiology and behavior.

The importance of phylogenetic trees, or estimates of evolutionary history, are that they allow biology to be predictive. Much as a chemist can use the periodic table of elements to predict chemical reactions, biologists can use phylogenetic trees to analyze biological variation and make predictions about behavior, morphology, and physiology, as well as biomolecular structure and other biological attributes.

The applications of molecular systematics in medicine are particularly important. The ability to predict the course of evolution allows scientists to track epidemic **pathogens**, research zootonic viruses (animal viruses that are transmissible to humans), understand the evolution of pharmaceuticals and drug resistance, and make predictions about emerging diseases. For example, phylogenetic studies of a form of influenza called influenza A have revealed reliable evolutionary behavior that can be used to predict how the viruses that cause influenza will evolve. This allows scientists to prepare vaccines for future strains in advance. Research into when simian immunodeficiency virus began to be transmitted to humans is vital to understanding how the transmission occurred and perhaps to prevent future zootonic transmissions.

Phylogeny is also an integral part of interpreting any coevolutionary relationships such as host and parasite. In the example of the **coevolution** of insects and their host plants, the plants evolve chemical defenses against the insects, who then evolve resistances to the chemicals. Because there are a limited number of chemical defenses available to the plants, researchers looked at whether insects are more likely to stay with the same plant as it evolves, or to switch to plants that contain chemicals to which they are already adapted. Studies of beetle phylogeny shows a closer match to plant chemistry than to plant phylogeny, indicating that the beetles have learned to switch plants as the host evolves new defenses.

Behavioral ecologists use phylogeny to reconstruct the evolution of behaviors. Molecular data can clarify the connections between animals previously thought to be unrelated. For example, flying foxes (*Pteropus*, also known as fruit bats), in contrast to other bats, have been shown to share significant features of brain organization with primates. These shared features lead scientists to believe that wings and flying evolved independently in these two lineages.

Evolution is not something that just happened in the past. It can be observed in the present and used to predict the future, by employing molecular systematics to compare data across genes, individuals, populations, and species.

Nancy Weaver

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pathogens disease-causing agents such as bacteria, fungi, and viruses

coevolution a situation in which two or more species evolve in response to each other



Molluska

fossil record a collection of all known fossils

phyla the broad, principal divisions of a kingdom

herbivores animals who eat plants only

invertebrates animals without a backbone

exoskeleton a hard outer protective covering common in invertebrates such as insects

mantle the tissue in mollusks that drapes over the internal organs and may secrete the shell

epidermis the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

calcium a soft, silvery white metal with a chemical symbol of Ca

gastropods mollusks that are commonly known as snails

The phylum Molluska is one of the largest of all animal groups. Not only does it contain about 110,000 living species, the **fossil record** indicates a long and extensive history.

The major mollusk groups, called classes by most taxonomists (scientists who study the relationships of plants and animals), are the Gastropoda (snails and slugs), the Bivalvia (clams, mussels, and shipworms), the Cephalopoda (squid, octopuses, cuttlefish, and nautilus), the Polyplacophora (chitons), the Scaphopoda (tooth shells), the Monoplacophora (a single-shelled animal), and the little-known Aplacophora (a questionable mollusk).

Of all animal **phyla**, the mollusks are perhaps the most difficult to describe in terms of a “typical” mollusk. In fact, no one characteristic is unique to the mollusks and shared by all species. Their body shapes are immensely different. In terms of feeding and behavior, mollusks range from docile, grazing **herbivores** to stealthy and aggressive predators. Most mollusks are marine, except for a few snails and clams that are found in damp terrestrial or freshwater environments.

Some characteristics of mollusks are unique to the group, but many are characteristic of **invertebrates** in general. However, researchers have identified a suite of characteristics that are combined in some generalized way within the mollusks. Mollusks do not have a central rod or backbone-type support. They do not have an **exoskeleton**.

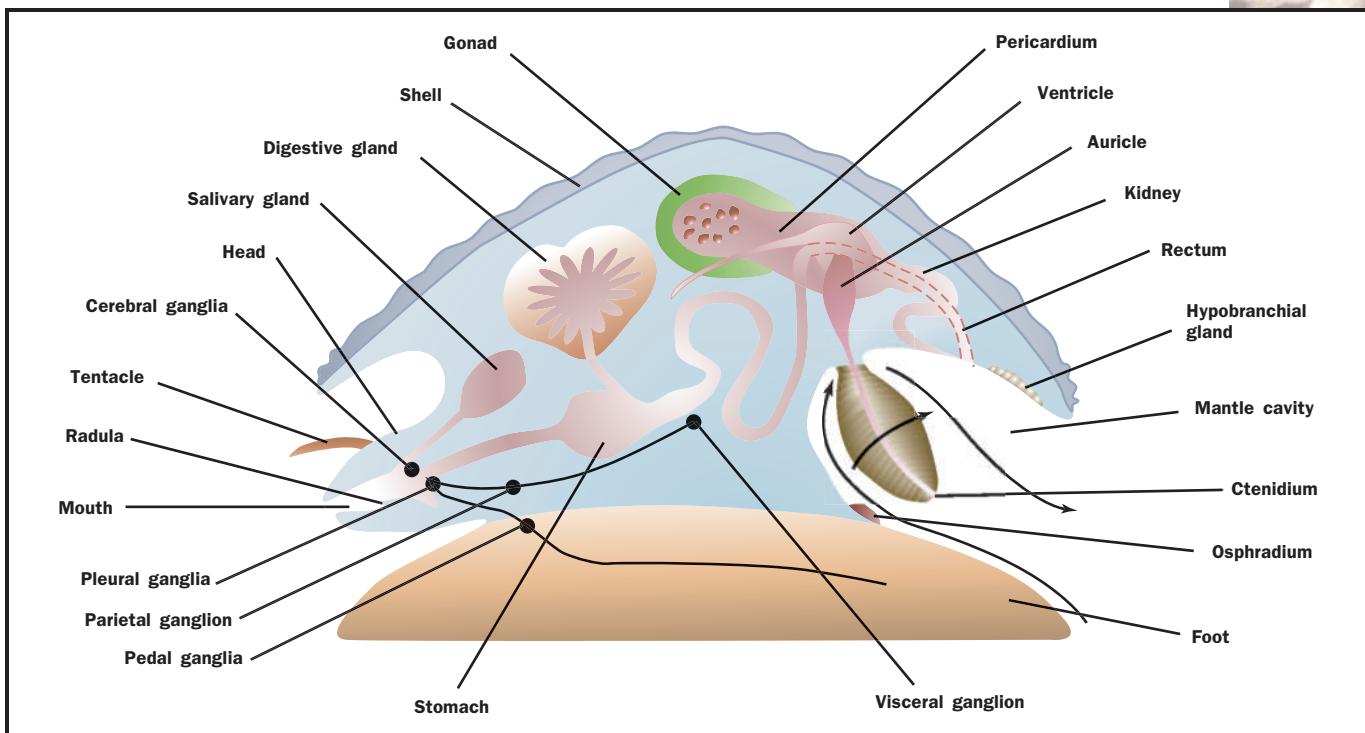
Perhaps the most important characteristic of mollusks is the presence of a specialized tissue called the **mantle**. The mantle is part of the **epidermis**, or skin, of the mollusk. It is filled with mucous glands and is very slippery to the touch. The mantle contacts the shell only at the outer edges. The inner epidermis where the shell is no longer in contact with the mantle is filled with fluid and acts as a sort of protective cushioning for the mollusk’s soft body.

The major function of the mantle is to secrete a substance that hardens into a three-layered shell. The outermost layer of the shell is a tough, solid deposit of **calcium** carbonate and is called the periostracum. The middle layer is a strengthening sheet of more calcium carbonate crystals. The innermost layer is made of organic chemicals that, when seen alone, capture light and appear to be multicolored. This layer is called the nacreous or prismatic layer. The beautiful appearance of this layer as seen in the inner shell of an abalone. The nacreous layer is also responsible for pearls. When a foreign particle penetrates the mantle, the shell-secreting cells in the mantle attach to the particle and build up layers of pearl around it.

The influence of the mantle and the resulting shell development is one of the most distinctive characteristics of the mollusks. Most living mollusk species have shells, although many have adapted to life without it. Remnants of the primitive shell can be found in the bodies of mollusks like the slugs and squids.

Gastropods

The **gastropods**, the snails and slugs, are one of the most familiar groups of mollusks. The name comes from a misunderstanding. Early biologists be-



lieved that the stomach of the gastropod was located in the muscular single “foot” on which the animals move, and that the animals ate with this foot. As a result, they named them “stomach-foot” (gastro-pod). Today we know gastropods do not eat with their “foot,” but the name remains.

The body of a gastropod body rests on this single muscular “foot.” The foot looks somewhat like a pedestal, and is the organ responsible for locomotion, or movement from place to place. Many species can withdraw their foot into their shell for protection, as gastropods are considered a tasty food item for many predators, including humans. Often, a gastropod will simply pull its shell over the foot for protection from predators.

The head end of the foot contains the sensory organs and often a set of retractable antennae. In most snails the mouth is lined with a sharp, zipperlike structure called a radula. The radula is used for scraping algae off rocks. However, there are many predatory species in which the mouth is located on the end of a proboscis, or long snout. This proboscis is used to bore into the shells of other animals. Some species also inject poison into the soft bodies of their prey before using the mouth to consume it.

The shells of gastropods are the most spectacular part of the gastropod body. Over millions of years, gastropods evolved elaborately coiled and brightly colored shells as protection for their soft internal organs. The diversity of coiling shapes, from plain spirals to intricate towers, makes these animals valuable for shell collectors. Unfortunately, this has led to severe **population** reductions in many species. The beautiful shell of the sea conch, which is often depicted in pictures and movies as a type of musical instrument, is a prized collector’s item, and the conch is rapidly becoming hard to find.

Cross-section of a mollusk. Redrawn from Grove and Newell, 1969.

population a group of individuals of one species that live in the same geographic area



lungs sac-like, spongy organs where gas exchange takes place

hermaphroditic having both male and female sex organs

operculum a flap covering an opening

body plan the overall organization of an animal's body

The gastropods are one of the successful groups of mollusks, so much so that they are considered to be pests in many areas. Pulmonates, a group that includes slugs and snails who have evolved **lungs**, can survive in almost any temperate climatic region. They have been so successful, in part, because of their reproductive strategies. Most mollusks are either male or female. One onate, the familiar garden snail, is **hermaphroditic**, with both male and female reproductive organs. Being hermaphroditic allows the snail to reproduce anywhere at any convenient time.

Many snails live in freshwater ponds and lakes. The rest of the mollusks, with the exception of some clams, are all marine. The fact that snails live on land is important for many researchers who study climatic fluctuations, as many species are intolerant of even slight climatic changes. Snail fossils are often studied to interpret temperature and humidity in the past.

Slugs—gastropods that do not have shells—are also pulmonates. The pulmonates are considered to be the most derived of the mollusks. The most primitive mollusks are the Prosobranchia. These gastropods are the largest and oldest group of gastropods. They have an **operculum**, which is a small shell flap used to cover the foot when withdrawn into the shell cavity. They usually have a pair of gills and the sexes are mostly separate. The Opisthobranchia are a small group of gastropods who are very diverse in body form and function. In the opisthobranchs the body shell is greatly reduced. Some are small and round giving rise to the name bubble shell. All are marine. Many of the members of this group are burrowers who cause a lot of damage to rocks and the wood of many sailboats.

Many opisthobranchs have lost their shell entirely. Some of these animals are called the nudibranchs, who are probably the most beautifully colored animals on Earth. They have colorful projections on their backs that can be used for respiration, digestion, or protection if they contain stinging cells.

Bivalvia

The bivalves, or clams, are another highly successful mollusk group. Bivalves have two shells, or valves, that are compressed on either side of the body. The shells are made from the excretions of the mantle as in gastropods, but are very different in shape and some functions.

The two shells enclose most of the body, and strong muscles inside the shell keep the two valves tightly closed. The shells open only to take in and release water or to allow the foot to extend into the sand.

Like gastropods, bivalves have a strong muscular foot that protrudes from the valves. However, bivalves do not use their foot as much for moving from place to place. Many bivalves do use the foot for moving through the sand, but it is more often used to anchor the animal in the fine sediments where it lives.

The **body plan** of bivalves is similar to that of gastropods but has many basic differences. The gills are paired and very large, and gas exchange occurs on the surface of these structures. The gills actually evolved primarily for the purpose of food gathering and their gas exchange function is secondary. The circulatory system is open, which means that blood is

pumped by the heart through arteries into openings or sinuses. It is recaptured by veins and pumped back to the heart. The blood simply diffuses over the organs at the sinuses. Bivalve blood is poor in **hemoglobin**, the oxygen-carrying chemical in blood, but this deficiency is compensated for by the large surface area of the gills. Fortunately, the sedentary lifestyle of the bivalve does not require great amounts of oxygen.

Bivalves are **filter feeders** who take in water through a front opening, called an in-current siphon, and release it through an ex-current siphon. The digestive system includes an esophagus, stomach, long intestine, and an anus. Once the water is taken in, it passes over the gills, and mucus that coats the gills captures organic debris in the water. This organic material is transported to the esophagus by **cilia**.

Bivalves do not have a very evolved sensory system, but are limited to a few ganglia that respond to environmental stimuli. They have no antennae. Pectens, or scallops, are the only bivalves that have eyes complete with lenses, corneas, and **retinas**.

Bivalves have separate sexes. Reproduction occurs by releasing sperm and eggs in the water. In some species, the **gametes** (sperm and egg) are taken into the body and **fertilization** occurs within. In others, fertilization takes place in the external environment of the water.

All bivalves are **aquatic**. Some forms live in freshwater, but it is more common to find them in marine environments. Their diversity is largely based on the way they feed, the structure of their gills, and where they live.

Cephalopoda

Cephalopods include the squid, octopus, cuttlefish, and the survivor of an ancient lineage—the nautilus. Their variety of forms and functions is so varied that entire books have been written about specialized groups of cephalopods.

Shells, which are so typical of mollusks, appear to be absent in the cephalopods. In both squid and cuttlefish, an internal vestige of the shell remains inside the soft body. Anyone who has ever seen the “cuttlebone” used in parakeet and parrot cages may not realize that this is the remnant of the ancient mollusk shell. The squid have an even more reduced shell that exists as a simple clear plasticlike film that runs the length of the body. The octopus has the vestige of a shell that has been put to use as mouthparts that are quite effective for biting prey.

The sensory systems of the nautilus, octopus, and squid are highly developed. These animals are extremely intelligent and have shown that they have memory and can solve problems of a simple nature. They are acutely aware of their environments and can respond to threats with a wide array of defense tactics. The octopus and squid are well-known for squirting dark colored “ink” into the water to confuse a predator, then darting away in the flash of an instant.

Cephalopods are the swiftest mollusks. While most mollusks are sedentary or sluggish, cephalopods can swim quite fast at times and are masters of deep-ocean living. Locomotion is accomplished by means of jet propulsion in which a strong ex-current siphon spouts out water to propel the animal away from danger. Cephalopods sneak up on their prey, using their

hemoglobin an iron containing protein found in red blood cells that binds with oxygen

filter feeders animals that strain small food particles out of water

cilia hair-like projections used for moving

retinas layers of rods and cones that line the inner surface of the eye

gametes reproductive cells that only have one set of chromosomes

fertilization the fusion of male and female gametes

aquatic living in water



tentacles to stealthily reach out towards the victim or to delicately slide along the ocean bottom.

Squid, octopus, and cuttlefish are very unlike the nautilus. The relationship between an octopus and a nautilus is hard to see unless the animals are closely examined, but both animals have similar tentacles, which they use for grasping prey. The tentacles can wrap around a prey item such as a shrimp and pull it to the mouth.

ammonites an extinct group of cephalopods with a curled shell

Scientists know little about the soft body evolution of the cephalopods, but the fossil record of coiled shell species is well documented. The ancestors of the nautiloids are the **ammonites**, animals with spirally coiled shells that, unlike gastropod shells, have separate chambers. These chambers functioned in gas regulation and allowed the animal to move up and down in the water column. Some ammonites are believed to have dived so deeply down into the water searching for prey that, as a result of increasing water pressure, they developed very intricate infoldings of the shell. The infoldings increased the surface area of the fragile shell, which in turn increased its strength. These shells could have withstood enormous underwater pressures. The graceful and highly intricate shells of the ammonites are valued by people all over the world.

Other Mollusk Groups

It is easy to find general mollusk characteristics in other mollusk groups. The polyplacophorans, or chitons, are shelled grazing animals found on rocks in the intertidal zone. The scaphopods have shells that look like long pointed teeth. They live in the sand and filter food from the water. A rare, recently discovered monoplacophoran called neopilina is a single-shelled animal that is considered to be a “living fossil” as scientists had thought they were extinct. Scientists believe the monoplacophorans represent the primitive form of the mollusks.

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Molting

exoskeleton hard outer protective covering common in invertebrates such as insects

One of the general characteristics that defines the phylum Arthropoda (which includes insects, spiders, and crustaceans) is an external skeleton, also called an **exoskeleton**. The arthropod exoskeleton completely covers the outside of the body and the muscles inside adhere to it. Exoskeletons are hard and protect the body. Because the exoskeleton is hard and rigid, an arthropod cannot grow unless it sheds its old exoskeleton and secretes a new one. This process is called molting.

Arthropod growth is limited to molting, so growth happens in steps rather than continuously. The stages between moltings are called instars.



A cockroach shown after molting, next to the skin it shed.

The extent of an individual's growth between molts and the length of time between molts are related to the temperature as well as to the amount of food and water an individual gets.

Warmer temperatures and more food and water can shorten the instar length and make the individual bigger. Other cues, such as the length of the day, are used to determine the timing of molting. Most insects have a specific end point to their growth, and after their final molt they are sexually mature adults. Most insects with wings acquire wings only in their adult stage. For example, except for the absence of wings, baby crickets are born looking exactly like adult crickets but are tiny in size. Crickets undergo several molts and live through several instars as they grow bigger. In their final molt, they become sexually mature and gain wings for flight.

Beneath the exoskeleton is an underlying cell layer called the epidermis, which secretes the exoskeleton, also called the cuticle. The exoskeleton is noncellular and made of **chitin** and proteins, which give the exoskeleton its rigid and protective properties. The exoskeleton and the epidermis together form the **integument** of an arthropod.

The molting process is a series of steps. It is controlled by the hormone **ecdysone**. Ecdysone is secreted from glands behind the brain. Once it is released the molting process begins. The arthropod builds a new exoskeleton underneath the old one. The epidermis pulls away from the existing exoskeleton. This creates a space between the epidermis and the exoskeleton. This space is filled with a gel that promotes shedding of the old exoskeleton.

Under this gel, the epidermis secretes a new cuticle. This requires a lot of energy. The new cuticle is secreted in various layers, and many biochemical processes change the newly excreted cuticle from cellular secretions into the insoluble form of the new exoskeleton. At this point, the new exoskeleton is still soft and pliable.

The gel that is between the new and old cuticles contains digestive **enzymes**. These enzymes start to break down the old exoskeleton once the new cuticle has been made insoluble and can resist being damaged by these

chitin a complex carbohydrate found in the exoskeleton of some animals

integument a natural outer covering

ecdysone a hormone that triggers molting in arthropods

enzymes proteins that act as catalysts to start biochemical reactions





ecdysis shedding the outer layer of skin or exoskeleton

enzymes. These digestive enzymes dissolve the inside of the old exoskeleton and the products are reabsorbed by the individual and used in making the new cuticle. This recycling of material reduces the amount of energy needed for molting. Only the inside of the old exoskeleton can be reused. The outside of the exoskeleton is shed in a process called **ecdysis**.

Ecdysis consists of splitting the exoskeleton, usually along the back of the arthropod, and crawling out of the old exoskeleton. Old exoskeletons of insects can be found in nature. They look just like the insect did but are hollow inside.

When an individual first emerges from the old exoskeleton following ecdysis, it is very vulnerable because the new exoskeleton is quite soft. Newly emerged individuals are wrinkly and whitish. The swallowing of air by the individual expands the cuticle. This pulls out the wrinkles and makes the individual become larger during molting. After expansion of the cuticle, another biochemical process takes place that hardens and darkens the exoskeleton. This biochemical process is a reaction to oxygen in the air. It can take several hours for an individual to undergo expansion and hardening.

Even though molting happens only occasionally, most arthropods continue to add layers to the inside of the exoskeleton all the time. Some insects do this every twenty-four hours and form growth rings similar to those of trees. **SEE ALSO** SKELETONS.

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Morphological Evolution in Whales

Whales are the only group of mammals to have adopted an exclusively **aquatic** lifestyle. Their entire life cycle, from birth until death, is carried out in an aquatic **habitat**. The terms “whale” and “cetacean” are usually used interchangeably, cetaceans being the scientific term for whales, dolphins, and porpoises. However, “whale” is also sometimes used to distinguish some of the larger species of the order Cetacea from the other two major groups, the dolphins and porpoises.

Cetaceans are found in almost all oceans and their connecting seas, as well as in **estuaries** (wide tidal river mouths) and rivers. Whales range in size from the 1-meter-long (3 feet) dolphins and porpoises to the 30-meter-long (100 feet) blue whale. The seventy-seven **extant** species of whales each belong to one of two suborders, the Odontoceti (toothed whales) and the Mysticeti (**baleen** whales). The toothed whales—porpoises, dolphins, and most of the smaller whales—have **homodont** (uniform in size and shape) teeth or are toothless. The odontocetes use their teeth to feed on fish and **crustaceans**. The mysticetes are toothless, but strain **plankton**.



This humpback whale emerges from underneath the water's surface in Glacier Bay National Park, Alaska. The anatomical structures of the whale's front flippers are very similar to that of the human hand.

and small crustaceans using a dense fringe of bristled plates called baleen (whalebone) that hangs from the roof of their cavernous mouth.

The extinct Archaeoceti appeared in the early part of the Eocene epoch (about 50 million years ago). Although they do not show all the specialized body characteristics of the odontocetes and mysticetes, their spindle-shaped body and horizontal tail show that they were well adapted to an aquatic lifestyle. Unlike the extant whales, archaeocetes have **heterodont** (different in size and shape) teeth and their nostrils are located midway along the snout. Based on the fossil evidence, archaeocetes went extinct slowly, disappearing sometime during the Pliocene epoch (2.5 to 7 million years ago).

Morphological Specializations of Extant Whales

Whale form and structure departed dramatically from that of terrestrial mammals, adopting a fishlike appearance. The whale body is streamlined, with a large head and nondifferentiated neck, and has a **dorsal** fin made up of **connective tissue** and skin on the back. The tail is a T-shaped, horizontally flattened, boneless fluke, which serves as the major propulsive force during locomotion. Whales swim using an up-and-down wavelike motion rather than the side-to-side bending motion used by most fish.

Like other mammals, whales have **lungs** and breathe air. They inhale and exhale through a single nostril or a pair of nostrils on top of their head, toward the back. The waterspout that emerges from this “blowhole” is simply water vapor expelled from the lungs during exhalation along with a small amount of water collected near the edges of the blowhole.

The whale skull has undergone other changes in addition to the relocation of the nostril(s) and the development of homodont teeth and baleen.

heterodont teeth differentiated for various uses

dorsal the back surface of an animal with bilateral symmetry

connective tissue cells that make up bones, blood, ligaments, and tendon

lungs sac-like, spongy organs where gas exchange takes place





phalanges bones of the fingers and toes

ungulate animal with hooves

ruminants plant eating animals with a multi-compartment stomach such as cows and sheep

phlogenetic relating to the evolutionary history

genome an organism's genetic material

The upper jaw is thicker at the back end, while the lower jaw is a horizontal bar rather than an L-shape, such as in humans. The cranium and brain have become wider so that their widths are greater than their lengths, a very unusual situation in mammals. This elongation of the cranium and the brain is referred to as a “telescoping of the skull.” The relative sizes and shape of the various skull bones have changed as a result of this telescoping.

Whale skin is hairless except for a few tactile hairs. In addition, the skin lacks sweat or oil glands and feels like smooth rubber. A thick layer of blubber lies underneath the skin, aiding in buoyancy, insulating the body, and storing energy in the form of fat.

When compared to the limbs of terrestrial mammals, whale forelimbs have been transformed into flippers, while the hind limbs have been lost. The bones of their upper forelimbs have been reduced in size and the number of **phalanges** in each digit has increased, resulting in elongated “hands.” Although whales do not have hind limbs, all species have a pelvic bone, and a few species have thighbones.

Fossil Evidence for the Origin of Whales

Certain details concerning the evolution of whales remain unknown. Scientists agree that whales evolved from some kind of primitive **ungulate** (hoofed mammal), but because we do not have a fossil of the animal that was intermediate between the terrestrial and aquatic whale ancestors, it is difficult to classify whales relative to their closest mammalian relatives, the artiodactyls (camels, pigs, **ruminants**, and hippopotamuses). Fossil data suggests that whales and artiodactyls share a recent ancestor, but whales differ from other ungulates in a number of significant skeletal characteristics.

The important morphological differences between the two orders of extant whales, the odontocetes and the mysticetes, also lead scientists to believe that the branch that eventually gave rise to modern whales split off from the rest of the mammalian tree long ago. The first fossil representatives of both orders appeared during the Oligocene epoch (about 38 to 25 million years ago). Some paleontologists look for clues about whale origins in the Cenozoic era, particularly in the Paleocene and early Eocene epochs (50 to 65 million years ago). Other paleontologists who believe that a Paleocene or Eocene origin would not have allowed sufficient time for the extreme morphological changes look for answers within the Cretaceous period of the Mesozoic era (65 to 130 million years ago).

Molecular Evidence for the Origin of Whales

Molecular DNA studies performed during the 1990s provide a more precise placement of whales on the mammalian **phylogenetic** tree (diagram representing the evolutionary relationships between mammal groups). Several different scientific teams working on different parts of the cetacean **genome** have all concluded that whales should be classified as artiodactyls, not as a sister group as suggested by the fossil evidence. The molecular evidence indicates that whales are most closely related to hippopotamuses. The affinity to water exhibited by hippopotamuses has led some scientists to wonder about the aquatic tendencies of the most common ancestor of whales and hippos.

Despite the agreement of the results drawn of molecular studies performed on cetacean DNA, certain aspects of the origin of whales remain under dispute. Paleontologists maintain that whales should not be classified as artiodactyls and warn against drawing conclusions about the nature of whale ancestors based on a hypothesized relationship between whales and hippos. SEE ALSO FOSSIL RECORD; GEOLOGICAL TIME SCALE; MORPHOLOGY.

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Morphology

Morphology, broadly defined as the study of animal form, is a field that helps us understand animal diversity and animal history. For centuries, scientists have been interested in how animals are put together and how the parts work together to make functioning organisms that can run, fly, swim, eat, and survive. Early scientific efforts focused on descriptive methods in which scientists dissected specimens and described the musculoskeletal and other body systems with words and detailed drawings.

As new techniques were developed, scientists began to specialize along the lines of various subdisciplines, including **functional morphology** and ecological morphology. Morphologists moved beyond what had started as a purely descriptive science and began to ask and answer more complex questions.

Functional morphology emphasizes the mechanics of a particular structure—how it works. For example, a functional morphologist might examine the pattern of musculoskeletal activity involved in an activity such as running. Using techniques such as high-speed video, X-ray video, force-platform measurements, and EMGs (electromyographs, or recordings of electrical activity in muscles), the scientist can determine a joint's range of motion, the duration and intensity of muscle activity, and the order in which the muscles activate to produce a pattern of movement.

Functional morphologists are often interested in the performance limits of a particular system. They ask questions such as: How much force can the human jaw produce? How fast can a lizard sprint on an inclined surface? How much weight can a thigh bone stand before it breaks?

Ecological morphology (also called "ecomorphology") considers the structure of an organism in the context of its **habitat** and ecological role. Ecological morphologists are more interested in how structures are actually used in nature than in the limits to which structures can be pushed in an artificial laboratory setting. Ecological morphologists distinguish between a structure's biological role and its function. Therefore, they usually

functional morphology
study of form and function

habitat physical location where an organism lives in an ecosystem



spend some time familiarizing themselves with the habits and natural surroundings.

Ecological morphologists ask questions such as: How does the shape of a hawk's beak help it tear through the flesh of its prey? How does the shape of fish larvae help them disperse along wave-swept shores? How does the shape of a bat's wing help it maneuver while catching insects at night?

Although these specific research areas are worthy of pursuit in and of themselves, many scientists promote an integrative approach to the study of morphology that brings together these and other aspects of morphological research. Evolutionary morphology draws lessons from functional and ecological morphology to determine how structures evolved. Using a comparative method, morphologists put structures into a historical context and draw conclusions about how a structure came to exist based on structural and/or functional similarities and differences between related animals.

When variations in environmental pressures and biological roles are taken into account, morphological differences can lend insight into the origin of animal diversity. As animals evolve over time, their morphology adapts to specific selective pressures such as prey type and abundance, predator type and abundance, **climate**, and habitat characteristics. The diversity of animal form reflects the complex interactions between animals and their environment. **SEE ALSO ADAPTATION; MORPHOLOGICAL EVOLUTION IN WHALES.**

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climate long-term weather patterns for a particular region

enzymes proteins that act as catalysts to start biochemical reactions

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Mouth, Pharynx, and Teeth

The digestive system functions to receive, store, and break down food to absorb nutrients. Both physical and chemical digestion processes begin in the mouth. The presence of food in the mouth causes the salivary glands to deliver saliva into the mouth. Often even the smell or anticipation of food will cause activation of the salivary glands. Digestive **enzymes** in saliva begin to moisten, soften, and dissolve the food before passing it to the next stage of the digestive system. Saliva also contains mucin, which protects the mouth from abrasion, and buffers, which prevent dental cavities by neutralizing acid in the mouth. The tongue is used to taste and manipulate food during chewing.

Fish, amphibians, and reptiles principally use teeth to grip prey and prevent it from escaping until it can be swallowed whole. Birds have no teeth, but many have bills with serrated edges for shredding. Often the upper bill is hooked for seizing and tearing apart prey. Other bill shapes are designed for seed eating and fishing. Because snakes have no limbs, their

mechanism of feeding has been modified. Rapid strikes, venom, and constriction are used to immobilize prey. Backward-curving fangs also help snakes to seize and hold prey. Snakes tend to eat large prey items, and they are able to unhinge their jaws to swallow them. For some animals, the physical reduction of food is necessary to release nutrients from indigestible components and to increase the surface contact between food and digestive juices. Physical reduction of food in the mouth is accomplished by the chewing, rasping, and grinding of teeth. The function and type of teeth depend upon the specialized food habits of the animal.

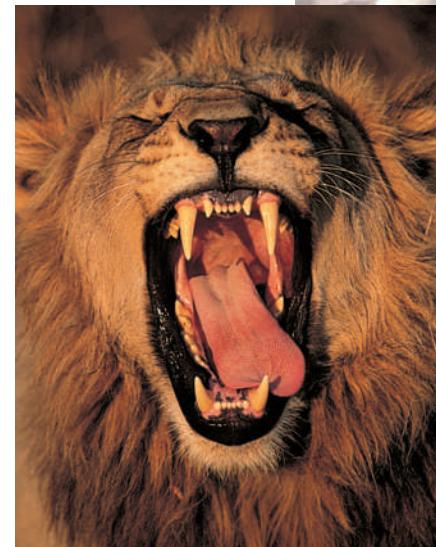
Mammals exhibit true mastication, meaning that their teeth are involved in chewing as opposed to just tearing or crushing. Mammals typically have four types of teeth. The incisors at the front of the mouth are used for biting, cutting, and stripping; the canines are used for seizing, piercing, and tearing. Further back in the mouth, premolars and molars are used for grinding and crushing. Carnivores have well-developed canines for seizing prey and tearing meat. **Herbivores** have reduced canines, but well-developed molars for grinding. Their teeth help them break apart the tough cellulose walls of plants to access nutrients. Rodents have self-sharpening incisors that grow throughout life and must be worn away by gnawing to keep them from growing too long.

The teeth of some **vertebrates** have evolved to serve functions other than feeding. For example, elephant tusks are modified upper incisors used for defense, attack, and rooting for food. Male wild boars have modified canines that are used as weapons in male-to-male combat. Elk use specialized teeth to make mating and territorial calls.

After food is physically and chemically reduced in the mouth, it passes to the next stage of digestion. Food is swallowed when the tongue pushes the food to the back of the mouth and into the pharynx. The pharynx acts as an intersection between the esophagus and the **trachea**. The esophagus leads to the stomach, whereas the trachea leads to the **lungs**. The epiglottis, a **cartilaginous** flap, covers the trachea during swallowing to prevent food and fluid from entering the lungs. Food then enters the esophagus and **involuntary muscles** contract to push food into the stomach.

Invertebrates have comparable feeding and digestive mechanisms to those of vertebrates. Invertebrates do not possess true teeth. However, they often have beaks or toothlike structures for biting and holding. Insects have three pairs of appendages on the head that serve multiple functions. The first pair, the mandibles, are primarily for crushing. The second pair, the maxillae, serve as grasping jaws, and the third, the labia, as probing and tasting tongues. Food that has been broken down into smaller pieces enters the mouth, often with the help of extended maxillae. As with vertebrates, salivary glands produce enzymes to help break down food. The reduced food then enters the crop, an organ similar to the vertebrate stomach, for further digestion.

In insects, the form and structure of mouthparts varies dramatically depending upon the type of feeding. Locusts eat leaves and have grinding and cutting mandibles. Mosquitoes and butterflies have sucking or siphoning mouthparts. The common housefly has spongelike mouthparts with which they lap up food they have liquefied with salivary secretions.



This yawning lion in Botswana displays sharp and dangerous teeth. Since the lion is carnivorous, its long canines are predominant features of its mouth.

herbivores animals who eat plants only

vertebrates animals with a backbone

trachea the tube in air-breathing vertebrates that extends from the larynx to the bronchi

lungs sac-like, spongy organs where gas exchange takes place

cartilaginous made of cartilage

involuntary muscles muscles that are not controlled by will

invertebrates animals without a backbone



carnivorous term describing animals that eat other animals

chitinous made of a complex carbohydrate called chitin

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

mollusks a large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

vertebrate an animal with a backbone

fascicles close clusters

sarcomeres segments of striated muscle fibrils which are divided by thin dark bands

myofilaments any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

actin a protein in muscle cells that works with myosin in muscle contractions

myosin the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

voluntary muscles muscles with fibers of cross bands usually contracted by voluntary action

Other invertebrates have interesting structures used for procuring and reducing food. For example, *Nereis*, a **carnivorous** polychaete (marine worm), have a muscular pharynx with **chitinous** jaws that they turn inside out quickly to seize prey. The pharynx then retracts and the prey is swallowed. **Crustaceans** often reduce the size of food using shredding devices like the tearing, beaklike jaws in cephalopod **mollusks** (i.e., squid). Snails have a radula, a rasping structure in the mouth, for scraping algae off rocks.

SEE ALSO **DIGESTIVE SYSTEM**.

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Muscular System

Independent movement is a unique characteristic of animals. Most animal movement depends on the use of muscles. Together, muscles and bones make up what is known as the musculoskeletal system. This combination provides protection for the body's internal organs and allows for many kinds of movement. Whether the movement is as simple as opening the eyes or as complex as flying, each is the result of a series of electrical, chemical, and physical interactions involving the brain, the central nervous system, and the muscles themselves.

Muscle is the flesh, minus the fat, that covers the skeleton of **vertebrate** animals. Muscles vary in size and shape and serve many different purposes. Large leg muscles such as hamstrings and quadriceps control limb motion. Other muscles, like the heart and the muscles of the inner ear, perform specialized involuntary functions. Despite the variety in size and function, however, all muscles share similar characteristics.

At the highest level, the entire muscle is composed of many strands of tissue called **fascicles**. These are the strands of muscle that can be seen in red meat or chicken. These strands are made up of very small fibers. These fibers are composed of tens of thousands of threadlike myofibrils, which can contract, relax, and lengthen.

The myofibrils are composed of up to ten million bands laid end-to-end called **sarcomeres**. Each sarcomere is made of overlapping thick and thin filaments called **myofilaments**. The thick and thin myofilaments are made up of contractile proteins, primarily **actin** and **myosin**.

Types of Muscle Tissue

Muscles are categorized as either voluntary or involuntary. The muscles that animals can deliberately control are known as **voluntary muscles**. Those that cannot be controlled by the animal, such as the heart, are called **in-**

voluntary muscles. Vertebrates also possess several different types of muscle tissue: cardiac, smooth, and striated or skeletal.

The muscle types are classified on the basis of their appearance when viewed through a light microscope. **Striated muscle** appears striped (striated) with alternating light and dark bands. Smooth muscle lacks the alternating light and dark bands.

Cardiac muscle. Cardiac muscle makes up the wall of the heart, which is called the myocardium. In humans the heart contracts approximately seventy times per minute and can pump nearly 5 liters (4.5 quarts) of blood each minute. The fibers of the heart muscle are branched and arranged in a netlike pattern. The involuntary heart contraction is stimulated by an electrical impulse within the heart itself at the sinoatrial node.

Smooth muscle. Smooth muscle cells are organized into sheets of muscle lining the walls of the stomach, intestines, blood vessels, and diaphragm, and parts of the urinary and reproductive systems. The smooth muscle contractions push food through the digestive system, regulate blood pressure by adjusting the diameter of blood vessels, regulate the flow of air in the **lungs** and expel urine from the urinary bladder. These body functions are involuntary and controlled by the **autonomic nervous system**.

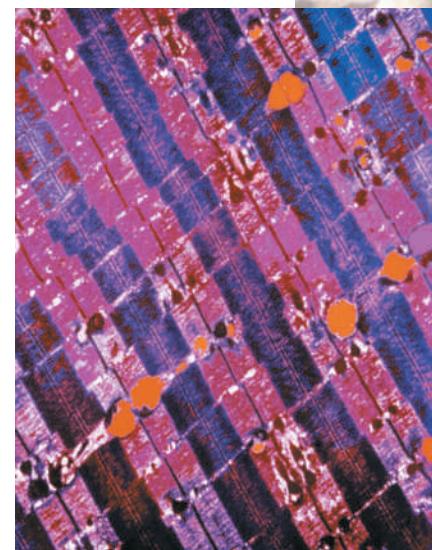
Skeletal or striated muscle. Skeletal muscle, which is muscle tissue attached to bones, makes up a large portion of an animal's body weight—sometimes between 40 and 60 percent. Skeletal muscles move parts of the skeleton in relation to each other. They contain abundant blood vessels that transport oxygen and nutrients, nerve endings that carry electrical impulses from the central nervous system, and nerve sensors that relay messages back to the brain. Skeletal muscles are responsible for the conscious or voluntary movements of the trunk, arms and legs, respiratory organs, eyes, and mouth—parts of the animal. They are used for such actions as running, swimming, jumping, and lifting.

These distinctive muscle types can be observed throughout the evolution of vertebrates, however the arrangement of muscles varies according to differing environmental and survival needs. In fish, for example, most of the skeletal muscles fan out from either side of the backbone. Muscle makes up nearly 60 percent of the fish's body and nearly all of it is involved in moving the tail and spine.

As vertebrates evolved and adapted to life on land, the down-the-spine muscle arrangement began to change. More muscle power was needed for moving the limbs. Limb muscles became both bigger and longer. Some muscle fibers in a frog's hind legs can be nearly a quarter as long as the frog's body, which is proportionately much longer than the muscles in many fish. More muscles developed in the chest to be used for breathing, as vertebrates began spending more time on land. In mammals, this led to the development of the diaphragm, an involuntary muscle that helps to bring air into the lungs.

How Muscles Contract

Nerves connect the spinal column to the muscle. The place where the nerve and muscle meet is called the **neuromuscular junction**. Inside the muscle fibers, a signal from the nervous system stimulates the flow of calcium, which



The electrograph displays the interaction of actin-myosin filaments.

involuntary muscles
muscles that are not controlled by will

striated muscle a type of muscle with fibers of cross bands usually contracted by voluntary action

lungs sac-like, spongy organs where gas exchange takes place

autonomic nervous system division of the nervous system that carries nerve impulses to muscles and glands

neuromuscular junction
the point where a nerve and muscle connect





invertebrates animals without a backbone

hormones chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

cilia hair-like projections used for moving

flagella cellular tail that allow the cell to move

aquatic living in water

flagellum cellular tail that allows cells to move

cnidarians aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

arthropods members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

mollusks large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, muscles, and octopuses

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

exoskeleton hard outer protective covering common in invertebrates such as insects

bivalve mollusks mollusks with two shells such as clams

causes the thick and thin fibers (myofibrils) to slide across one another. When this occurs, the sarcomere shortens, which generates a force. The contraction of an entire muscle fiber results when billions of sarcomeres in the muscle shorten all at once.

The “sliding-filament theory” suggests that these thin and thick filaments become linked together by molecular cross bridges, which act as levers to pull the filaments past each other during the contraction of the muscle fiber. Myosin molecules have little pegs, called cross bridges, that protrude from the thick filament. During contraction, another molecule, called actin, appears to “climb” across these bridges.

Movement in invertebrates. Movement occurs in all animals, including those without highly developed musculoskeletal systems. Nearly all groups of animals, including relatively simple organisms such as jellyfish and flatworms, have rudimentary muscle fibers that are specialized to move parts of the body. The number of muscles is not necessarily related to the size of the organism or the presence of a skeletal system. For example, a caterpillar may have 2,000 separate muscles compared with some 600 muscles in the human body.

Movement in **invertebrates** is caused by the same contractile proteins, actin and myosin, that function in the muscles of vertebrates. This primitive muscle tissue is triggered into action by nerves, **hormones**, or the built-in rhythm of the organism.

Simple protozoans such as the *Ameoba*, can either contract or extend their one-celled body in any direction. Other protozoans move by means of contractile fibers contained in **cilia** and **flagella**. Cilia are minute, hairlike, projections that stick out from the cells of some animals. Cilia allow protozoa to move freely through their **aquatic** environment. Another adaptation is the **flagellum** (pl., flagella), a whiplike structure found in sponges. A flagellum moves by a beating pattern that mimics a snakelike undulation.

Both smooth and striated muscle are present in invertebrate animals ranging from **cnidarians** to **arthropods**. Flatworms have muscle fibers in three directions, the contraction of which will move the body in multiple planes much like a human tongue. The body wall of earthworms contains both an outer and an inner layer. Contraction of the outer layer causes the body to lengthen and the action of the inner layer shortens it, producing the wiggling motion of the worm.

The only invertebrates without this layered arrangement of muscle tissue are the **mollusks**, **crustaceans**, and insects. They do, however, have many separate muscles, varied in size, arrangement, and attachments, that move the body segments and the parts of the jointed legs and other appendages. These muscles are fastened to the internal surfaces of the **exoskeleton**. Clams and other **bivalve mollusks** use strong muscle contractions to keep their shells tightly shut at high tide. Once the shell-closing muscles have contracted, they can remain tightly shut for hours without tiring. SEE ALSO LOCOMOTION; SKELETONS.

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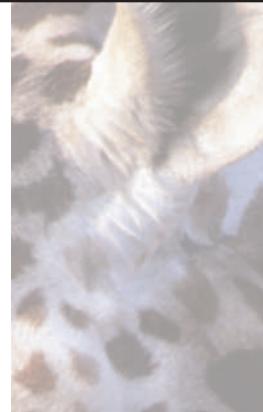
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Museum Curator

Museum curators care for, manage, organize, and develop the objects in a museum. Museum curators may do some or all of the following tasks:

- acquire new items for the museum's collection;
- examine items for the collection to determine their condition and whether they are authentic;
- identify and classify items;
- keep and maintain inventory records about all items in the collection;
- arrange and oversee conservation and restoration work for the items;
- make sure that climate and pest control issues are seen to at all times to protect the items in the collection;
- organize and prepare displays, which can include traveling and arranging for loan exhibitions;
- conduct research or oversee research on collection pieces;
- educate the public about the collections, which generally involves lecturing and writing;
- raise funds for the museum, which can include applying for grants and attending social events with private museum donors;
- supervise a staff, which can consist of volunteers, interns, students, collection managers, technicians, junior curators, and secretarial staff.

As this list shows, museum curators must not only be experts in their field but also have very good people skills and writing skills. A museum curator must be very dedicated, often spending long hours traveling and weekends and evenings at social events raising money for the museum.

To become a museum curator, one must follow a long period of training in a discipline. Generally, at a museum, a person starts as an assistant and works her or his way up to associate, then to full (or senior) curator. Museum curators may specialize in a specific discipline such as art, natural history, science, or technology.

Museum curators need a well-rounded education. In high school, one should take courses in English, literature, creative writing, history, art, the sciences, business, and foreign language. Math and computer skills are also essential. Museum curators must have a bachelor's degree, and most museums require their chief curators to have a doctoral (Ph.D.) degree. Museums generally hire curators who have degrees in fields related to the



This museum curator prepares the bones of an Allosaurus for public display.



museum's specialty. While some persons attend college and obtain degrees in museum studies (museology), most get degrees in their particular areas of interest, such as biology or paleontology. Earning two graduate degrees, in museum studies and a specialized subject, can make a person a more valuable curator. In order to get hands-on experience, college students can apply for internship programs at a museum. These internships generally last a year or less and involve work on a project identified by the museum. Also, volunteering at a museum is a good way to get experience.

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N

Natural Resources

Natural resources are those elements of the environment that are considered valuable to humans. These can be raw materials, such as trees for lumber and ore for manufacturing, or things that are directly consumed, such as groundwater to drink and animals to eat. The word “natural” means that there has been no modification by humans. A “resource” is something that is necessary for growth and reproduction. Natural resources can be divided into three categories: perpetual resources, like the Sun; potentially renewable resources, like forests; and nonrenewable resources, like fossil fuels.

While a resource can be something that is necessary for an animal as well as a human, the term “natural resource” is always used in the human context. The use of this term has increased with the growing awareness of the need to manage the use of these resources to ensure their existence in the future. Many of these resources grow or form at a much slower rate than the rate at which humans are using them, and so their future is in peril. Methods to protect natural resources are complex, involving education, reduction in demand, and large-scale recycling. Global cooperation will be vital to the success of all of these tactics.

Perpetual Resources

In the context of human usage, natural resources can be divided into three categories based on the possibility of resource renewal. The first category is perpetual resources. Phenomena such as solar rays, wind, tides, and flowing water will always exist within the scope of human existence. The Sun, which drives many of these phenomena, is not likely to burn out for billions of years. Harnessing solar energy or the motion of the wind or water will not decrease the quantity of these resources, which is the obvious advantage of perpetual resources.

Solar cells take the energy from the Sun's rays and turn them into electricity that can charge batteries and drive household equipment and even



some specially designed automobiles. Windmills produce energy generated by the turning of their blades. But neither solar nor wind energy is commonly used because other energy sources, such as coal and gas, are less expensive in proportion to the amount of energy produced. Until a worldwide financial demand for alternative energy sources develops, technologies for exploiting these sources will lag behind common energy sources in their relative efficiency.

There are difficulties in harnessing some perpetual energy sources. One example is hydroelectric power, which is generated from flowing water that spins turbines which in turn generate electricity. The problem here is that to create enough energy for a large-scale hydroelectric plant, it is necessary to build huge dams. These dams must increase the potential energy of the water. They must also ensure that energy delivery does not stop during seasonal decreases in water flow on the rivers upon which the dams are built.

These huge dams allow sediments in the water to settle out so that ultimately, in anywhere from 40 to 300 years, the system becomes clogged. Also, the lake that is formed inundates the upstream shallow **habitat** on

Solar panels on top of houses are becoming a more common instance and source of natural power in the United States.

habitat physical location where an organism lives in an ecosystem



which many fishes rely, changes the downstream flow patterns, and does not allow species to travel the full length of the river, which some species need to do for breeding purposes.

Renewable Resources

With the growing realization that some resources are being used up, there has been a focus on renewable resources, the second category of natural resources. This category includes plants, animals, fertile soils, and clean air and water. These may be more accurately described as potentially renewable, because in many places they are not being actively renewed. That is because in the short term it is more economical to exhaust one area and then go to a new one instead of renewing the resource.

Harvesting trees, for example, is most economical when the entire forest is harvested, which is known as clear-cutting. That way, machines have easier access to do the cutting and transport of the logs. Unfortunately, the cleared landscape does not support the same species that were there previously. In addition, this landscape is subject to extensive soil erosion. To maintain the forest in its prior state, some trees must remain standing to conserve the soil, and efforts must be made to replant the same species that were harvested. Both cost more money and take more time than simply moving to a new area to harvest.

Another example involves drinking water. In many areas, drinking water supplies are contaminated because of poor sewage systems and runoff from human activities like farming and industry. It is proving less expensive to haul water in from other areas than to correct the cause of the problem. Therefore, this approach is becoming more common. Until an increase in consumer demand for resources that are truly being renewed alters political action and financial motivation, many potentially renewable resources will continue to be threatened.

Nonrenewable Resources

The third and final category of natural resources is nonrenewable resources, which includes fossil fuels and minerals. These resources take extensive geological time to form, and are therefore essentially finite. Oil and natural gas are fossil fuels, which constitute an essential energy source of developed countries. They are burned to generate electricity and to power combustion engines, as in automobiles and airplanes. Minerals like iron and gold are mined from the earth as low-quality ore and then processed into pure forms that are used as building materials.

Nearly all the steps for obtaining and using nonrenewable resources are harmful to the environment. Drilling and mining to get the raw materials almost always drastically disturbs or destroys the area being explored. Processing the raw materials involves a great deal of energy and chemicals that produce toxic by-products. Finally, the use of fossil-fuel-based products like gasoline causes air and water pollution.

The conservation of natural resources involves many steps, the first of which is a global change of attitude toward conservation that places a priority on reducing consumption. The number of people and the amount of resources each person consumes must be reduced in order to lower the usage

of natural resources. This will be no easy matter. Reducing the number of people having an impact would be a difficult step for areas where large families are of religious or economic importance. Also, reducing the amount each person consumes is contrary to the notion of progress in the most developed countries. Hopefully, education will help reduce the demand for nonrenewable resources and increase the use of perpetual and renewable resources before shortages dictate these changes. SEE ALSO HABITAT; HABITAT LOSS.

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Natural Selection

Natural selection is the differential survival and reproduction of individuals with particular **phenotypes**, the physical manifestation of **genotypes**. Natural selection works only on the phenotypes of individuals. Natural selection produces adaptation when the phenotype is heritable. Natural selection is the most important cause of biological evolution.

Charles Darwin was the creator of the concept of evolution by natural selection. In his 1859 book, *On the Origin of Species*, the most important book on evolution, Darwin put forth his argument and supported it with multiple examples. Darwin's idea of natural selection was heavily influenced by an essay on human population growth written in 1798 by English economist Thomas Malthus. Malthus pointed out that every organism has the ability to produce more individuals than the environment can support, and that many individuals die without reproducing. Darwin recognized that variation among individuals is always present, and that some individuals with particular combinations of traits are more likely to survive than other individuals with different combinations of traits. With so much variation, and more individuals being produced than can survive, the individuals with the combination of traits that are best suited to their environment will survive better and reproduce more than other individuals. This is natural selection as Darwin described it.

Darwin also identified artificial selection, which works in the same way as natural selection except that humans are the selective force rather than the environment. Artificial selection, for example, has produced domesticated animals. One of the best illustrations of artificial selection is the breeding of dogs, as humans selectively bred dogs to have specific characteristics. Beagles were bred to bark as they chased after foxes. Labrador retrievers were bred to swim and to carry game birds that had been shot down over water back to shore. Other characteristics selected for included body size,

phenotypes the physical and physiological traits of an animal

genotypes the genetic makeup of different organisms

sexual selection selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

populations groups of individuals of one species that live in the same geographic area

habitat physical location where an organism lives in an ecosystem

ecosystems self-sustaining collections of organisms and their environments

color, hair length, and personality. Dogs are all the same species, but there are clearly huge amounts of variation among breeds.

Darwin also identified a third type of selection, **sexual selection**. Sexual selection is the differential ability of individuals to win mates and reproduce. Most animal species have sexual dimorphism, that is, the different sexes have different traits. Sexual dimorphism results from sexual selection. Bird songs, elaborate coloration, and the other characteristics that help males attract mates are sexually selected traits. For example, male guppies have bright spots of pigmentation that attract females. Males that are more brightly colored mate with more females.

There are three forms of selection: directional, stabilizing, and diversifying. Directional selection changes the average value of a trait in some **populations**. For example, female guppies that prefer to mate with male guppies that have more orange spots will increase the average number of orange spots on males in the next generation. Stabilizing selection reduces variation in a population by selecting against the extreme individuals. In a similar example, females liked males that had only five spots of orange, but disliked males with more or less than five spots. Diversifying selection increases the variation in a population by favoring the extreme individuals, for example males with lots of orange spots or with no orange spots, and disfavoring males with average amounts of orange spots. SEE ALSO ADAPTATION; BIOLOGICAL EVOLUTION; DARWIN, CHARLES.

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Nematoda

The Phylum Nematoda consists of the species commonly known as roundworms. There are approximately 12,000 described species, but the actual number could be many times higher. Nematode worms are extremely abundant; often, several hundred species, and as many as a million individuals, inhabit a square yard of soil. Nematodes are also extremely varied ecologically. They are found in almost every imaginable **habitat**, including terrestrial (land-based), freshwater, and saltwater **ecosystems**, as well as within other organisms as parasites. Nematodes can be herbivorous, carnivorous, or parasitic, and include both generalists (who make use of a wide variety of resources) and specialists (who make use of only particular resources). They play a particularly critical role in decomposition and nutrient cycling, where they are often the intermediate decomposers that partly break down organic materials so that they can then be dealt with by bacterial decomposers.



A pinworm. Adult pinworms live in the large intestine of humans.

Characteristics of Nematodes

Roundworms are small, slender, unsegmented worms which are tapered at both ends. They have a circular cross section. Different species of nematodes are often difficult to distinguish because of their fairly uniform external morphology, or outer appearance.

Nematodes are characterized by an external (outer) layer of cuticle that is secreted by the hypodermis underneath it. The cuticle is somewhat rigid. However, it is flexible enough to permit bending and stretching, and can be penetrated by gases and water. The cuticle is **molted**, or shed, several times during the worm's growth. The hypodermis underlying the cuticle is a syncitium—that is, it consists of large cells with more than one nucleus. A layer of muscle cells is found beneath the hypodermis. All nematode muscle fibers run lengthwise along the animal's body. This single, unvaried orientation limits nematodes to their characteristic, and somewhat awkward, pattern of movement, a flailing whiplike motion that is produced by alternate contractions (shortenings and thickenings) of muscle cells on either side of the animal's body. The rigidity of the cuticle layer also limits the motion of nematodes.

Nematodes lack a true **coelom** (body cavity) since their internal cavity is not lined by cells originating from the embryonic mesoderm. Instead, they possess a fluid-filled pseudocoel (incomplete coelum) that contains the intestine and reproductive organs.

The nematode nervous system is characterized by a rear nerve ring around the area of the pharynx (area deep inside the mouth cavity) and two pairs of lengthwise nerve cords that run down the body. There are also **dorsal** (back) and **ventral** (belly) nerve cords as well as a set of lateral nerve cords across the body. These nerve cords transmit sensory information and coordinate movement. Nematodes have a variety of sensory receptors, including tactile (touch) receptors at the front and back ends of the body, and chemosensory (chemical-sensitive) cells at the front end. They also have light-sensitive organs organized either in ocelli (simple eyes) or distributed along the surface of the body.

molted the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

coelom a body cavity

dorsal the back surface of an animal with bilateral symmetry

ventral the belly surface of an animal with bilateral symmetry





diffusion the movement of molecules from a region of higher concentration to a region of lower concentrations

dioecious having members of the species that are either male or female

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

Nematodes have a complete gut with a mouth and an anus. Teeth, which are used to pierce animal or plant matter, aid in obtaining food. The pharynx is muscular and pumps food through the gut, and nutrients are absorbed in the intestine. There is no internal system of circulation, so the transport of nutrients and wastes is achieved by **diffusion** (scattering). Specialized cells for excretion, which are known as rennette cells and are unique to the phylum, remove nitrogen-laden wastes. These are expelled from the nematode directly through the body wall, in the form of ammonia.

Nematodes breathe across their entire body surface. This gas exchange strategy is adequate because of the small size of the worms, which means they have a high ratio of surface area to volume.

The majority of nematodes are **dioecious**; that is, the sexes are separate. Some species, however, are hermaphroditic, having both male and female reproductive organs. In dioecious species, males have a specialized spine for **sexual reproduction** that is used to open the female's reproductive tract and to inject sperm. Nematode sperm is unusual in that the sperm cells do not have flagella, and move using an amoeboid motion (crawling). While some species are live-bearing, most lay eggs. Eggs escape through a mid-body hole called the gonopore in the female. There is no distinct larval stage. Eggs develop directly into juveniles that generally resemble the adults except that they lack mature reproductive organs. Nematodes are also characterized by an unusual feature called "eutely," in which every individual of a given species has exactly the same number of cells. This cell number is achieved by the end of the developmental period, so that subsequent growth of the animal involves increases in cell size rather than in cell number.

Nematodes of Particular Interest

Some well-known nematode parasites include hookworms, pinworms, and heartworms. Also included are *Trichinella spiralis*, which is responsible for trichinosis and uses both pigs and humans as hosts, and filarial worms, which are the primarily tropical parasites responsible for the diseases elephantiasis and river blindness.

The nematode *Caenorhabditis elegans* is one of the most well-studied living species and has served as a biological model organism for genetic and developmental studies. It was the first multicellular organism for which a complete DNA sequence was obtained.

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Nervous System

The nervous system is a highly precise and complex system of cells that allows animals to sense, process, and react to cues from the physical environment. The fundamental duty of the nervous system is to transfer information at relatively high speed from one part of the animal to another. Every animal has at least a rudimentary nervous system. Although plants and fungi are able to sense and respond to aspects of their environment, they do this based solely on chemical **physiological** responses and not because of the combined activity of specialized cells. The means by which a nervous system transfers information is through electrochemical signal transmission. Single nerve cells, neurons, can receive information in the form of a chemical and electrical signal, and transfer this information to other **neurons**, as well as to **somatic** cells, non-neurons.

The reason and the means by which animals originally developed a nervous system are very difficult to ascertain. Certainly, ancestral animals gained an advantage by being able to sense their environment, and as multicellular organisms became very large, a fast efficient system of communication was needed. However, the function and identity of the first neuron remains a mystery.

Components of the Nervous System

The nervous system of **vertebrates** is functionally divided between the central nervous system, consisting of the brain and **spinal cord**, and the **peripheral nervous system**, including all neurons that do not have their cell bodies within the brain or spinal cord. Primarily, the nervous system is composed of four cell types: neurons, Schwann cells, oligodendrocytes, and astrocytes.

Neurons are the information transfer cells that perform the primary activity of the nervous system. Schwann cells, oligodendrocytes, and astrocytes are support cells for neurons. Schwann cells are located only in the peripheral nervous system, but they have the same function as oligodendrocytes, which are located solely within the central nervous system. Both cell types wrap a fatty myelin sheath around the axon, the electrical signal, to insulate it and thereby increase the speed of conduction. This axonal covering is white, whereas the neuron is gray, so that nerves composed primarily of **axons** look white because of the myelin, and regions formed mostly by cell bodies look gray.

Support cells can also absorb excess neurotransmitter and provide certain precursor molecules that the neurons will use to construct essential proteins and metabolites. Astrocytes appear only in the central nervous system, and their function is to absorb nutrients from the bloodstream and conduct them to the neurons. Data suggests that support cells are also instrumental in directing immature neurons into their correct location during development, as well as ensuring the integrity of **synapses** and guiding regrowth of axons after injury.

The brain and nervous system are composed of grouped functional systems. This means that neurons can be categorized based on what kind of information they convey. These like-neurons are organized into pathways of conduction punctuated by processing nodes. The conduction pathways

physiological the basic activities that occur in the cells and tissues of an animal

neurons nerve cells

somatic having to do with the body

vertebrates animals with a backbone

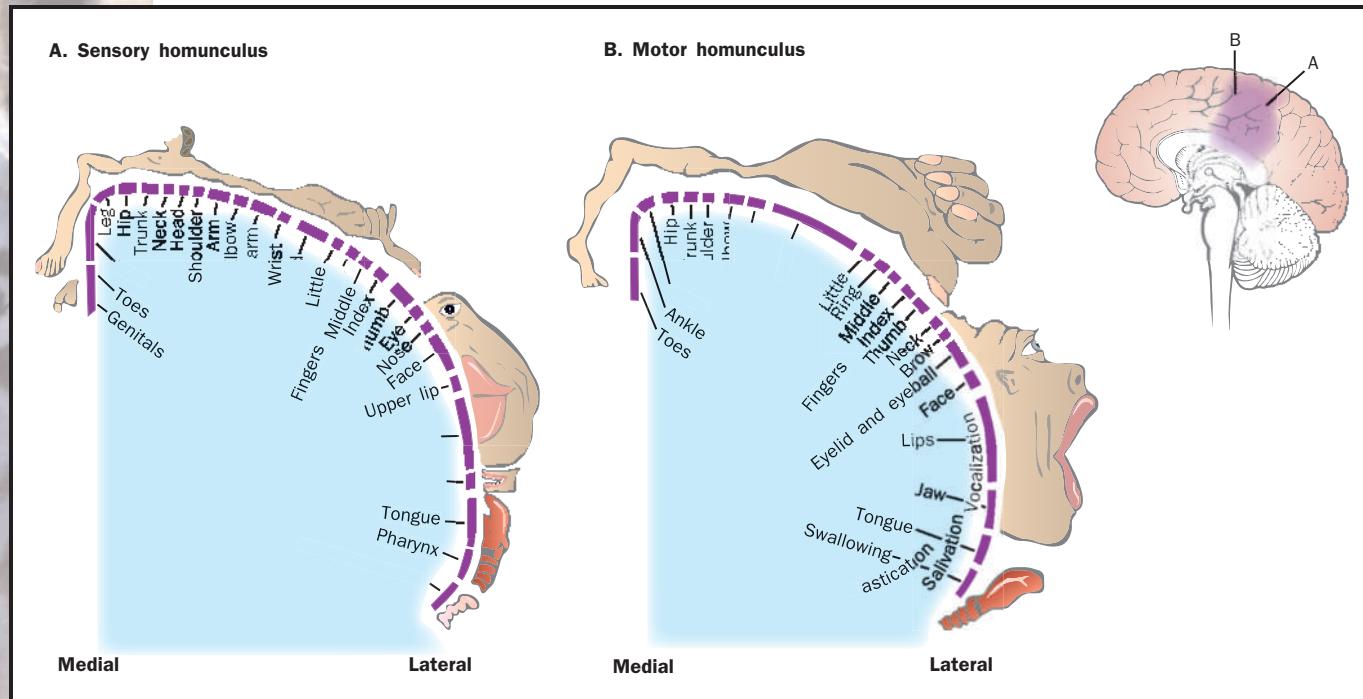
spinal cord thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

peripheral nervous system the sensory and motor nerves that connect to the central nervous system

axons cytoplasmic extensions of a neuron that transmit impulses away from the cell body

synapses spaces between nerve cells across which impulses are chemically transmitted





Homunculus. Redrawn from Kandel, et. al, 2000.

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

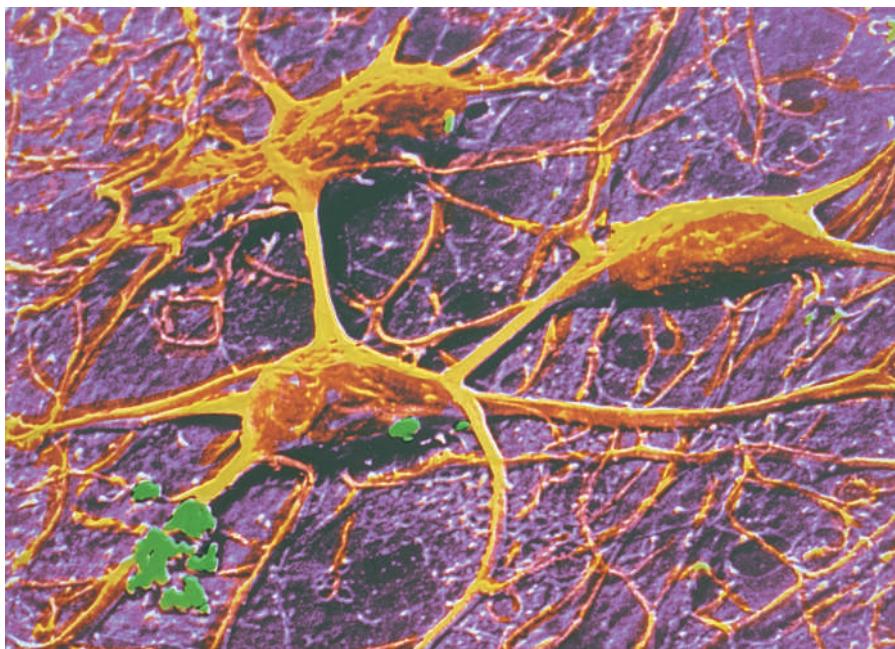
action potential a rapid change in the electric charge of the cell membrane

are formed of nerves or fibers containing primarily neuronal axons. The nodes, called ganglia or brain nuclei, are mostly composed of neuronal cell bodies and **dendrites**. Because information is transferred along pathways, and each node processes the information in a characteristic manner, the nervous system is referred to as a labeled-line system.

The nervous system is also called a parallel pathway system, because sensations such as sounds and visual inputs are transferred to the brain in an organized manner within separate nerves. For instance, sounds are divided up into their respective frequencies, and each frequency travels in its own fiber, parallel to the other frequency fibers grouped together within the auditory nervous system. The different sounds thus remain segregated until they are processed in the cortex. Finally, although distinct regions of the brain perform unique tasks, many overall concepts that are important psychologically to humans are not located in any one region of the brain. Memory, emotion, intelligence, and personality are all examples of emergent properties, meaning that they result from the coordinated activities of many brain regions.

Neurons carry information in the form of an **action potential**, which is a rapid (several milliseconds long) change in the electrical conduction of the cell membrane. When a neuron produces an action potential, it is described as firing, and a single action potential is called a spike. Action potentials are the primary form of communication between neurons, and the entire nervous system is mediated by this signal.

One may then wonder how perception can be so complex. This is because many factors contribute to the information encoded by the action potentials, including the frequency of action potentials, the probability of an action potential in any particular cell, the morphology (shape) of the neuron, the number and location of neurons that contribute the information,



This micrograph depicts three human nerve cells of the cerebral cortex and their branching fibers.

the number and location of neurons that receive the information, the type of neurotransmitter it uses, and the contributions of support cells. Furthermore, although each individual neuron can only produce an action potential for communication, this signal can have a different shape and character for different neurons.

The opposite of an action potential is a **hyperpolarizing potential**. This is instigated by inhibitory neurons, which release a neurotransmitter that decreases the probability that the neuron will fire. There may be thousands of inputs to a single neuron, or just one, and the contributions of all the factors listed above allow the combinatory activity of all the neurons in the ordered nervous system to produce consciousness, cognition (knowing), behavior, sensation, and **homeostasis** (maintenance of an organism's general health) in animals.

hyperpolarizing potential any change in membrane potential that makes the inside of the membrane more negatively charged

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

Peripheral nervous system. In vertebrates the peripheral nervous system is composed of both motor neurons, which instigate muscle movement and activity, and sensory neurons, which convey information about the external and internal state of the organism. Furthermore, interneurons are important intermediates in both sensory and motor pathways, because they connect different circuits and can modify a signal as it follows a particular course. All subdivisions of the peripheral nervous system are comprised of these three neuronal types. The peripheral nervous system can be further divided into the autonomic nervous system and the **somatic nervous system**. Because it mediates the activity of heart muscle, smooth muscle, and exocrine glands, the autonomic nervous system is also referred to as the involuntary nervous system. The somatic nervous system is called voluntary because it controls the skeletal muscles.

somatic nervous system a part of the nervous system that controls the voluntary movement of skeletal muscles

Autonomic nervous system. The autonomic nervous system is made up of the sympathetic, parasympathetic, and enteric divisions. The enteric system is a subsection of the peripheral nervous system located in the gas-



parasympathetic divisions part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

somatosensory information sensory information from different parts of the body except for the eyes, tongue, ears, and other primary sense organs

dorsal root ganglia nervous tissue located near the backbone

innervate supplied with nerves

trointestinal tract of the gut and is responsible for mediating digestive reflexes. The high number and dense compaction of neurons in this system, and its autonomy with respect to the brain, cause some scientists to qualify it as a primitive “second brain.”

The sympathetic and **parasympathetic divisions** of the peripheral nervous system are functional opposites. Whereas the parasympathetic division is responsible for homeostatic activities, such as maintaining a basal respiratory pattern, heartbeat, and normal metabolism, the sympathetic division governs the body’s reaction to extreme situations. It instigates emergency measures in response to stress from strong emotions, athletic exertions, battle, severe temperature change, and blood loss. The sympathetic division thus increases activity in the heart and other organs, the sweat glands, the vascular system, and certain smooth muscle groups. Because the autonomic division controls day-to-day bodily functions, it has been characterized as controlling “rest and digest” activities, whereas the sympathetic division is responsible for “fight or flight” reactions.

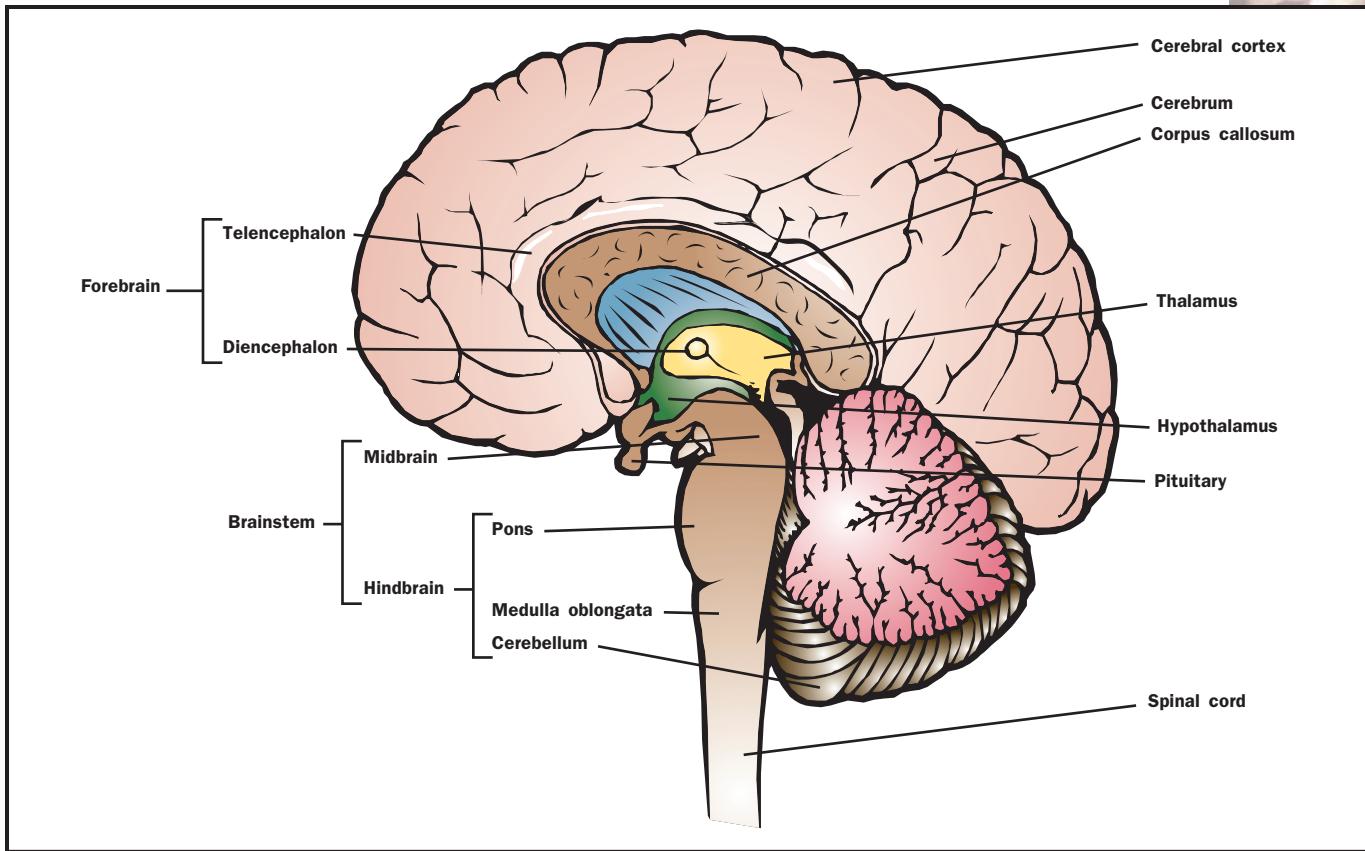
Somatic nervous system. The somatic nervous system allows vertebrates to monitor and control skeletal muscle output and to consciously sense aspects of the environment. Sensations originating at the skin or muscles of the trunk and limbs of an animal are called **somatosensory information**. Neurons located in the skin, muscle, joints, and ligaments of the body are specialized for transmitting somatosensory information to the central nervous system. Conveying the position of the limbs, muscle exertion, joint stress, temperature, tickle, pain, and tactile information, these sensory neurons enter the spinal cord via the **dorsal root ganglia**. The term “dorsal” means “toward the back of the body,” whereas “ventral” means “toward the front of the body.” Ganglia are congregations of neuronal cell bodies located outside of the brain. All sensory information enters the spinal cord from the dorsal side and then travels up to the brain.

Motor nerves controlling muscle movement descend from the brain and send axons out of the ventral side of the spinal cord. There are ventral roots that contain motor axons, but, unlike the somatosensory nerves, there are no motor ganglia. Motor neurons in the somatic nervous system **innervate** (connect with) skeletal muscles and can be controlled by a mix of voluntary and involuntary impulses.

Sensation and motor control of the face, head, and neck do not enter the brain through the spinal cord, but instead are transmitted through cranial nerves that pass through holes in the skull. When animals plan to make a movement, the cerebral cortex sends a message down through the brain to the spinal cord and out to that muscle. Sensory neurons located within the muscle sense its movement and send that information back up to the brain through the somatosensory pathway.

The Brain

The vertebrate brain is housed in the skull, at the rostral end of the organism, whereas the tail end of the animal is the caudal end. Quadrupedal, four-legged, animals have distinct rostral (head), caudal (tail), dorsal (back), and ventral (stomach) poles. At a point in human development, the brain bends 90° so that humans may stand vertically with face pointing forward, whereas



the quadruped's head and brain remain in the straight axis of the spinal cord. Thus, below this bend, dorsal refers to the back and ventral to the chest sides of the body; but, above the bend, dorsal refers to the upward direction and ventral points downward.

All vertebrates have a **bilaterally symmetrical** brain, meaning that specialized regions on one side of the brain are mirrored on the other side. Although animals with more complex brains contain several specialized structures and pathways that differ from one hemisphere to the other, for the most part this mirror image organization is conserved.

The brain is divided into three basic regions, the hindbrain, midbrain, and forebrain. The hindbrain contains the pons, cerebellum, and medulla oblongata. At the top of the spinal cord is the medulla oblongata, a thickened region of neural tissue responsible for basic life processes such as breathing, digestion, and control of heart rate. Directly above (rostral to) the medulla is the pons, which conducts information relating to movement, gustation (taste), respiration, and sleep. The cerebellum, a large, highly folded structure composed of six tissue layers, lies dorsal to the pons and medulla. The cerebellum smoothens and coordinates muscle movements and is responsible for learned motor patterns, such as riding a bicycle.

The midbrain lies rostral to the hindbrain, and between these regions is the cephalic flexure, the bend that disrupts the longitudinal axis of the human central nervous system. The midbrain, primarily a relay site for motor and sensory neurons, is the focus of clinical research for its involvement in motor dysfunction diseases such as Parkinson's. Additionally, it is

Anatomy of the human brain.

bilateral symmetry

characteristic of an animal that can be separated into two identical mirror image halves



becoming increasingly clear that complex signal properties for sensory systems are established in the midbrain, rather than higher up, in the cortex.

The forebrain can be subdivided into the diencephalon and the telencephalon. The diencephalon is situated directly rostral to the midbrain. It contains the thalamus, which is a nexus for all information destined for the cerebral cortex, and the hypothalamus. The hypothalamus serves to integrate autonomic signals and endocrine activity with the organism's behavior. It regulates body temperature, eating and digestion rates, hormonal control of mating and pregnancy, and the sympathetic division of the autonomic nervous system.

The telencephalon houses the basal ganglia, hippocampus, amygdaloid nuclei, and cerebral cortex. The first three of these structures are buried in the center of the brain, surrounded by the cerebral cortex, cerebellum, and midbrain. The basal ganglia are essential for regulating motor performance. The hippocampus is implicated in short-term memory, and with aspects of long-term memory storage. The amygdala and its associated nuclei coordinate emotion and the effect of emotional state on autonomic and endocrine functions.

The cerebral cortex is involved with higher functioning, association formation, conscious perception, thought, memory, and emotion. The two hemispheres are divided but are interconnected by a bridge called the corpus callosum. Each hemisphere is divided anatomically into four lobes that are separated by prominent folds in the tissue: the occipital, parietal, temporal, and frontal lobes. The occipital lobe is the most dorso-caudal, located at the back of the skull. It contains primary processing centers for vision. The parietal lobe, centrally located on the dorsal cortex, processes sensory and motor information from the body. A distinct fold in the cortex called the central sulcus separates the primary motor cortex (just rostral of the sulcus) from the primary sensory cortex (just caudal of the sulcus). These thin strips of cortex extending from the top of the brain around the lateral sides encode sensation and motor input to every body region in a highly predictable manner. The amount of cortex dedicated to a particular body region is in direct proportion to the amount of motor control or sensory input from that region. The temporal lobe angles down ventrally on the lateral sides of the brain. It contains higher processing centers for audition, vision, and memory. The frontal lobe is the most rostral, and it contains association areas that may be a site for the storage of long-term memories.

Specialized Systems in Animals

The nervous systems of particular animals are specialized to the life habits of those animals. For example, some migratory animals may rely on detection of electromagnetic cues from Earth's crust to guide them over great distances. Weakly electric fish sense their environment and communicate with each other through emission of electrical impulses. These specialized senses require a specialized nervous system to collect and interpret information from the environment. Marine **invertebrates**, such as the giant squid, have very different neurons from those of vertebrates. The nerve cells are unmyelinated (not myelin-containing support cells), and thus the diameter of the axon must be very large sufficiently to increase conduction speed of the neuron.

Invertebrates animals without a backbone

Most invertebrates, including insects, have a centralized brain, but the most primitive animals instead have a diffuse distribution of distinct ganglia within each of their segments. These ganglia interact to control organismal activities, but there is no central processing center, as in vertebrates. Studying the simpler nervous systems of invertebrates aids in the understanding of their biological processes. SEE ALSO GROWTH AND DIFFERENTIATION OF THE NERVOUS SYSTEM; NEURON; SENSE ORGANS.

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Neuron

Neurons are highly specialized cells in both form and function. They contain the same suite of **organelles** as other cells, including the nucleus, endoplasmic reticulum, **mitochondria**, and **bilipid membrane**. Unlike many cells, however, neurons are polar cells, meaning that one side of the cell has a different form and function than the other side of the cell. The **dendrites** are located at one extremity, and the **axon** is at the other end. Dendrites are an extension of the neuronal membrane. This extension stretches out from the cell body like a tree with many branches. Each “twig” of the dendritic tree is in contact with another neuron, and the function of the dendrites is to receive information from these other neurons. It is not uncommon for thousands of neurons to contact a single dendritic arbor. The axon, at the opposite pole of the cell, is generally long and unbranched until its tip, where it may have several small branches. After the dendrites pass information through the cell body to the axon, the axon passes this information to the dendrites of other neurons.

Neurons must maintain a particular internal environment. They actively pump positively charged sodium molecules from their **cytoplasm** to their extracellular space, at the same time bringing positively charged potassium ions in. This is accomplished by the sodium/potassium pump, a molecular exchange protein in the membrane that creates different concentrations of ions outside and inside the neuron. The result is that the inside of the cell is negatively charged with respect to the outside of the cell. The difference in charge between the inside and outside of the cell membrane is known as the membrane potential. If the cell is depolarized,

organelles membrane-bound structures found within a cell

mitochondria organelles in eukaryotic cells that are the site of energy production for the cell

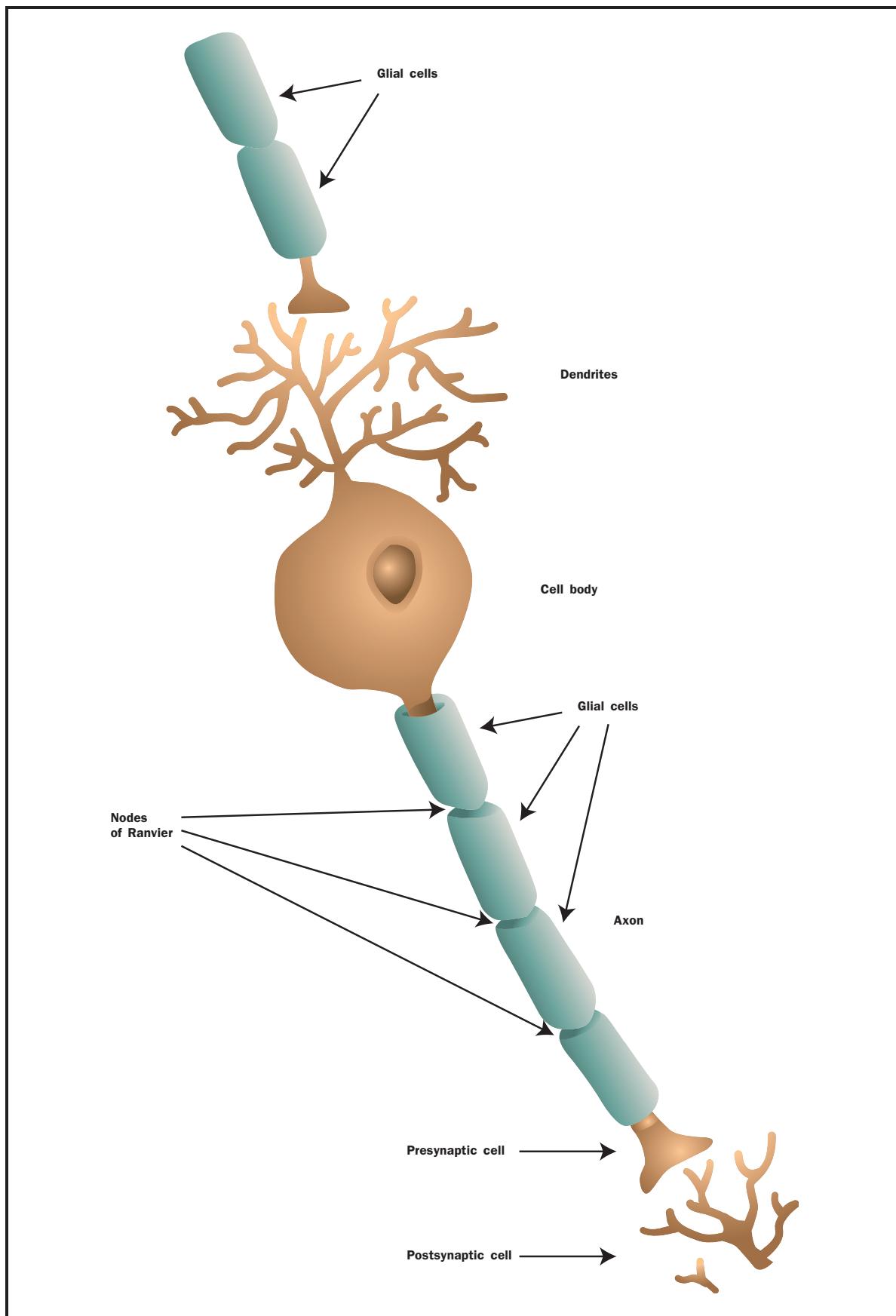
bilipid membrane a cell membrane that is made up of two layers of lipid or fat molecules

dendrites branched extensions of a nerve cell that transmits impulses to the cell body

axon cytoplasmic extension of a neuron that transmits impulses away from the cell body

cytoplasm fluid in eukaryotes that surrounds the nucleus and organelles





Anatomy of the neuron.

the inside of the cell contains more positive charge than normal. If the cell is hyperpolarized, the inside contains more negative charge than normal. If a neuron were disconnected from all other neurons, its membrane potential would remain constant, but when a neuron is in contact with other neurons, it receives many depolarizing signals at its dendrites. The depolarization is caused by allowing more sodium molecules to enter the cell, thereby making the inside more positively charged than normal. The depolarization begins at the tip of the dendrites and travels toward the cell body. If the depolarization is strong enough, it will not die off before reaching the cell body. If the depolarization is very strong, it will reach the axon at the other side of the cell body.

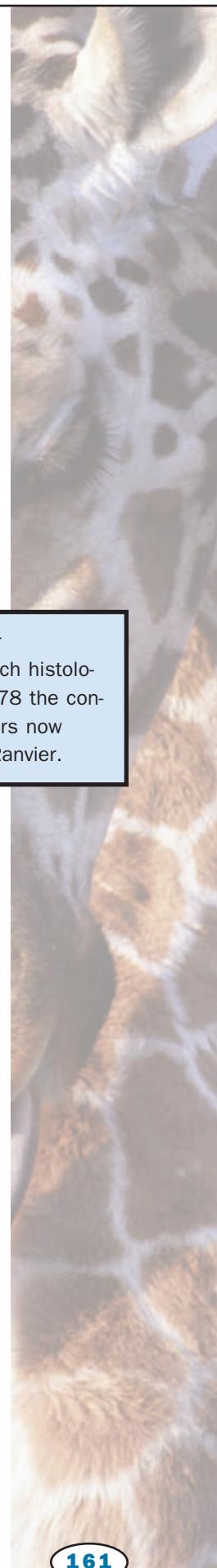
When depolarization reaches the axon, it causes an electrical chain reaction that reaches to the tip of the axon. This **action potential**, or spike, occurs as an active process by which specific ion channels open, allowing positively charged molecules into or out of the cell. First, the base of the axon becomes slightly depolarized from the dendritic signal. This causes specific sodium channels to open. Sodium then enters the axon, increasing the amount of depolarization. Soon the sodium channels fatigue and close, as potassium channels open, allowing positively charged potassium ions to leave the cell. The potassium ion flow cancels the depolarization and even hyperpolarizes the cell a little before potassium channels close and the membrane returns to its normal potential. This electrical event passes along the axon like a wave. The axon is covered by a number of specialized cells called glial cells. These cells wrap around the neuron and insulate it from ion exchange, except at small gaps called the nodes of Ranvier. Because ions can enter or leave the cell only at the nodes of Ranvier, the action potential jumps from node to node, thereby increasing its speed. Because the electrochemical signal moves so quickly through the neuron, the transmission of a signal along the axon is called firing.

The manner by which one neuron's axon stimulates another neuron's dendrite is through a signal molecule called a neurotransmitter. This occurs at the synapse, a specialized region that includes the tip of one neuron's axon and the conjoining region of another neuron's dendrite. **Neurotransmitters** are stored within the axon tip in pouches of membrane called vesicles. When an action potential travels down the axon and reaches the synapse, it triggers the release of neurotransmitter-containing vesicles into the synaptic cleft, the region of space between the axon of one neuron and the dendrite of another. The neuron that releases the neurotransmitter from its axon is called the presynaptic cell and the neuron that receives the neurotransmitter at its dendrites is called the postsynaptic cell. The neurotransmitter diffuses across the synaptic cleft, the space between the pre- and postsynaptic cells, and binds to special neurotransmitter receptors in the dendrite of the postsynaptic neuron. These receptors open, allowing sodium ions to flow into the cell. This event is the origin of the dendritic depolarization. Neurotransmitters can be excitatory, meaning that they cause depolarization in the postsynaptic cell, or inhibitory, which means that they prevent depolarization in the postsynaptic cell. Inhibitory neurotransmitters cause a different set of receptors to open, allowing the entry of negatively charged ions such as chlorine. In this inhibition event, the negative charge hyperpolarizes the cell and decreases the probability that the postsynaptic

action potential a rapid change in the electric charge of the cell membrane

Louis-Antoine Ranvier (1835–1922), a French histologist, described in 1878 the constriction in nerve fibers now known as nodes of Ranvier.

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell





neuron will be depolarized by excitatory presynaptic neurons. SEE ALSO GROWTH AND DIFFERENTIATION OF THE NERVOUS SYSTEM; NERVOUS SYSTEM; SENSE ORGANS.

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Nocturnal

Nocturnal organisms are those that are active mainly at night and sleep during the day. Their activity pattern occurs in twenty-four hour cycles, known as a circadian rhythm. Nocturnal animals include bats, cats, owls, mice, scorpions, opossums, raccoons, coyotes, cockroaches, and moths.

niche how an organism uses the biotic and abiotic resources of its environment

diurnal active in the daytime

sonar the bouncing of sound off distant objects as a method of navigation or finding food

Nocturnal animals occupy a **niche** that is complementary to that of **diurnal** animals. For example, owls have a nighttime role similar to that of hawks during the day. Moths fill the same niche at night as butterflies do during the day.

Many nocturnal animals have specialized adaptations for their nighttime activities. The eyes of most nocturnal animals are larger than those of diurnal animals, helping them to function well in low light. Many nocturnal animals have large ears that are exceptionally sensitive. An acute sense of hearing is helpful when sight cannot be relied on in the darkness. Similarly acute senses of smell, taste, and touch also aid in overcoming the disadvantages of low light conditions.

Most bats have developed a special **sonar** system called echolocation. They make high frequency calls either out of their mouths or noses and then listen for echoes to bounce from the objects in front of them. This is an effective means of finding their way around in low light and catch their food (generally insects). Fruit bats, one of the few diurnal bats, lack the ability to echolocate. This demonstrates the evolution of characteristics favoring their particular niche, in this case daylight activity versus nighttime activity.

Cats' eyes are well adapted to nocturnal activity. The eyes are relatively large, with pupils that can open wide in the dark and narrow down to slits in the sunlight. The size and position of the eyes on the head allow as much light as possible to enter them and ensure a wide field of vision. These are important factors in hunting and nocturnal prowling. A cat cannot see in total darkness, but it can see better in dim light than can most other animals. Also, cats have large, erect ears that help in the detection of prey in the darkness. SEE ALSO DIURNAL.

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Oligocene

The Oligocene epoch (39 to 22 million years ago) is the transition period between the earlier and later Tertiary period (65 to 2 million years ago).

A key feature of evolution is the ripple effect created by geographical changes that influence **climate** and therefore vegetation and ultimately the ways in which animals develop. The most important geographical event separating the Oligocene from the preceding tropical and fairly stable Eocene was the splitting off of the Australasian landmass from Antarctica. As the oceans encircled the growing polar ice cap, the waters cooled. This cooling effect was spread around the globe by circulating currents that produced a dramatic drop in temperatures and, equally important, a new climate marked by seasonal fluctuations. Many animals of the Eocene that depended on a warm climate became extinct in the Oligocene, which is sometimes called “the great divide.” Changing seasons favored the rise of homeothermic (warm-blooded) animals, such as mammals, over those who could not control their metabolic temperatures, such as reptiles. Thus the lizards, turtles, and crocodiles who survived did not flourish in the way that mammals like rodents and all modern-hoofed animals did.

The climatic changes produced changes in vegetation as well. Most forests in northern latitudes (45°) became cooler, mixed coniferous-deciduous, in which the most successful mammals tended to be short-legged, stumpy-bodied browsers and **scavengers**. Fortunately for humans, tropical zones, though greatly diminished, still existed in parts of South America and Africa, where a few primates survived on the year-round fruit supply. Plentiful food sources and tropical climate allowed for the survival of the early primates.

Insect groups expanded to include the social ants and termites, followed rapidly by the appearance of **insectivores**. Now that whole colonies of foods were available in a single place, the previously scarce mouse-size mammals who fed on this food also grew in size and number.

The growth of the polar ice cap locked up more and more of the ocean water, causing sea levels to drop and connecting parts of Europe and Asia that had been separate. This allowed a mingling of species throughout Eurasia from which a number of **herbivores** did not recover. Archaic predators such as the condylarths and creodonts, which were hooved flesh eaters, began to decline and were replaced by giant, flightless, **carnivorous** birds. At over 2 meters (7 feet) tall, with deadly claws and ferocious, hatchet-like beaks, *Diatryma* and *Phorusrhacus* were the fearsome top predators of the Oligocene. They too disappeared, possibly because they were unable to protect their ground-dwelling young from the small, fast mammals that came along in the Miocene.

Just as the linking of landmasses tended to produce uniformity, so isolation produced spectacular diversity. Australia had sailed off with a few ancestral marsupials, mammals whose infants crawl into a pouch, or



climate long-term weather patterns for a particular region

scavengers animals that feed on the remains of animals that they did not kill

insectivores animals who eat insects

herbivores animals who eat plants only

carnivorous animals that eat other animals



Oligocene epoch and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Cenozoic	Quaternary	Holocene	0.01
		Pleistocene	1.6
	Tertiary	Pliocene	5.3
		Miocene	24
		Oligocene	37
		Eocene	58
		Paleocene	66

a

niche how an organism uses the biotic and abiotic resources of its environment

edentates lacking teeth

ungulates animals with hooves

marsupium, where they are suckled and grow to independence. Given an entire continent in which to experiment, the marsupials exploded in a riot of shapes and sizes, filling every conceivable evolutionary **niche** from herbivores and carnivores to scavengers and insectivores. Only a few of these species survive to the present.

South America also separated from the other land masses and developed its own unique mammals. The **edentates** (toothless mammals), which included anteaters, sloths, and armadillos, were enormous, slow-paced vegetarians and insectivores. For example, glyptopons (armadillos) were 3 meters (10 feet) long and baluchitheriums (rhinoceroses) were 5.5 meters (18 feet) tall and 8.2 meters (27 feet) long. A bizarre assembly of hoofed animals also flourished in this region until the Isthmus of Panama formed at the end of the Cenozoic (2 million years ago) and linked North and South America. This two-way land bridge allowed a few herbivores from the south to move north, but on the whole, the invasion of ruthless carnivores and more efficient **ungulates** (hoofed mammals) signaled the end of most of the uniquely southern mammals.

In the Atlantic and Pacific Oceans, separated by the Isthmus of Panama, whales continued to thrive, spreading from Europe to New Zealand where they were joined by sea cows and the first seals. SEE ALSO GEOLOGICAL TIME SCALE.

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Ontogeny

Ontogeny describes the entire life history of an organism from **fertilization** to death. It includes not only embryonic and prenatal development but also postnatal growth and development.

That patterns of ontogeny can provide fascinating insights into evolutionary history has long been recognized. Possibly the most famous concept linking the two areas is the “biogenetic law” of German biologist Ernst Haeckel (1834–1919), which states that “ontogeny recapitulates phylogeny.” Haeckel suggested that, in the course of its development, each organism recapitulates (repeats the stages of) its entire **phylogenetic** history by taking on the morphologies of all of its ancestors sequentially, from the most primitive ancestor to the most advanced. Haeckel favored a fairly stringent interpretation of the biogenetic law, and spent considerable time identifying the ancestors represented by different developmental stages. For example, he viewed the gastrula stage (an early embryonic stage during which the three embryonic tissue layers are formed) of **vertebrate** embryos as representing the morphology of their **invertebrate** ancestors. Later developmental stages were interpreted as representing “higher” ancestors. For example, all avian and mammalian embryos go through a developmental stage in which gill slits are highly prominent. Haeckel interpreted this stage as a recapitulation of the “fish stage.”

Haeckel’s biogenetic theory fell into disfavor in the early twentieth century, when increasing evidence on the ontogenetic patterns and phylogenetic histories of different species indicated that there was not, in fact, a direct correspondence between the two. However, Haeckel’s ideas are important because they stimulated considerable interest in embryological studies and because they emphasized the importance of links between ontogeny and evolution, an area that is still being actively studied today.

Current ideas regarding ontogeny and phylogeny rely on the concepts of another nineteenth-century scientist, Prussian-Estonian embryologist Karl Ernst von Baer. Von Baer noted that earlier developmental stages are simpler, with complexity increasing over time. He also emphasized development as a process in which related species diverge over time. That is, all species resemble each other fairly closely during the earliest stages of development, and gradually diverge in form over the course of ontogeny. The fertilized egg, the earliest stage of ontogeny, represents the time when different species are most similar.

Von Baer also stated that the “general” characteristics of a species appear before the “specific” ones, so that traits that characterize more inclusive groups, such as the phylum to which an individual belongs, appear earlier than those that characterize more restricted groups, such as the genus or species. This is apparent in human development in multiple ways. For example, the development of the neural tube, a trait possessed by all chordates, is a fairly early ontogenetic event, whereas the development of such species-specific features as the characteristic human facial or limb morphology appear much later.

There was a resurgence of interest in ontogeny as it relates to evolution in the late twentieth century. Stephen Jay Gould, an American paleontologist and evolutionary biologist, brought considerable attention to the

fertilization the fusion of male and female gametes

phylogenetic relating to the evolutionary history

vertebrate animal with a backbone

invertebrate animal without a backbone

Karl Ernst von Baer (1792–1876) was a pioneer of descriptive and comparative embryology.



natural selection

process by which organisms best suited to their environment are most likely to survive and reproduce

climate long-term weather patterns for a particular region

phyla the broad, principle divisions of a kingdom

niche how an organism uses the biotic and abiotic resources of its environment

bivalve mollusks mollusks with two shells such as clams

crustaceans arthropods with hard shells and jointed bodies and appendages that mainly live in the water

fossil record collection of all known fossils

field with the publication of his 1977 book, *Ontogeny and Phylogeny*. Of particular interest to evolutionary biologists and those who study morphology is the idea that the patterns and processes of development can channel or constrain the way in which evolution occurs. Several evolutionary biologists have attempted to explain morphological evolution as the product not only of **natural selection** but also of developmental constraints. SEE ALSO DARWIN, CHARLES; GOULD, STEPHEN JAY; HAECKEL'S LAW OF RECAPITULATION; PHYLOGENETICS SYSTEMATICS; VON BAER'S LAW.

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Ordovician

The Ordovician period (500 to 440 million years ago) comes after the Cambrian in the early Paleozoic era. The period is named for a Celtic tribe named the Ordovices who once lived in the area of Wales (in Britain) where the rocks were first studied. Ordovician limestones are over 6.4 kilometers (4 miles) thick in places and are found on all continents except Antarctica. The uniformity and thickness of the bed indicates a long period of warm and stable **climate** that allows them to develop.

In fact, the Ordovician period was as remarkable for the diversity of its species as the Cambrian period was for the appearance of most major **phyla**. A burst of evolutionary creativity in shape, size, and function tripled the number of marine species that appeared. Specialization became the dominant theme of life, with new forms filling every possible **niche**.

The appearance of highly efficient predators such as the nautiloids and the lobster-size sea scorpions forced the marine community to evolve protective strategies or disappear. Various species responded by developing larger size, thicker shells, or more elaborate defenses. A proliferation in the shapes of the shells of **bivalve mollusks** allowed them to burrow deeply into sand or mud. Other mollusks learned to swim freely by rapidly clapping their valves together. And still others developed intricate teeth-and-socket arrangements that allowed them to close so tightly that they were almost impossible to open.

Exploring the oceans of the Ordovician world would have been quite similar to exploring the oceans of today. Sea urchins, starfish, and sea lilies lived in profusion among the rocks. The first great coral reefs appeared and gave shelter to **crustaceans** of all kinds. Sea mats, sea snails, and sea cucumbers abounded in the tide pools. A huge diversity of bivalve mollusks made their slow way across the muddy ocean floor, leaving their tracks and burrows in the **fossil record**.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missippian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

Ordovician period and surrounding time periods.

The very first primitive fishes appeared, slow and heavily armored, without fins or heads with brains. These agnathans (jawless fishes) were the first animals to have a **notochord** (flexible rod spine), a precursor of a true spinal chord. These chordates were the ancestor of all animals with backbones.

While almost all animals of the Ordovician were marine, another remarkable occurrence is recorded in the rocks of northwest England. There, arthropods (animals with jointed legs) that lived in shallow, freshwater pools left the first tracks in fossilized mud. Scientists speculate that evaporation of their pools forced these centipede-like creatures to adapt to terrestrial conditions. From this point on, the arthropods, a group that includes insects, spiders, and crabs, ruled the land for 40 million years.

The massive Ordovician limestone ends abruptly with a jumble of glacial till, indicating an ice age that so disrupted Earth's climate that more than half of all species became extinct. This first great extinction wiped out huge numbers of **trilobites**, with their precise and sensitive eyes, **brachiopods**, **crinoids**, and other marine **invertebrates**. The life-forms that survived the cataclysmic end of the Ordovician contributed to the genetic makeup of the animal kingdom to the present. SEE ALSO **GEOLOGICAL TIME SCALE**.

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notochord a rod of cartilage that runs down the back of chordates

trilobites an extinct class of arthropods

brachiopods a phylum of marine bivalve mollusks

crinoids an echinoderm with radial symmetry that resembles a flower

invertebrates animals without a backbone

Osmosis See *Transport*.

Osteichthyes

Osteichthyes, or bony fishes, includes two major groups: Sarcopterygii, or lobe-finned fishes, and Actinopterygii, or ray-finned fishes. The characteristics that unite this diverse group include **lungs** or a gas-filled swim bladder derived from lungs, segmented fin rays, bone, and bony scales. Although the tetrapods (including birds, reptiles, mammals, and amphibians)

lungs sac-like, spongy organs where gas exchange takes place



are formally within the Sarcopterygii, they are discussed within their own entries; only animals commonly thought of as “fishes” are discussed here.

Sarcopterygii (Lobe-Finned Fishes)

Although only eight sarcopterygian fish species exist today, they are interesting because scientists believe they are the likely descendants of the fishes that gave rise to the terrestrial **vertebrates**, or tetrapods. The defining feature supporting this notion is a limblike fin with supporting bones that attach to the pelvic and **pectoral** girdles. There are six species of lungfish (Dipnoi or Dipneusti) found in Africa, South America, and Australia. Lungfish have true lungs, which allow them to live in stagnant water. African lungfish can survive for many months in a dry lake bed, protected by a mucus cocoon.

Coelacanths (Crossopterygii) were thought to have gone extinct 70 million years ago along with the dinosaurs until they were rediscovered near South Africa in 1938. There are two species, both large, up to 2 meters (7 feet) long, which prey on fish and squid in the deep waters of the Indian Ocean. Coelacanths are thought to rest on their lobed fins on the ocean floor. They have apparently evolved from a shallow-water, air-breathing ancestor, but their lunglike swim bladders are now filled with fat.

Actinopterygii (Ray-Finned Fishes)

With over 21,000 species distributed over the fresh and salt waters of the world, actinopterygians match the diversity of birds, mammals, reptiles, and amphibians put together. The fins of ray-finned fishes are attached to their body by fin rays, rather than lobes.

About thirty-five species are “primitive” actinopterygians. The Chondrostei have a **cartilaginous** skeleton and lack true scales, and they have an **asymmetrical** tail like a shark’s. They include the sturgeons, noted for their caviar and among the largest fishes found in freshwater, and the filter-feeding paddlefish of the Mississippi River. Gars (Semiionotiformes, family Lepisosteidae) are sit-and-wait predators restricted to the fresh and **brackish** waters of North America. Gars have a cylindrical body covered with armorlike scales and a long snout lined with sharp teeth. Their large swim bladder functions as a lung, allowing them to live in stagnant water. The alligator gar, found in the southern United States and Mexico, reaches 3 meters (10 feet) in length. The single existing species in the last major group of “primitive” actinopterygians, the bowfin (Amiiformes), is also a sit-and-wait predator restricted to North American freshwaters.

The remaining actinopterygians are teleosts, characterized by a symmetrical tail, highly maneuverable fins, and jaws adapted for sucking.

Bony-Tongues, Eels, and Herring

Most bony-tongues (Osteoglossomorpha) are African electric fishes (Mormyridae), which forage and communicate by producing electrical fields. The group also includes the large arapaima of South America and the moon-eye and goldeneye of the upper Mississippi drainage. Tarpon and eels are familiar representatives of the Elopomorpha, characterized by larvae called

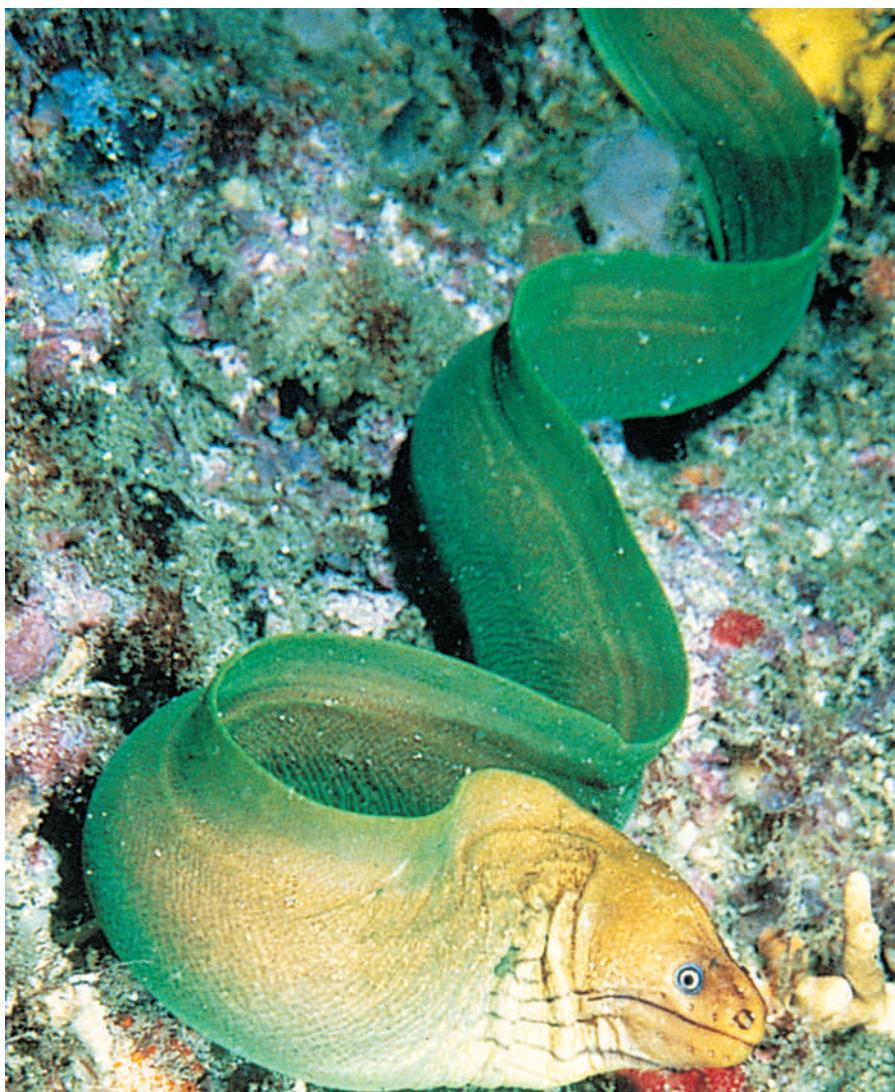
vertebrates animals with a backbone

pectoral of, in, or on the chest

cartilaginous made of cartilage

asymmetrical lacking symmetry, having an irregular shape

brackish a mix of salt water and freshwater



A moray eel in Wreck Bay, Australia.



leptocephali, which are transparent, very slender-bodied, and leaflike. Eels are long, small-headed fishes with sharp teeth, adapted for living in tight crevices or burrows.

Freshwater eels (family Anguillidae) spend most of their lives preying on fishes and **invertebrates** in freshwater. They then migrate to specific breeding grounds in the ocean, usually a distance of thousands of kilometers, and can even travel on land if conditions are damp enough. European and North American eels from the Atlantic slope all migrate to the deep waters of the Sargasso Sea area of the North Atlantic Ocean to spawn. The clupeomorphs include some of the most abundant vertebrates, shad, herring (Clupeidae), and anchovies (Engraulidae). Most species in this group school (live in groups) in open water. They filter-feed on **plankton** that they catch on modified gill rakers, specialized structures associated with the gills.

invertebrates animals without a backbone

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

Pikes and Salmon

Pikes (family Esocidae) are sit-and-wait predators restricted to northern Eurasia and North America. The largest of the pikes, the muskellunge of



pharyngeal having to do with the tube that connects the stomach and the esophagus

nocturnal active at night

dorsal the back surface of an animal with bilateral symmetry

habitats physical locations where an organism lives in an ecosystem

the North America Great Lakes region, can be as much as 1.8 meters (6 feet) long and weigh as much as 36 kilograms (80 pounds). These long, sharp-toothed fishes grab their prey sideways, turn it around, and swallow it headfirst.

There are only about 150 species of salmonids (Salmoniformes), but they are the dominant fishes of cold-water streams and lakes in northern regions and are of substantial economic importance for food and sport fishing. Familiar salmonids include trout, largely restricted to freshwater lakes and streams, and salmon, most of which spend most of their lives at sea. They use a sophisticated sense of smell to detect the stream they were born in and return there to spawn a single time and die.

Ostariophysi

About one-quarter of all known fishes belong to this diverse group, which dominates Earth's freshwaters. Three main features characterize the Ostariophysi: (1) **Pharyngeal** teeth, located in the throat behind the gills, are used for processing food once swallowed and allow for specialization on different food types. (2) Weberian ossicles, a series of bones connecting the swim bladder (which acts like an eardrum) to the inner ear, allow for sensitive hearing, (3) *Schreckstoff*, or "fright substance," is a chemical they give off when injured that causes other fish of the same species to dive for cover or swim closer together. These three features may account for the success of Ostariophysi, particularly in murky lakes and streams where visibility is limited.

The 1,600 species in Cyprinidae (minnows and carps) are the dominant freshwater fishes in Eurasia, Africa, and North America but are absent from South America and Australia. They are mostly small, tapered, silvery fishes, although some, like the Colorado squawfish, can attain lengths of 2 meters (7 feet). Male North American shiners (genus *Notropis*) turn bright red or orange and defend nests. Suckers (Catostomidae), found in North America and Asia, have extendable, fleshy lips specialized for sucking algae and other food from the bottom. The order Characiformes, which includes tetras, piranhas, and pencilfishes, is a diverse group of 1,200 species restricted to South America, southern North America, and Africa. The order Siluriformes (2,000 species) is made up of the catfish, most of which are **nocturnal** and characterized by sensitive barbels on the snout that look like cat whiskers.

Cod, Anglerfishes, Killifishes, and Livebearers

The diverse group Paracanthopterygii includes the abundant and economically important codfishes (Gadiformes, 700 species), elongated fishes with three **dorsal** fins and a chin barbel, which are mostly found in open oceanic waters. Anglerfishes and frogfishes (Lophiiformes) are cryptic, bottom-dwelling fishes. They have a structure that looks like a fishing pole growing out of the head. The top of the "fishing pole" looks like a fish or invertebrate, and the fish uses the pole and "fish" to entice prey. The Atheriniformes include many small, colorful freshwater fishes popular in the aquarium trade. The Atherinidae include the silversides of North American brackish waters and the Australian rainbowfishes. Killifishes (Cyprinodontidae and related families) are often found in very confined **habitats** such as

desert springs. Some species live in tiny puddles in the rain forest and jump from puddle to puddle during rains.

The African and South American species restricted to temporary pools have the shortest life spans of any vertebrate. Eggs can remain dormant in dry mud for most of the year, but the fish hatch and grow rapidly to maturity during the rainy season, sometimes living only three months before ponds dry up again. Livebearers (Poeciliidae and Goodeidae), restricted to the New World, include the mosquitofish, introduced worldwide and a threat to native wildlife, and the colorful guppies and swordtails.

Acanthopterygii

With about 9,000 species, this group of “spiny-rayed fishes” is composed of the dominant fishes of the oceans as well as numerous inhabitants of freshwater. The Gasterosteiformes are mostly long, covered in armored plates, and characterized by males that share parental duties. They include the sticklebacks (Gasterosteidae), whose males build and defend nests, as well as the seahorses and pipefishes (Syngnathidae), whose males carry the eggs and hatchlings in specialized pouches on their belly. The Scorpaeniformes include 1,000 species of mostly bottom-dwelling fishes such as sculpins and rockfish. The group is characterized by very spiny dorsal and anal fins, often associated with venom glands, which in some tropical scorpionfishes can cause death to humans. The 500 species of flatfishes (Pleuronectiformes) such as sole, halibut, and flounders, are uniquely adapted to life on the ocean bottom. When they are larvae they look like most other fish larvae, but as they develop they undergo a **metamorphosis** in which one eye migrates to the other side of the head. As a result, the adult flatfish has a bottom side with no eyes and a top side with two eyes. The top side can sometimes change color to match the background of the ocean bottom. The Tetraodontiformes include the pufferfishes and triggerfishes, which are slow-swimming, heavily armored fishes with “beaks” that they use to feed on coral and invertebrates. Some, like the balloonfish, can inflate rapidly with water when confronted with a predator.

metamorphosis a drastic change from a larva to an adult

The ruling perches, or Perciformes, are 7,000 species characterized by spiny fins and a two-part dorsal fin. They include the North American basses and sunfishes (Centrarchidae) and the family Percidae, which includes the perches of Eurasia and the walleyes and brightly colored darters of North America. Drums (Sciaenidae) are mostly coastal fishes that use low-frequency sounds during courtship. Cichlids (Cichlidae) have greatly diversified throughout the New World and African tropics; the Rift Lakes of Africa contain hundreds of species of cichlids restricted to each lake, many of which are highly specialized to a particular feeding task. For example, some fishes eat only the scales on the left sides of other fishes, while others have mouths specialized for sucking out the eyes of other fishes. Closely related marine fishes include the colorful wrasses (Labridae) and parrotfishes (Scaridae), in which some individuals can change sex from female to male. The cleaner wrasse specializes in removing parasites from other fishes. The colorful damselfishes (Pomacentridae) are unusual among marine fish in that they care for their young; males in some species build and defend nests. The group includes the anemonefish, which have developed an immunity to the sting of the anemone and can live and reproduce within its tentacles. The





more than 800 species of gobies (Gobiidae) are small fishes found in fresh and salt water; their pelvic fins are fused to form a sucking disk. These fishes have colonized habitats such as small crevices among rocks, tide pools, and streams above waterfalls, and some, like the mudskipper, can travel on land. Tuna and mackerel (Scombridae) are “warm-blooded” for efficient muscle activity and rapid swimming.

Other Actinopterygians

filter feeders animals that strain small food particles out of water

The Stenopterygii include the bristlemouths, small, luminescent **filter feeders** that live in the deep oceans and may be the world’s most abundant vertebrate. Lanternfishes (Scopelomorpha) use luminous lures to catch prey. Lizardfishes (Cyclosquamata) are well-camouflaged sit-and-wait predators who live on coral reefs. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Gil G. Rosenthal

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P

fossil record a collection of all known fossils

vertebrate an animal with a backbone

invertebrate an animal without a backbone

Paleontologist

Paleontologists study the history of life on Earth as shown in the **fossil record**. Fossils are the traces of organisms that lived in the past and are preserved in Earth’s crust. Paleontology involves the identification and naming of fossil species and organisms and the determination of the environment in which they lived. Paleontology is considered a subcategory of geology. It is a very broad science that uses biology, geology, chemistry, and physics. There are many subdivisions in the field of paleontology, including:

- **vertebrate** paleontology, the study of fossils of animals with backbones;
- **invertebrate** paleontology, the study of fossils of animals without backbones;
- micropaleontology, the study of fossils of single-celled organisms;
- paleobotany, the study of plant fossils;
- paleoecology, the study of ancient environments;
- biostratigraphy, the study of the fossils in rock layers from different areas to determine their relative ages.

As can be seen by this list, paleontology is more than just the study of dinosaurs. Modern paleontology attempts to understand life-forms as they are related to extended family trees, some of very ancient origins. Thus, paleontologists are frequently involved in studies of evolutionary biology and can be considered systematists, which means that they study the evolutionary relationships among organisms.



A paleontologist cleans the remains of the jawbone of a *Tyrannosaurus rex*.



Most paleontologists work in geology programs of colleges or universities. They do research and teach classes. Smaller numbers of paleontologists work in museums. There, they carry out their own research and sometimes teach and assist with exhibits. A much smaller number of paleontologists work for government geological surveys. Until recently, paleontologists found work with oil companies, helping to search for oil. However, this field has declined as a source of employment for paleontologists.

Research in paleontology generally involves doing fieldwork, analyzing the fossils, and writing up one's findings for publication and presentation. Analysis of fossils begins with carefully measuring and describing them. Next, the fossils are dated by various methods. Then the fossils and the rocks in which they were found are used to learn information about the history of Earth. Finally, the fossils are used to fill in missing information about the fossil record and are related to present-day organisms.

A paleontologist must have a doctoral (Ph.D.) degree. A bachelor's degree can be obtained in either geology or biology. Graduate schools generally require a full year of chemistry, physics, and mathematics (through calculus) at the undergraduate level. It is also important to have strong writing and computer skills. After getting a bachelor's, one can get a master's and then a doctoral degree or, alternatively, enter a doctoral program directly. If an individual has not had much experience with research in college (such as writing a senior thesis), then it might be best to get a master's degree first. It generally takes from two to three years to complete the master's program. A Ph.D. program usually takes from four to six years if the candidate already has a master's, and from six to eight years if he or she does not. The courses most important to paleontology include mineralogy, stratigraphy and sedimentation, sedimentary petrology, invertebrate paleontology, **ecology**, invertebrate and vertebrate zoology, evolutionary biology, and genetics. SEE ALSO PALEONTOLOGY.

Denise Prendergast

ecology study of how organisms interact with their environment

fossil record a collection of all known fossils

vertebrate an animal with a backbone

invertebrate an animal without a backbone

ecosystems self-sustaining collections of organisms and their environments

taxonomy the science of classifying living organisms

phylogenetic relating to the evolutionary history of species or group of related species

extant still living

flora plants

fauna animals

scavengers animals that feed on the remains of animals they did not kill

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Paleontology

Paleontology is the study of the history of life as revealed in the **fossil record**. Fossils are remnants or traces of living organisms from past geologic ages that have become preserved in Earth's crust. They include not only the skeletons or shells of deceased creatures, but also burrows, footprints, eggs, and fossilized feces (excrement), known as coprolites.

Paleontology draws extensively from both biology and geology. Some subdisciplines of paleontology are defined by the types of organisms that are studied. Examples are **vertebrate** paleontology, **invertebrate** paleontology, paleobotany, and micropaleontology (study of single-celled fossils). Paleoecologists study extinct **ecosystems**. Related areas include biostratigraphy, the study of fossil distributions in different strata (rock layers), and taphonomy, which examines the process of fossil formation. Biological disciplines in which contributions of paleontology are particularly critical include systematics and **taxonomy**. They focus on determining **phylogenetic** relationships (the sequence of branching events in evolutionary history which have resulted in the production of divergent species) between extinct as well as **extant** organisms. Another such discipline is comparative anatomy, which examines the morphology (form) and structure of organisms. Still another is evolutionary biology, which examines how biological organisms change over time.

The study of the fossil record also permits the identification of periods of major change in biological diversity. Sudden shifts in **flora** and **fauna** result from major events involving the extinction of organisms, such as the one that eliminated the dinosaurs at the end of the Cretaceous period. In fact, geological eras are bounded by these sudden changes.

Taphonomy examines the processes by which fossils are formed. Any event that occurs between the death of an organism and its fossilization is of interest to taphonomists. The first step to fossilization is burial. Burial can occur in a number of ways; corpses may be buried by sediments in rivers, by sand, or in the bottoms of lakes or oceans. After burial, corpses may be compressed and distorted by the surrounding sediment. There is also a lengthy period of remineralization following burial. During this time, bone is replaced by minerals carried through the rock by water. Remineralization does not necessarily obscure fine detail because the replacement occurs on a minute scale.

During the process of fossilization, much information about the biology of organisms is lost. Damage to the corpse, either by **scavengers** or from weather or erosion, may occur prior to burial, and distortion from a

number of sources can occur afterwards. Soft parts of organisms are fossilized much less frequently than hard parts, and information on color, **physiology**, or behavior is particularly likely to be lost. It is because of the incompleteness of most fossils that paleontologists have developed a well-deserved reputation for inferring (deducing) huge amounts of information on the biology of organisms from fragmentary, or partial, remains.

The proper dating of fossil material is often critical to paleontological studies. Relative dating considers the relative placement of different rock strata; younger rock layers are formed on top of older layers. Also, similar sequences of strata that are found in different locations are likely to date from the same period. Absolute dates for fossil material are usually estimated using radioisotopes. This method makes use of the fact that radioactive atoms decay into more stable atoms at a known rate. **SEE ALSO** FOSSIL RECORD; GEOLOGICAL TIME SCALE; PALEONTOLOGIST.

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Parasitism

Parasitism describes a relationship between two species, a parasite and its host, in which the parasite benefits, while the host is harmed. Parasitism is one form of **symbiosis**, which more generally describes any situation involving a close relationship between organisms of different species.

Parasites are different from predators and parasitoids (which also derive benefits from certain interspecific interactions while harming the other participant) in that the host of a parasite is not necessarily killed. Instead, parasites derive benefits from their hosts, most often nutritional resources and shelter, over a longer period of time. It is in fact advantageous to parasites if they do not harm their hosts too badly, because that prolongs the period during which parasites can obtain benefits from hosts. However, in some cases, the impact of parasites on a host is great enough to cause disease, and in extreme cases, the death of the host may also occur.

physiology study of the normal function of living things or their parts

symbiosis any prolonged association or living together of two or more organisms of different species

Parasitism is a common survival strategy among biological organisms, and many species are characterized by parasitic lifestyles for all or part of their lives. All the major kingdoms of life include some parasitic species. In addition, there are very few biological species that are free of parasites altogether.

Categories of Parasites

Parasites may be grouped by any of several traits. **Ectoparasites** live outside the body of the host, usually on the body surface. Well-known ectoparasites include fleas, ticks, and leeches. **Endoparasites** live within the host's body. Endoparasites can further be divided into those that live within

ectoparasites organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

endoparasites organisms that live inside other organisms and derive their nutrients directly from those organisms





obligatory parasites animals that can exist only as parasites

facultative parasites organisms that can survive either as parasites or free-living

microparasites very small parasites

macroparasites parasites that are large in size

vertebrates animals with a backbone

monoxenous a life cycle in which only a single host is used

progeny offspring

heteroxenous a life cycle in which more than one host individual is parasitized

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

host cells (bacteria and viruses), and those that live in spaces in the host's body (all other, generally larger, endoparasites).

Parasites may also be grouped depending on whether they are **obligatory parasites**, which must have a host in order to survive, or **facultative parasites**, species for which a parasitic lifestyle is optional. Facultative parasites adopt parasitic lifestyles if the opportunity arises, but they are also able to live free of a host organism.

Parasites are also grouped based on their size. **Microparasites** include viruses, bacteria, and fungi. These reproduce within the host and are characterized by comparatively small size and short life cycles. Microparasites also induce an immune response in the host, so that the ability to exploit a certain individual may be temporary. **Macroparasites**, on the other hand, typically describe larger parasites such as insects, worms, or **vertebrates**. They are larger in size (usually visible to the eye) and do not reproduce in the body of the host. Instead they release offspring which then find and infect new hosts.

Parasites may derive any of a number of benefits from their interactions with host species. Some obtain only nutrients, while others also gain shelter and a site for reproduction. They also vary in the closeness of their relationship to their host. Mosquitoes, for example, visit vertebrate hosts only to feed. Certain mites, on the other hand, remain intimately associated with their hosts throughout their lives.

Parasitic Life Cycles

Life cycles of parasites may be simple or complex. Parasites that are characterized by a simple or direct life cycle have only one host and are described as **monoxenous**. The parasite generally spends most of its life in or on the host, and may reproduce within the host. Because offspring must be transmitted to other hosts, however, the parasite or its **progeny** must have some way of leaving the host, surviving in the external environment for some period, and locating and infecting a new host. Parasites with simple life cycles have both parasitic and free-living life stages. The proportion of the total life cycle spent in each stage varies according to the parasite.

Parasites with more complex life cycles involving multiple hosts are described as having indirect or **heteroxenous** life cycles. The primary host of a heteroxenous species is the one in which adult parasites live and reproduce. The secondary or intermediate host is used by immature life stages of the parasite and is also essential. In many cases, the parasite passes through critical developmental stages in the intermediate host. The intermediate host may also aid in transmitting parasites to their final host. Fleas, for example, are sometimes intermediate hosts for mammalian parasites such as tapeworms.

A well-studied parasite with a complex life cycle is the liver fluke. Parasitic flukes reach adulthood in the bile duct of a primary host species such as a sheep or a cow. Flukes can cause extensive damage to the liver. During reproduction, eggs are released by flukes into the host's digestive system, ultimately passing out of the host in fecal material. Once the eggs hatch, immature juveniles infect a snail as an intermediate host. In the intermediate host, development and **asexual reproduction** occurs. At a further de-



velopmental stage, the parasite leaves the intermediate host and encysts on local vegetation. When the parasites are ingested, along with the vegetation, by a sheep or cow, they enter the intestine and then migrate to the liver and bile duct, ready to begin a new generation.

Some parasites are transmitted directly from one host to another by species, often insects, described as vectors. One particularly effective vector for vertebrate parasites is the mosquito, which plays a role in the transmission of numerous parasites including heartworm, the viruses that cause yellow fever and encephalitis, and *Plasmodium*, the **protozoan** that causes malaria.

Examples of Parasites

Species in countless taxonomic groups have parasitic lifestyles. The protozoans include several well-known parasite groups, such as amoebas and the organisms responsible for malaria. Malaria is a serious disease that occurs in large portions of the world, particularly in tropical areas. The malaria protozoan has a complex life cycle that involves **asexual reproduction** in humans and other vertebrate species, and **sexual reproduction** in mosquitoes. Mosquitoes also act as vectors for malaria, transmitting the parasites from one vertebrate host to another.

There are several groups of parasitic worms. The flat, ribbonlike parasitic worms of the class Cestoda are known as tapeworms. Tapeworms reside in the small intestines of their hosts, where they live in a constant bath of well-processed nutrients. For this reason, tapeworms do not need and have lost several **physiological** systems such as the circulatory and digestive systems. Food **absorption** occurs directly across the entire body surface of tapeworms.

Nematodes, or roundworms, include many important parasitic species. Well-known nematode parasites include pinworm, the large human roundworm, hookworm, and heartworm, which affects dogs and cats. In addition, parasitic nematodes cause diseases such as river blindness and elephantiasis, which results in blocked lymph flow and causes swellings in the body. *Trichinella spiralis*, which causes the disease trichonosis following the ingestion of uncooked, infected pork, is also a nematode worm.

A third group of parasitic worms are the trematodes, or flukes. Aside from the liver flukes mentioned above, trematode species are responsible for schistosomiasis and other significant diseases in humans.

There are also vertebrate parasites. One example is the lamprey, a primitive fish species that feeds by attaching to other fishes with a circular tooth-filled mouth and sucks blood and other bodily fluids. Lampreys are often ultimately fatal to their hosts.

Many plant species are parasitic. The most famous of these is probably mistletoe, which infests various species of trees. Its “roots” tap into the tree’s phloem network in order to intercept resources. Mistletoe is spread by birds, which transport the sticky white seed-berries from tree to tree.

Brood Parasitism

One special form of parasitism is brood parasitism. Brood parasites are species, most commonly birds, that lay their eggs in nests of another species.

protozoan a member of the phylum of single-celled organisms

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

sexual reproduction reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

physiological the basic activities that occur in the cells and tissues of an animal

absorption the movement of water and nutrients



The host species devotes the considerable energy required to brood eggs till hatching and to feed the chicks.

Brood parasites include species such as wydahs, cuckoos, and the brown cowbird of North America. Often, brood parasites increase their chance of success by laying eggs that resemble those of the host. Some brood parasites raise their own nest in addition to leaving eggs in the nests of other individuals, while others are exclusively parasitic. Some brood parasites are very specific about the hosts they exploit, while others use a wide variety of hosts. The brown cowbird, for example, is known to leave eggs in the nests of more than 200 different songbird species. Brood parasites will sometimes eject an egg from the host nest as they deposit their own egg. In addition, newly hatched brood parasite nestlings may eject eggs or step-siblings as well.

Parasitic nestlings elicit automated feeding behaviors from their adoptive parents by calling and opening their beaks wide. Classic photos of brood parasitism often show smallish parents feeding chicks that are significantly larger than they are. In some instances of brood parasitism, the energy devoted to raising a parasite prevents parents from raising chicks of their own. In others, brood parasites manage to coexist with the host offspring.

Certain potential host species can detect the addition of a foreign egg by a brood parasite and will abandon the nest and begin again elsewhere. In some cases, seeing adult brood parasites near their nest is enough to trigger abandonment.

Social Parasitism

Social parasitism is a special form of parasitism unique to certain social insects, particularly ants. Socially parasitic ants derive some or all of their resources from other ant species. In some cases, this involves no more than the stealing of food resources from other ant colonies, either of the same species or of a different species. However, in more extreme cases, socially parasitic ant species do not build their own nests or raise their own offspring. Instead, their strategies involve killing the queen of another colony and then making use of the workers, or stealing and enslaving workers from other colonies. In the most extreme case, the socially parasitic species actually lives within the nest of a host species, using host workers to raise young and obtain resources.

The Importance of Parasitism in the Evolution of Species

Parasitism is hypothesized to affect the evolution of many biological species. For example, parasitism may play a role in group size—larger groups of conspecific organisms are known to be more vulnerable to infestation by parasites. The naked mole rat, a highly social rodent species in which individuals live in large colonies, is probably “naked” (that is, practically hairless) because hairlessness reduces opportunities for parasite invasion. On the other hand, parasitism may promote the evolution of sociality by encouraging such social behaviors as reciprocal grooming or cleaning. This occurs in numerous mammalian species, including many primates, where individuals can be seen picking lice and other parasites from each other’s fur.



Cuckoo birds are brood parasites. These birds leave their eggs to be raised by other bird species, thereby avoiding the high energy expenditure required to monitor eggs and feed chicks.

The evolution of parasites and their hosts is also one of the best examples of **coevolution**, a situation in which there are two species, each of whose evolution depends upon and responds to the evolution of the other. Other pairs of species that may coevolve are predators and their prey, and flowering plants and their insect pollinators.

Coevolution between parasites and their hosts is antagonistic, and is sometimes described as an “evolutionary arms race,” because each species attempts to evolve in such a way as to foil the other. That is, hosts are constantly evolving to avoid parasites, while parasites are evolving so that they can continue to exploit their hosts.

Another situation in which parasitism is hypothesized to play an important role is in the mating behaviors of species. One theory of **sexual selection**, called the handicap hypothesis, depends on parasitism as the critical evolutionary factor. The handicap hypothesis attempts to explain the evolution of brightly colored males, or males with elaborate ornamentation, in many species of animals. The peacock is a classic example of this—think of the gaudy coloration and elaborate tail of male peacocks.

Why do males evolve these traits, which make them highly visible and hence vulnerable to predators? The explanation seems to be that colorful or ornamented males are preferred as mates by females, so that male reproduction depends on the evolution of these traits. Why do females prefer colorful males? The handicap hypothesis argues that only very healthy males would be able to develop and maintain bright colors or ornaments. It is believed that parasites would make males sickly, and prevent them from devoting the resources necessary to maintain their bright plumage.

Consequently, by mating with males who are brightly colored and in generally good shape, females are more likely to end up with mates that carry fewer parasites. These males may also be relatively parasite-free because they

coevolution a situation in which two or more species evolve in response to each other

sexual selection
selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes



have “good genes,” which might then be passed on to the female’s offspring.
SEE ALSO INTERSPECIES INTERACTIONS.

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Passive Transport *Transport*.



Louis Pasteur is known as the “father of bacteriology.”

Pasteur, Louis

French Chemist and Microbiologist
1822–1895

Louis Pasteur, the father of modern bacteriology, was born on December 27, 1822, in Dôle in eastern France. Pasteur proved that microorganisms cause fermentation and disease; he also originated the process known as pasteurization. Pasteur created vaccinations for rabies, anthrax, and chicken cholera. He is also credited with saving the beer, wine, and silk industries in France during his time.

Pasteur, the son of a tanner, attended primary and secondary schools in Arbois and Besançon. As a boy he showed more interest in art than science. Pasteur attended the Royal College in Besançon, earning his bachelor of arts degree in 1840 and bachelor of science degree in 1842. The following year, he attended the École Normale Supérieure in Paris, earning his master of science degree in 1845, and his doctor of philosophy degree in 1847. By the age of twenty-six, Pasteur was famous for his work on the structure of crystals. In 1848 he received an appointment as professor of physics at the Dijon Lycée. Shortly thereafter, he became a professor of chemistry at the University of Strasbourg. This was the start of a distinguished career at various French universities. He married Marie Laurent, with whom he had five children. (Only two survived childhood.)

In 1854 Pasteur began his studies on fermentation, the chemical breakdown of substances by microbes. His work brought important improvements in brewing and winemaking. By the 1860s he had originated the process of

pasteurization, applying controlled heat to kill disease-causing microbes in wine, beer, vinegar, and milk. This made it possible to produce, preserve, and transport these goods without their becoming ruined. Pasteur studied the mysteries of bacteriology and was the first to show that living things come only from living things. Before that, many scientists had believed in spontaneous generation, a theory that life could come from things that are not alive.

In 1865 Pasteur began studying a disease of silkworms that was devastating the silk industry. He isolated the germ that caused the disease and found methods of preventing contagion and detecting diseased stock, thus saving the silk industry. In the 1880s Pasteur began to realize that disease was spread by microorganisms (microscopic-sized organisms). His germ theory of disease was one of the greatest scientific discoveries of the nineteenth century. He went on to develop vaccinations for preventing the disease anthrax in sheep, chicken cholera in fowl, and rabies in humans. Pasteur was admired by his countrymen and honored by the French Parliament in many ways. He died on September 28, 1895.

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PCR

PCR (**polymerase** chain reaction) is a method used by scientists to increase the amount of purified DNA in a sample. It is a highly specific procedure that amplifies one particular gene from within a large sample of undesirable DNA, DNA that the scientist does not wish to replicate. Before PCR, it was very difficult and time consuming to obtain particular fragments of DNA from a sample, and practically impossible to amplify, produce many copies of, that fragment. With PCR, scientists can copy a specific stretch of DNA billions of times in a few hours.

PCR was invented in 1983 by American biochemist Kary B. Mullis, who received the 1993 Nobel Prize for chemistry (with Canadian biochemist Michael Smith) in recognition of this inestimable contribution to science. Mullis invented PCR while working for the Cetus Corporation, a biotechnology firm located in California. His discovery proved so essential to biological research that when Cetus closed down in 1991, the pharmaceutical company Hoffman-La Roche purchased the PCR patent for \$300 million.

polymerase an enzyme that links together nucleotides to form nucleic acid

DNA Replication

Under most natural conditions, DNA exists in the form of two entwined single strands, and each strand is formed of smaller molecules called **nucleotides**. The word “polymerase” in the name polymerase chain reaction comes from the term “polymer,” which refers to any large molecule composed of many smaller molecules. Thus DNA is a **polymer** of nucleotides. A polymerase is an enzyme that pieces together polymers from the smaller

nucleotides building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

polymer a compound made up of many identical smaller compounds linked together





nucleotide the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

genes segments of DNA located on chromosomes that direct protein production

codons the genetic codes for an amino acid that are represented by three nitrogen bases

enzymes proteins that act as catalysts to start biochemical reactions

primers short preexisting polynucleotide chains to which new deoxyribonucleotides can be added by DNA polymerase

denaturing breaking down into small parts

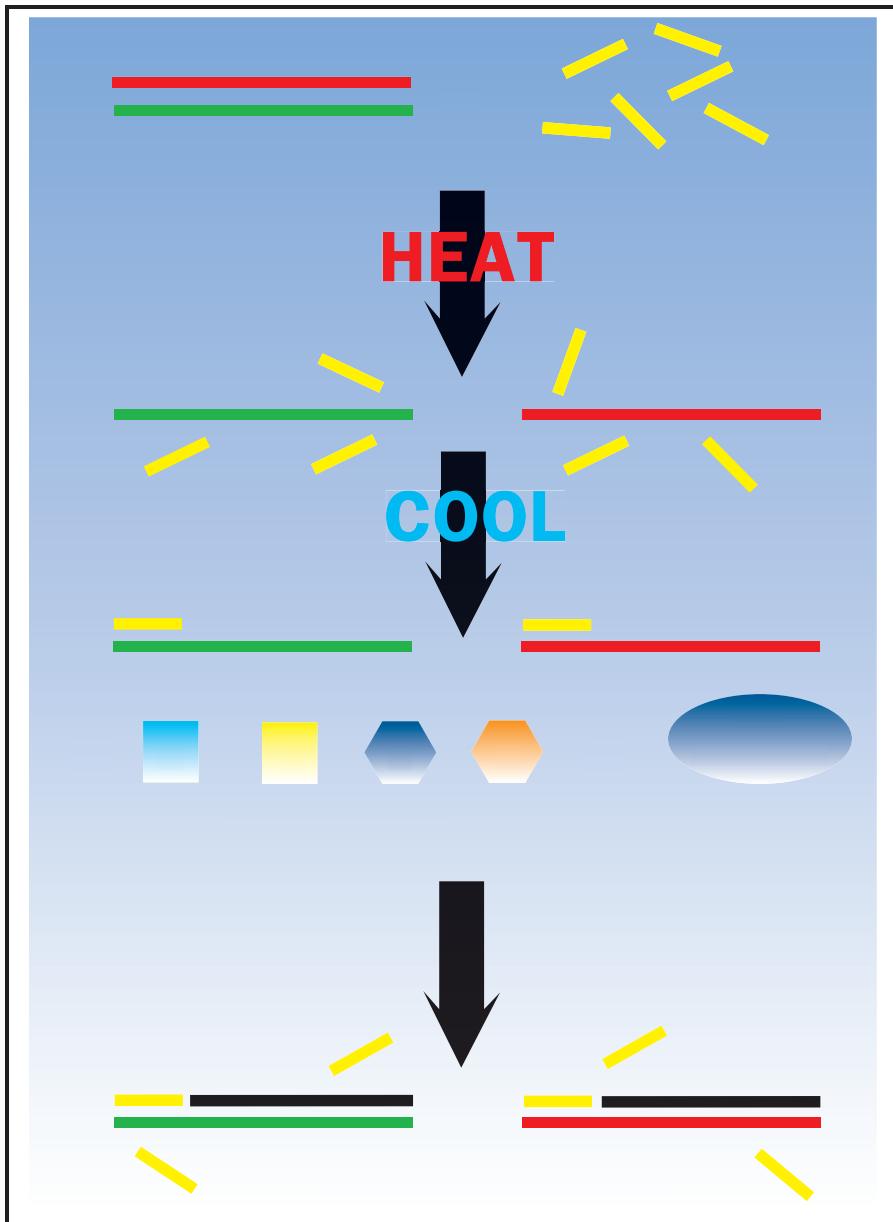
molecules. The strands of DNA must be separated before they can be copied, because the important information is contained along the center of the molecule, where the two strands are attached. Cells naturally synthesize new DNA in their nucleus through a process known as replication. During replication, the two parent strands unwind and separate and a new single daughter strand is built upon each of the existing parent strands. The two identical molecules of DNA that result from replication each contain one parent and one daughter strand. This is called semiconservative replication.

Scientists can find a particular gene (a sequence of nucleotides that encodes a unique protein) within a large sample of DNA by looking for the **nucleotide** sequences specific to that gene. The four basic nucleotides are adenine (A), guanine (G), thymine (T), and cytosine (C). An A on one strand always binds to a T on the other, and a G on one strand always binds to a C on the other. This makes it easy to determine the sequence of one strand of DNA when the sequence of the other strand is known. The beginnings and ends of all **genes** are defined by short sequences of three nucleotides called **codons**. The beginnings are marked by a “start” codon, and the ends by a “stop” codon. Special **enzymes** in the cell recognize the codons. These enzymes always begin at the start codon and end at the stop codon. Scientists can identify a particular gene by looking at the nucleotide sequence, and locate the place on the DNA where that gene begins by finding the start codon.

PCR Method

Almost any gene encoding almost any protein can be amplified using PCR. To replicate DNA in a laboratory environment, certain natural conditions must be reproduced. The necessary components are simple—the DNA to be replicated, DNA polymerase, **primers** complementary to both strands of DNA for that gene, and a mixture of the four nucleotides. DNA polymerase “reads” the nucleotide sequence and adds the correct nucleotides to the parent strand, thereby forming a complementary daughter strand. DNA polymerase can only build off a template, and it can add nucleotides only one by one, in one direction. DNA polymerase cannot begin without a primer, a short nucleotide sequence attached at one end of the DNA. For PCR, the primers must be present in very large quantities to increase the likelihood of replication. In a cell, a special enzyme builds primers for DNA, but the process is not specific for any one gene. By using synthetic primers that are complementary to the gene they want to replicate, scientists can replicate only that gene and not the remaining DNA.

PCR can be conducted with as little as one fragment of DNA in solution. By applying a high heat to the DNA solution, the bonds between the parent strands are broken, and the strands float apart. This process is called **denaturing** the DNA. In the first cycle of PCR amplification, the DNA is denatured, and the primers are added to the solution. The temperature is then lowered so that the primers can bind to the denatured strands. If the temperature is not lowered, the primers will not be able to function. After this, the temperature is raised slightly so that DNA polymerase can bind to the primer. Once it binds, the polymerase pulls nucleotides from the solution and adds them to the template parent strand to form a daughter strand. The polymerase drops away from the newly synthesized DNA at the stop



Polymerase chain reaction. A mixture of DNA and primers is heated until the DNA denatures. After this, primers are added and the solution is allowed to cool. As the solution cools, the primers bind to the correct gene within the DNA. Nucleotides are added to the solution along with DNA polymerase. DNA polymerase adds nucleotides to the primer to form the daughter strands. Finally, the new strands of DNA are formed and the procedure may be repeated to create more DNA.

codon. This procedure creates two new molecules of DNA, which contain only the gene the scientist wants to replicate.

The first cycle of PCR generates twice the number of DNA molecules for the gene than there were in the original solution. Additional cycles are needed to greatly increase this number. The second cycle is very similar to the first—the DNA in solution is denatured in the presence of primers, which bind to the parent strands as they cool; polymerase builds the daughter strand with nucleotides from the solution; and the reaction completes itself. The result of this second cycle is that there are now four DNA molecules encoding the gene for every one original DNA molecule used. The cycles are repeated until the desired amount of DNA is attained. Scientists calculate the number of DNA molecules resulting from PCR amplification by employing the formula a^*2^n , where a is the number of original molecules





of DNA, and n is the number of cycles of PCR. When enough DNA is made, the scientist stops the reaction.

The DNA polymerase used for PCR must be able to function at a very high temperature, because a high temperature is needed to keep the parent strands apart so the daughter strands can be built upon them. Most DNA polymerases in nature cannot function at high temperatures, so PCR uses a polymerase found in certain archaeabacteria that live in hot springs, where the water temperatures are often well above 90°C (194°F). The most commonly used polymerase is called *Taq* polymerase, because it was originally isolated from the archaeabacterium *Thermus aquaticus*.

Applications of PCR

PCR is very useful for creating a large quantity of DNA from a very small initial sample. Applications of PCR can be used to identify a particular individual or even to map out the evolutionary history of a species. These applications are based on the concept that some DNA is unique to a particular individual, some genes are unique to a particular species, and certain genes are shared by all organisms. The unique DNA makes it possible to determine the exact individual from which a strand of DNA came, which is why PCR is used by forensic scientists to test skin cells and hair follicles found at crime scenes. Assuming that the DNA belongs to the person who carried out the crime, that person can be identified from among a group of suspects. PCR is used by archaeologists to determine the identity of ancient human remains and unidentifiable mummies, and by paleontologists to examine how the **genome** of an organism has changed over the course of evolution. PCR can also be used to test the relatedness of different species when body characteristics alone do not provide enough evidence. For example, PCR analysis revealed that red panda bears are more closely related to raccoons than to greater panda bears, a distinction that had previously been impossible to determine.

Other applications of PCR take advantage of its ability to accumulate large amounts of DNA to conduct statistically significant research experiments. The technique is often used in medical research, for example to amplify the DNA of a virus, such as HIV, to understand how it infects humans, or to replicate the DNA of a **hormone**, such as insulin, to understand how it functions. The biomedical industry relies on PCR for identifying viral and bacterial infections, especially for detecting infections like AIDS and leprosy in their early stages. PCR can also be used to detect hereditary medical conditions in babies or adults who do not yet show signs of impairment. The large quantities of DNA formed through PCR can be introduced into the genome of another organism to create a **transgenic organism**. Transgenic animals are important for creating animal models of human disease. For example, hereditary diseases such as Alzheimer's that do not normally occur in mice can be introduced into the mouse genome. When the mouse begins to show symptoms of the disease, scientists can administer different treatments to find out which is the most effective.

Transgenic plants can also be used instead of the application of toxic **pesticides**; the goal is to create a plant that can defend itself against insects by producing its own insecticides that are not harmful to humans. Then

genome an organism's genetic material

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

transgenic organism an organism that contains genes from another species

pesticides substances that control the spread of harmful or destructive organisms

fewer chemical pesticides would be needed, reducing the contamination of drinking water and harm to humans exposed to the chemicals.

Mark R. Hughes, deputy director of the National Center for Human Genome Research at the National Institutes of Health, the American base for the **Human Genome Project**, called PCR “the most important new scientific technology to come along in the last hundred years.” (Powledge 1998). Its principle limitation is that the primer sequence must be known so that primers can be synthesized prior to the first cycle of PCR. Furthermore, PCR is less accurate when used to replicate large gene sequences (greater than approximately 5,000 nucleotides long), which means that it is difficult to study complex proteins. Additionally, the procedure is expensive and currently too technically demanding to be carried out by nonprofessionals. These drawbacks are being addressed by developments that would fully automate PCR, or provide simpler and less expensive kits. These kits could be used, for example, by people who suspect they are developing cancer. Indeed, PCR is expanding beyond the world of research and will be increasingly available to people for direct independent analyses. **SEE ALSO GENES; GENETIC ENGINEERING; GENETICS.**

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Peppered Moth

The peppered moth (*Biston betularia*) is an inconspicuous member of the family Geometridae, a night-flying species thought to spend its days resting camouflaged among the lichens that grow on tree trunks. The moth's predominant form has white wings, “peppered” with black specks or faint black lines, perfect for blending in with its tree bark environment. Less common is a variant, *carbonaria*, which is a black-winged moth, with increased levels of melanin (black pigment) causing the color change. The peppered moth has come to play a significant role in two important stories in science.

In 1859 British **naturalist** Charles Darwin proposed a theory of evolution in his book *On the Origin of Species*. He based his theory on three observations he made while collecting data on plants and animals during a five-year trip around the world in the survey ship *Beagle*: that living things vary, that they can pass on their characteristics, and that they are involved in a struggle for survival which favors genetic **mutations** that are better adapted to their environment.

The **fossil record** is tantalizingly full of what appear to be gradual changes from one mineralized skeleton to the next, charting the evolution

naturalist a scientist who study nature and the relationships among the organisms

mutations abrupt changes in the genes of an organism

fossil record a collection of all known fossils



Two variations of peppered moths. The camouflage achieved by the darker moth on the darker background will act to protect the moth from predators.

natural selection the process by which organisms best suited to their environment are most likely to survive and reproduce

of species. The only problem with Darwin's theory was that there was no evidence of **natural selection** in action. Then, in the mid-1800s a phenomenon occurred that seemed to indisputably prove natural selection. A small moth commonly called the peppered moth, common to British woodlands, underwent dramatic color changes with the advent of pollution-darkened skies. As the industrial revolution proceeded across Britain, covering towns and countryside with soot, blackening tree trunks, and killing the lichens, the melanic, or black, variety of the moth increased in number and the original peppered variety all but disappeared. Photographs of the two types of moths on sooty and clean tree bark were dramatic evidence of the power of camouflage, and experiments clearly showed birds predating the uncamouflaged moths when given a choice. Industrial melanism was the name given to this example of evolutionary adaptation to smoky air.

In the 1950s, Oxford University biologist H. B. D. Kettlewell bred peppered moths in a lab and released close to a thousand of them in polluted and nonpolluted woods. When the moths were recaptured several nights later, there was a clear correlation of more black moths in the dark woods

and more white ones in the clean. Kettlewell further released hundreds of moths onto the bark of dark and light trees at dawn and photographed birds eating the more conspicuous species. He concluded, “The effects of natural selection on industrial melanism for crypsis (camouflage) in such areas can no longer be disputed. Birds act as selective agents as postulated by evolutionary theory. Had Darwin observed industrial melanism he would have seen evolution occurring not within thousands of years but in thousands of days.” (Holdrege 1999, p. 66) By the 1970s, following the passage of legislation that resulted in cleaner air, the **population** of dark moths decreased and light ones made a dramatic comeback. This seemed to provide proof of natural selection.

Also during the 1970s, some surprising evidence was introduced by British biologist Cyril Clarke that called into question some of the previous research involving the peppered moth. In twenty-five years of studying the peppered moth, Clarke found only two in daylight. The moth is notoriously difficult to locate and in fact no one knows where it lives by day, but it is certainly not on the lower trunks of trees. The peppered moth is **nocturnal** and its chief predators are bats. All of the peppered moths experimented with had been collected in traps at night and many of the ones eaten from tree trunks had been glued to the trees where they were found by opportunistic birds. The ones not glued had been released in early morning when they typically would fall asleep on the bark. Further confounding the earlier research was the discovery that an increase in the original peppered variety around both Liverpool and Detroit, Michigan, occurred despite no increase in the dark lichens assumed to be their hiding place.

The history of the peppered moth research is a reminder of how strongly people see what they look for. Kettlewell’s field experiments showed that birds feed on moths released onto tree trunks preferentially by degree of camouflage. Since the moths are not normally found on lower tree trunks during the day, this experiment created, as all experiments do, an artificial situation and then appeared to prove a hypothesis. Some evolutionary scientists such as Stephen Jay Gould are highly critical of the unwillingness of researchers to consider alternative concepts. If Kettlewell had not been so convinced of the truth of bird predation, he might have been more willing to question his results. When scientists have an uncritical acceptance of a certain theory there is a real danger of seeing what one believes and turning science into dogma. Dogmatic knowledge, teaching what is only an opinion as absolute fact, is the antithesis of science’s basic tenet of observation and questioning.

Biologist Craig Holdrege believes that instead of using experiments as a way of proving or disproving an idea, scientists could come to see them as a way of interacting with phenomena. To keep science alive, scientists need to remember to be aware of their own preconceptions and be wary of drawing general conclusions from a specific and contrived event. Experiments help scientists clarify ideas and formulate new questions. As such, they become more of a jumping-off point than an end. The peppered moth story points to the need for much greater basic natural history observation, difficult as that is. Where does the moth rest by day? How far does it fly? What do the larvae eat and could the melanism be an effect of a change in the larvae’s diet?

population a group of individuals of one species that live in the same geographic area

nocturnal active at night





The peppered moth is a reminder that science is an evolving process. Vitality comes from doubting conventional dogma, making new observations, and thinking with originality. Science is an ongoing exploration and renewal of ideas. Just as Darwin's hypotheses added to the richness of scientific thinking, so the peppered moth story is an excellent teacher of the evolution of the scientific process. **SEE ALSO CAMOUFLAGE; GENETIC VARIATION IN A POPULATION; SELECTIVE BREEDING.**

Nancy Weaver

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Glossary

abiogenic: pertaining to a nonliving origin

abiotic: nonliving parts of the environment

abiotic factors: pertaining to nonliving environmental factors such as temperature, water, and nutrients

absorption: the movement of water and nutrients

acid rain: acidic precipitation in the form of rain

acidic: having the properties of an acid

acoelomate: an animal without a body cavity

acoelomates: animals without a body cavity

acoustics: a science that deals with the production, control, transmission, reception, and effects of sound

actin: a protein in muscle cells that works with myosin in muscle contractions

action potential: a rapid change in the electric charge of the cell membrane

active transport: a process requiring energy where materials are moved from an area of lower to an area of higher concentration

adaptive radiation: a type of divergent evolution where an ancestral species can evolve into an array of species that are specialized to fit different niches

adenosine triphosphate: an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

aestivate: a state of lowered metabolism and activity that permits survival during hot and dry conditions

agnostic behavior: a type of behavior involving a contest of some kind that determines which competitor gains access to some resource such as food or mates

alkaline: having the properties of a base

allele: one of two or more alternate forms of a gene

alleles: two or more alternate forms of a gene



allometry: relative growth of one part of an organism with reference to another part

allopatry: populations separated by a barrier

alluvial: sediments from flowing water such as silt, sand, mud, and gravel

alpha: the dominant member of a group

altruistic behavior: the aiding of another individual at one's own risk or expense

alveoli: thin-walled sacs in the lungs where blood in capillaries and air in the lungs exchange gases

ameloblasts: cells that form dental enamel

amioite: embryo of a vertebrate that is surrounded by a fluid-filled sac

ammonites: an extinct group of cephalopods with a curled shell

amnion: the membrane that forms a sac around an embryo

amniote: a vertebrate which has a fluid-filled sac that surrounds the embryo

amniotes: vertebrates which have a fluid-filled sac that surrounds the embryo

anadromous: moving from the ocean up a river to spawn

analogous: a similarity in structures between two species that are not closely related

anemia: a condition that results from a decreased number of red blood cells

angiosperms: a flowering plant that produces seeds within an ovary

annelids: segmented worms

anoxic: an environment that lacks oxygen

anterior: referring to the head end of an organism

anterior pituitary: the front part of the pituitary gland that produces hormones that stimulate the production of sperm and testosterone in the testes

antibodies: proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

antigen: foreign substances that stimulate the production of antibodies in the blood

anurans: the order of amphibians that contains frogs and toads

aphrodisiac: a substance or object that is thought to arouse sexual desire

aphrodisiacs: substances or objects that are thought to arouse sexual desire

aposematic: a feature or signal that serves to warn

aposematic coloration: a bright coloration in animals with physical or chemical defenses that act as a warning to predators



appendicular: having to do with arms and legs

appendicular skeleton: part of the skeleton with the arms and legs

aquatic: living in water

aragonite: a mineral form of calcium carbonate

arboreal: living in trees

Archae: an ancient lineage of prokaryotes that live in extreme environments

arthropod: a phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

arthropods: members of the phylum of invertebrates characterized by segmented bodies and jointed appendages such as antennae and legs

artificial pollination: manual pollination methods

asexual reproduction: a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

asymmetrical: lacking symmetry, having an irregular shape

aural: related to hearing

autonomic nervous system: division of the nervous system that carries nerve impulses to muscles and glands

autotroph: an organism that makes its own food

autotrophs: organisms that make their own food

axial skeleton: the skeleton that makes up the head and trunk

axon: cytoplasmic extension of a neuron that transmits impulses away from the cell body

axons: cytoplasmic extensions of a neuron that transmit impulses away from the cell body

B-lymphocytes: specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

bacterium: a member of a large group of single-celled prokaryotes

baleen: fringed filter plates that hang from the roof of a whale's mouth

Batesian mimicry: a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

behavioral: relating to actions or a series of actions as a response to stimuli

benthic: living at the bottom of a water environment

bilateral symmetry: characteristic of an animal that can be separated into two identical mirror image halves

bilaterally symmetrical: describes an animal that can be separated into two identical mirror image halves

bilateria: animals with bilateral symmetry

bilipid membrane: a cell membrane that is made up of two layers of lipid or fat molecules

bio-accumulation: the build up of toxic chemicals in an organism

bioactive protein: a protein that takes part in a biological process

bioactive proteins: proteins that take part in biological processes

biodiversity: the variety of organisms found in an ecosystem

biogeography: the study of the distribution of animals over an area

biological control: the introduction of natural enemies such as parasites, predators, or pathogens as a method of controlling pests instead of using chemicals

biological controls: introduction of natural enemies such as parasites, predators, or pathogens as a method of controlling pests instead of using chemicals

biomagnification: increasing levels of toxic chemicals through each trophic level of a food chain

biomass: the dry weight of organic matter comprising a group of organisms in a particular habitat

biome: a major type of ecological community

biometry: the biological application of statistics to biology

biotic: pertaining to living organisms in an environment

biotic factors: biological or living aspects of an environment

bipedal: walking on two legs

bipedalism: describes the ability to walk on two legs

birthrate: a ratio of the number of births in an area in a year to the total population of the area

birthrates: ratios of the numbers of births in an area in a year to the total population of the area

bivalve mollusk: a mollusk with two shells such as a clam

bivalve mollusks: mollusks with two shells such as clams

bivalves: mollusks that have two shells

body plan: the overall organization of an animal's body

bone tissue: dense, hardened cells that makes up bones

botany: the scientific study of plants

bovid: a member of the family bovidae which is hoofed and horned ruminants such as cattle, sheep, goats and buffaloes

bovids: members of the family bovidae which are hoofed and horned ruminants such as cattle, sheep, goats and buffaloes



brachiopods: a phylum of marine bivalve mollusks

brackish: a mix of salt water and fresh water

brood parasites: birds who lay their eggs in another bird's nest so that the young will be raised by the other bird

buccal: mouth

budding: a type of asexual reproduction where the offspring grow off the parent

buoyancy: the tendency of a body to float when submerged in a liquid

Burgess Shale: a 550 million year old geological formation found in Canada that is known for well preserved fossils

calcified: made hard through the deposition of calcium salts

calcite: a mineral form of calcium carbonate

calcium: a soft, silvery white metal with a chemical symbol of Ca

capture-recapture method: a method of estimating populations by capturing a number of individuals, marking them, and then seeing what percentage of newly captured individuals are captured again

cardiac: relating to the heart

cardiac muscle: type of muscle found in the heart

cardiopulmonary: of or relating to the heart and lungs

carnivorous: describes animals that eat other animals

carrying capacity: the maximum population that can be supported by the resources

cartilage: a flexible connective tissue

cartilaginous: made of cartilage

catadromous: living in freshwater but moving to saltwater to spawn

character displacement: a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

chelicerae: the biting appendages of arachnids

chemoreceptors: a receptor that responds to a specific type of chemical molecule

chemosynthesis: obtaining energy and making food from inorganic molecules

chemosynthetic autotrophs: an organism that uses carbon dioxide as a carbon source but obtains energy by oxidizing inorganic substances

chemotrophs: animals that make energy and produce food by breaking down inorganic molecules

chitin: a complex carbohydrate found in the exoskeleton of some animals

chitinous: made of a complex carbohydrate called chitin

chloroquine: a drug commonly used to treat malaria

chromosomes: structures in the cell that carry genetic information

cilia: hair-like projections used for moving

circadian rhythm: daily, 24-hour cycle of behavior in response to internal biological cues

clades: a branching diagram that shows evolutionary relationships of organisms

Class Branchiopoda: a group of marine bivalve mollusks

Class Malacostraca: crustaceans such as lobsters, crabs, and shrimp

Class Maxillopoda: crustaceans such as barnacles, ostracods, and copepods

Class Merostomata: crustaceans such as horseshoe crabs and eurypterids

Class Pycnogonida: crustaceans such as sea spiders

cleavage: the process of cytokinesis in animal cells; as cells multiply, the plasma membrane pinches off to make two cells from one

climate: long-term weather patterns for a particular region

cnidaria: a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

cnidarians: aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

codominance: an equal expression of two alleles in a heterozygous organism

codon: the genetic code for an amino acid that is represented by three nitrogen bases

codons: the genetic code for an amino acid that is represented by three nitrogen bases

coelom: a body cavity

coevolution: a situation in which two or more species evolve in response to each other

coexist: live together

commensal: a symbiotic relationship wherein which one species benefits and the other is neither helped nor harmed

competitive exclusion principle: the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently and have a reproductive edge and eventually eliminate the other species

compound eye: a multifaceted eye that is made up of thousands of simple eyes

compound eyes: multifaceted eyes that are made up of thousands of simple eyes



concentric: having the same center

conchiolin: a protein that is the organic basis of mollusk shells

coniferous, conifers: having pine trees and other conifers

connective tissue: cells that make up bones, blood, ligaments, and tendons

consumers: animals that do not make their own food but instead eat other organisms

continental drift: the movement of the continents over geologic time

contour feather: a feather that covers a bird's body and gives shape to the wings or tail

contour feathers: feathers that cover a bird's body and give shape to the wings or tail

controversy: a discussion marked by the expression of opposing views

convergence: animals that are not closely related but they evolve similar structures

copulation: the act of sexual reproduction

crinoids: an echinoderm with radial symmetry that resembles a flower

critical period: a limited time in which learning can occur

critical periods: a limited time in which learning can occur

crustaceans: arthropods with hard shells, jointed bodies, and appendages that mainly live in the water

ctenoid scale: a scale with projections on the edge like the teeth on a comb

cumbersome: awkward

cytoplasm: fluid in eukaryotes that surrounds the nucleus and organelles

cytosolic: the semifluid portions of the cytoplasm

death rate: a ratio of the number of deaths in an area in a year to the total population of the area

deciduous: having leaves that fall off at the end of the growing season

denaturing: break down into small parts

dendrites: branched extensions of a nerve cell that transmit impulses to the cell body

described: a detailed description of a species that scientists can refer to identify that species from other similar species

desiccation: drying out

detritus: dead organic matter

deuterostome: animal in which the first opening does not form the mouth, but becomes the anus

deuterostomes: animals in which the first opening does not form the mouth, but becomes the anus

diadromous: animals that migrate between freshwater and saltwater

differentiation: differences in structure and function of cells in multicellular organisms as the cells become specialized

diffusion: the movement of molecules from a region of higher concentration to a region of lower concentration

dioecious: having members of the species that are either male or female

diploblastic: having two germ layers; ectoderm and endoderm

diploid cells: cells with two sets of chromosomes

direct fitness: fitness gained through personal reproduction

diurnal: active in the daytime

DNA replication: the process by which two strands of a double helix separate and form two identical DNA molecules

dominance hierarchies: the structure of the pecking order of a group of individuals of a group where the multiple levels of dominance and submission occur

dominant: an allele that is always an expressed trait

dorsal: the back surface of an animal with bilateral symmetry

dorsal root ganglia: nervous tissue located near the backbone

dorsoventrally: flattened from the top and bottom

dysentery: inflammation of the intestines that is characterized by pain, diarrhea, and the passage of mucous and blood

ecdysis: shedding the outer layer of skin or exoskeleton

ecdysone: hormone that triggers molting in arthropods

echinoderms: sea animals with radial symmetry such as starfish, sea urchins, and sea cucumbers

ecological: relating to an organism's interaction with its environment

ecology: study of how organisms interact with their environment

ecosystem: a self-sustaining collection of organisms and their environment

ecosystems: self-sustaining collections of organisms and their environments

ecotourism: tourism that involves travel to areas of ecological or natural interest usually with a naturalist guide

ectodermal: relating to the outermost of the three germ layers in animal embryos

ectoparasite: an organism that lives on the surface of another organism and derives its nutrients directly from that organism



ectoparasites: organisms that live on the surfaces of other organisms and derive their nutrients directly from those organisms

edentates: lacking teeth

El Niño: a periodic condition characterized by a warming of the central Pacific Ocean and the changes in global weather patterns that are brought about

emit: to send out or give off

endocrine system: the grouping of organs or glands that secrete hormones into the bloodstream

endoparasite: an organism that lives inside another organism and derives its nutrients directly from that organism

endoparasites: organisms that live inside other organisms and derive their nutrients directly from those organisms

endoskeleton: a skeleton that is surrounded by muscle tissue

endosymbionts: the hypothesis that certain organelles in eukaryotes are prokaryotes that have a symbiotic relationship and live within the eukaryote

endotrophic: deriving nourishment from within

enterocoelous: a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

enzyme: a protein that acts as a catalyst to start a biochemical reaction

enzymes: proteins that act as catalysts to start biochemical reactions

epidermis: the protective portion of the outer portion of the skin found in some animals, it is composed of two layers of cells where the outer layer is continuously shed and replaced by the inner layer

epistasis: a phenomenon in which one gene alters the expression of another gene that is independently inherited

epithelial cells: cells that occur in tightly packed sheets that line organs and body cavities

epithelial lining: sheets of tightly packed cells that cover organs and body cavities

epitope: a localized region on an antigen that is recognized chemically by antibodies

equilibrium: a state of balance

erythrocytes: red blood cells, cells containing hemoglobin that carry oxygen throughout the body

estuaries: an area of brackish water where a river meets the ocean

ethology: animal behavior

eucoelomates: animals that have a true body cavity that is completely surrounded by mesoderm

eukaryota: a group of organisms containing a membrane bound-nucleus and membrane-bound organelles

eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles

eukaryotic cells: contains a membrane-bound nucleus and membrane-bound organelles

eutraphine: animals that can live in a wide range of salt concentrations

eusocial: animals that show a true social organization

evaporites: rocks formed from evaporation of salty and mineral-rich liquid

excrescence: an abnormal growth

excrescences: abnormal growths

exons: the coding region in a eukaryotic gene that is expressed

exoskeleton: a hard outer protective covering common in invertebrates such as insects

exoskeletons: hard outer protective coverings common in invertebrates such as insects

exponential growth: a population growing at the fastest possible rate under ideal conditions

extant: still living

facilitated diffusion: the spontaneous passing of molecules attached to a carrier protein across a membrane

facultative parasites: organisms that can survive either as a parasite or free-living

falconry: a sport where falcons are used for hunting

fascicle: a close cluster

fauna: animals

fertilization: the fusion of male and female gametes

fibroblasts: type of cells found in loose connective tissue that secretes the proteins for connective fibers

fight or flight response: an automatic, chemically controlled response to a stimulus that causes increased heart and breathing rates for increased activity

filter feeders: animals that strain small food particles out of water

fission: dividing into two parts

fixed action pattern: behaviors that are common to all members of a species

flagella (flagellum): cellular tail that allows the cell to move

flagellae: cellular tails that allow cells to move



flora: plants

fossil record: a collection of all known fossils

frequency-dependant selection: a decline in the reproductive success of a particular body type due to that body type becoming common in the population

frugivores: fruit-eating animals

functional morphology: studying form and function

fusion: coming together

gametes: reproductive cells that only have one set of chromosomes

gametocyte: cell that produces gametes through division

gametocytes: cells that produce gametes through division

ganoid scale: hard, bony, and enamel covered scales

gastropods: mollusks that are commonly known as snails

gastrovascular cavity: a single cavity where digestion occurs

gastrulation: the formation of a gastrula from a blastula

gene therapy: a process where normal genes are inserted into DNA to correct a genetic disorder

genes: segments of DNA located on chromosomes that direct protein production

genetic trait: trait related to biological inheritance

genetics: the branch of biology that studies heredity

genome: an organism's genetic material

genomes: the sum of all genes in a set of chromosomes

genotype: the genetic makeup of an organism

germ cell: an egg or sperm cell, a gamete

germ cells: egg or sperm cells, gametes

gill arches: arches of cartilage that support the gills of fishes and some amphibians

gill filaments: the site of gas exchange in aquatic animals such as fish and some amphibians

gills: site of gas exchange between the blood of aquatic animals such as fish and the water

gizzard: the muscular part of the stomach of some animals where food is ground

global warming: a slow and steady increase in the global temperature

glycoprotein: an organic molecule that contains a carbohydrate and a protein

gonad: the male and female sex organs that produce sex cells

gonads: the male and female sex organs that produce sex cells

granulocytes: a type of white blood cell where its cytoplasm contains granules

green house effect: a natural phenomenon where atmospheric gases such as carbon dioxide prevent heat from escaping through the atmosphere

habitat: the physical location where organisms live in an ecosystem

habitat loss: the destruction of habitats through natural or artificial means

habitat requirement: necessary conditions or resources needed by an organism in its habitat

habitats: physical locations where organisms live in an ecosystem

Hamilton's Rule: individuals show less aggression to closely related kin than to more distantly related kin

haplodiploidy: the sharing of half the chromosomes between a parent and an offspring

haploid cells: cells with only one set of chromosomes

hemocoel: a cavity between organs in arthropods and mollusks through which blood circulates

hemocyanin: respiratory pigment found in some crustaceans, mollusks, and arachnids

hemoglobin: an iron-containing protein found in red blood cells that binds with oxygen

hemolymph: the body fluid found in invertebrates with open circulatory systems

herbivore: an animal that eats plants only

herbivores: animals that eat only plants

herbivorous: animals that eat plants

heredity: the passing on of characteristics from parents to offspring

heritability: the ability to pass characteristics from a parent to the offspring

hermaphodite: an animal with both male and female sex organs

hermaphroditic: having both male and female sex organs

heterodont: teeth differentiated for various uses

heterotrophic eukaryotes: organisms containing a membrane-bound nucleus and membrane-bound organelles and do not make their own food

heterotrophs: organisms that do not make their own food

heteroxenous: a life cycle in which more than one host individual is parasitized



heterozygote: an organism whose chromosomes contain both genes of a contrasting pair

heterozygote advantage: a condition where a heterozygous individual has a reproductive advantage over a homozygous individual

Hippocrates: a central figure in medicine in ancient Greece, he is considered the father of modern medicine

home range: the area where an animal lives and eats

homeostasis: a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

homeothermic: describes animals able to maintain their body temperatures

hominid: belonging to the family of primates

hominids: belonging to the family of primates

homodont: teeth with a uniform size and shape

homologous: similar but not identical

homology: correspondence in the type of structure and its origin

homoplastic: similar but of different origins

homozygote: an animal with two identical alleles for one trait

hormone: a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

hormones: chemical signals secreted by glands that travel through the bloodstream to regulate the body's activities

Horseshoe crabs: "living fossils" in the class of arthropods

Hox genes: also known as selector genes because their expression leads embryonic cells through specific morphologic development

Human Genome Project: a study by U.S. Department of Energy and the National Institutes of Health to map the entire human genome by 2003

hunting season: a period of time during which hunting is permitted

hunting seasons: periods of time during which hunting is permitted

hybrid: offspring resulting from the cross of two different species

hydrostatic skeleton: a pressurized, fluid-filled skeleton

hyperpolarizing potential: any change in membrane potential that makes the inside of the membrane more negatively charged

hypothalamus: part of the upper end of the brain stem that regulates activities in the nervous and endocrine systems

IgA: immunoglobulin A; a class of proteins that make up antibodies

IgD: immunoglobulin D; a class of proteins that make up antibodies

IgE: imunoglobin E; a class of proteins that make up antibodies

IgG: imunoglobin G; a class of proteins that make up antibodies

IgM: imunoglobin M; a class of proteins that make up antibodies

inbreeding depression: loss of fitness due to breeding with close relatives

incomplete dominance: a type of inheritance where the offspring have an intermediate appearance of a trait from the parents

incus: one of three small bones in the inner ear

indirect fitness: fitness gained through aiding the survival of non-descendant kin

infrared: an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red; heat is carried on infrared waves

innate behavior: behavior that develops without influence from the environment

innervate: supplied with nerves

inoculation: introduction into surroundings that support growth

insectivore: an animal that eats insects

insectivores: animals that eat insects

instars: the particular stage of an insect's or arthropod growth cycle between moltings

integument: a natural outer covering

intercalation: placing or inserting between

intraspecific: involving members of the same species

introns: a non-coding sequence of base pairs in a chromosome

invagination: a stage in embryonic development where a cell layer buckles inward

invertebrates: animals without a backbone

involuntary muscles: muscles that are not controlled by will

isthmus: a narrow strip of land

iteroparous: animals with several or many reproductive events in their lives

k-selected species: a species that natural selection has favored at the carrying capacity

k-selecting habitat: habitat where there is a high cost of reproduction and is sensitive to the size of the offspring

key innovation: a modification that permits an individual to exploit a resource in a new way

keystone species: a species that controls the environment and thereby determines the other species that can survive in its presence



krill: an order of crustaceans that serves as a food source for many fish, whales, and birds

lancelet: a type of primitive vertebrate

lancelets: primitive vertebrates

lateral inhibition: phenomenon that amplifies the differences between light and dark

lateral line: a row of pressure sensitive sensory cells in a line on both sides of a fish

learned behavior: behavior that develops with influence from the environment

learning: modifications to behavior motivated by experience

leukocytes: a type of white blood cells that are part of the immune system

life history strategies: methods used to overcome pressures for foraging and breeding

life history strategy: methods used to overcome pressures for foraging and breeding

lipids: fats and oils; organic compounds that are insoluble in water

logistic growth: in a population showing exponential growth the individuals are not limited by food or disease

lungs: sac-like, spongy organs where gas exchange takes place

lymphocytes: white blood cell that completes development in bone marrow

macroparsite: a parasite that is large in size

macroparasites: parasites that are large in size

macrophages: white blood cell that attacks anything foreign such as microbes

malleus: the outermost of the inner ear bones

mantle: the tissue in mollusks that drapes over the internal organs and may secrete the shell

mantles: tissues in mollusks that drape over the internal organs and may secrete the shell

matrix: the nonliving component of connective tissue

megachiroptera: fruit bats and flying foxes

meiosis: a specialized type of cell division that results in four sex cells or gametes that have half the genetic material of the parent cell

merozoite: a motile stage in some parasitic protozoa

mesenchyme: the part of the mesoderm from which the connective tissues (bone, cartilage, and vascular system) arise

mesenteries: the membrane that suspends many internal organs in the fluid-filled body cavity of vertebrates

mesoderm: the middle layer of cells in embryonic tissue

messenger RNA: a type of RNA that carries protein synthesis information from the DNA in to the nucleus to the ribosomes

metamorphose: to change drastically from a larva to an adult

metamorphoses: changes drastically from its larval form to its adult form

metamorphosing: changing drastically from a larva to an adult

metamorphosis: a drastic change from a larva to an adult

metazoan: a subphylum of animals that have many cells, some of which are organized into tissues

metazoans: a subphylum of animals that have many cells, some of which are organized into tissues

microchiroptera: small bats that use echolocation

microparasite: very small parasite

microparasites: very small parasites

midoceanic ridge: a long chain of mountains found on the ocean floor where tectonic plates are pulling apart

mitochondria: organelles in eukaryotic cells that are the site of energy production for the cell

Mitochondrial DNA: DNA found within the mitochondria that control protein development in the mitochondria

mitosis: a type of cell division that results in two identical daughter cells from a single parent cell

modalities: to conform to a general pattern or belong to a particular group or category

modality: to conform to a general pattern or belong to a particular group or category

molecular clock: using the rate of mutation in DNA to determine when two genetic groups split off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups split off

mollusks: large phylum of invertebrates that have soft, unsegmented bodies and usually have a hard shell and a muscular foot; examples are clams, oysters, mussels, and octopuses

molten: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

molting: the shedding of an exoskeleton as an animal grows so that a new, large exoskeleton can be secreted

monoculture: cultivation of a single crop over a large area

monocultures: cultivation of single crops over large areas



monocytes: the largest type of white blood cell

monophyletic: a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

monotremes: egg-laying mammals such as the platypus and echidna

monoxenous: a life cycle in which only a single host is used

morphogenesis: the development of body shape and organization during ontogeny

morphological: the structure and form of an organism at any stage in its life history

morphological adaptation: an adaptation in form and function for specific conditions

morphological adaptations: adaptations in form and function for specific conditions

morphologies: the forms and structures of an animal

mutation: an abrupt change in the genes of an organism

mutations: abrupt changes in the genes of an organism

mutualism: ecological relationship beneficial to all involved organisms

mutualisms: ecological relationships beneficial to all involved organisms

mutualistic relationship: symbiotic relationship where both organisms benefit

mutualistic relationships: symbiotic relationships where both organisms benefit

mutualists: a symbiotic relationship where both organisms benefit

myofibril: longitudinal bundles of muscle fibers

myofilament: any of the ultramicroscopic filaments, made up of actin and myosin, that are the structural units of a myofibril

myosin: the most common protein in muscle cells, responsible for the elastic and contractile properties of muscle; it combines with actin to form actomyosin

natural selection: the process by which organisms best suited to their environment are most likely to survive and reproduce

naturalist: a scientist who studies nature and the relationships among the organisms

naturalists: scientists who study nature and the relationships among the organisms

neuromuscular junction: the point where a nerve and muscle connect

neuron: a nerve cell

neurons: nerve cells



neurotransmitters: chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

niche: how an organism uses the biotic and abiotic resources of its environment

nocturnal: active at night

notochord: a rod of cartilage that runs down the back of Chordates

nucleotide: the building block of a nucleic acid that is composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

nucleotide chain: a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides: building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

obligative mutualism: an animal that must exist as part of a mutually beneficial relationship

obligatory parasites: an animal that can only exist as a parasite

olfactory: relates to the sense of smell

omnivorous: eating both plants and animals

ontogeny: the embryonic development of an organism

oocyst: a cyst in sporozoans that contains developing sporozoites

operculum: a flap covering an opening

operculum chamber: space covered by a flap

organelles: membrane-bound structures found within a cell

ornithology: the study of birds

osmoregulatory functions: controlling the water balance within an animal

osmoregulatory system: system that regulates the water balance between an organism and its environment

osmosis: the diffusion of water across a membrane

ossification: deposition of calcium salts to form hardened tissue such as bone

osteoblasts: potential bone forming cells found in cartilage

oviparous: having offspring that hatch from eggs external to the body

ovoviparity: having offspring that hatch from eggs retained in the mother's uterus

ovoviviparous: having offspring that hatch from eggs retained in the mother's uterus

paleoanthropology: the study of ancient humans

parasitology: the study of parasites



parasympathetic division: part of the nervous system that generally enhances body activities that gain and conserve energy such as digestion and heart rate

parental imprinting: a process by which a gene's expression in a child depends on which parent donated it before development

passive diffusion: the passing of molecules across a membrane from an area of higher concentration to an area of lower concentration without any energy input

pathogens: disease-causing agents such as bacteria, fungi, and viruses

pecking order: the position of individuals of a group wherein multiple levels of dominance and submission occur

pectoral: of, in, or on the chest

pedipalps: one pair of short appendages near the mouth in some arthropods used for feeding and copulation

pericardial cavity: the space within the membrane that surrounds the heart

peripheral nervous system: the sensory and motor nerves that connect to the central nervous system

peritoneum: the thin membrane that lines the abdomen and covers the organs in it

pesticide: any substance that controls the spread of harmful or destructive organisms

pesticides: substances that control the spread of harmful or destructive organisms

pH: a measure of how acidic or basic a substance is by measuring the concentration of hydrogen ions

phalanges: bones of the fingers and toes

pharyngeal: having to do with the tube that connects the stomach and the esophagus

phenotype: physical and physiological traits of an animal

phenotypes: the physical and physiological traits of an animal

phenotypic: describes the physical and physiological traits of an animal

phenotypic trait: physical and physiological variations within a population

phenotypic variation: differences in physical and physiological traits within a population

pheromones: small, volatile chemicals that act as signals between animals that influence physiology or behavior

phlogenetic: relating to the evolutionary history

phospholipid: molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water



photoreceptors: specialized cells that detect the presence or absence of light

photosynthesis: the combination of chemical compounds in the presence of sunlight

photosynthesizing autotrophs: animals that produce their own food by converting sunlight to food

phyla: broad, principle divisions of a kingdom

phylogenetic: relating to the evolutionary history of species or group of related species

phylogeny: the evolutionary history of a species or group of related species

physiological: relating to the basic activities that occur in the cells and tissues of an animal

physiology: the study of the normal function of living things or their parts

placenta: the structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placental: having a structure through which a fetus obtains nutrients and oxygen from its mother while in the uterus

placoid scale: a scale composed of three layers and a pulp cavity

placoid scales: scales composed of three layers and a pulp cavity

plankton: microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

plate tectonics: the theory that Earth's surface is divided into plates that move

platelet: cell fragment in plasma that aids clotting

platelets: cell fragments in plasma that aid in clotting

pleural cavity: the space where the lungs are found

plumose: having feathers

pluripotent: a cell in bone marrow that gives rise to any other type of cell

poaching: hunting game outside of hunting season or by using illegal means

poikilothermic: an animal that cannot regulate its internal temperature; also called cold blooded

polymer: a compound made up of many identical smaller compounds linked together

polymerase: an enzyme that links together nucleotides to form nucleic acid

polymerases: enzymes that link together nucleotides to form nucleic acid

polymodal: having many different modes or ways

polymorphic: referring to a population with two or more distinct forms present



polymorphism: having two or more distinct forms in the same population

polymorphisms: having two or more distinct forms in the same population

polyploid: having three or more sets of chromosomes

polysaccharide: a class of carbohydrates that break down into two or more single sugars

polysaccharides: carbohydrates that break down into two or more single sugars

population: a group of individuals of one species that live in the same geographic area

population density: the number of individuals of one species that live in a given area

population dynamics: changes in a population brought about by changes in resources or other factors

population parameters: a quantity that is constant for a particular distribution of a population but varies for the other distributions

populations: groups of individuals of one species that live in the same geographic area

posterior: behind or the back

precursor: a substance that gives rise to a useful substance

prehensile: adapted for seizing, grasping, or holding on

primer: short preexisting polynucleotide chain to which new deoxyribonucleotides can be added by DNA polymerase

producers: organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

progeny: offspring

prokaryota: a group of organisms that lack a membrane-bound nucleus and membrane-bound organelles

prokaryotes: single-celled organisms that lack a true cell nucleus

prokaryotic endosymbionts: single-celled organisms that lack a true cell nucleus that live inside of other cells

proprioceptors: sense organs that receive signals from within the body

protostome: animal in which the initial depression that starts during gastrulation becomes the mouth

protostomes: animals in which the initial depression that starts during gastrulation becomes the mouth

protozoa: a phylum of single-celled eukaryotes

protozoan: a member of the phylum of single-celled organisms

pseudocoelom: a body cavity that is not entirely surrounded by mesoderm

pseudocoelomates: animals with a body cavity that is not entirely surrounded by mesoderm

pterylae: feather tracks

quadrupedal: describes an animal with four legs

quadrupeds: animals with four legs

quinine: substance used to treat malaria

r-selected species: a species that shows the following characteristics: short lifespan; early reproduction; low biomass; and the potential to produce large numbers of usually small offspring in a short period of time

r-selecting habitat: the concept where a high reproductive rate is the chief determinant of life history

radially symmetric: wheel-like symmetry in which body parts radiate out from a central point

radially symmetrical: describes an animal that features a wheel-like symmetry in which its body parts radiate out from a central point

recessive: a hidden trait that is masked by a dominant trait

recombinant DNA: DNA that is formed when a fragment of DNA is incorporated into the DNA of a plasmid or virus

regeneration: regrowing body parts that are lost due to injury

relative abundance: an estimate of population over an area

rennin: an enzyme used in coagulating cheese; is obtained from milk-fed calves

resorbed: absorption of materials already in the body

resorption: absorbing materials that are already in the body

respiratory pigments: any of the various proteins that carry oxygen

restriction enzymes: bacterial proteins that cut DNA at specific points in the nucleotide sequence

retina: a layer of rods and cones that line the inner surface of the eye

riparian: habitats in rivers and streams

ruminants: plant-eating animals with a multicompartment stomach such as cows and sheep

sagital plane: a plane that runs long-ways through the body

salamanders: four-legged amphibians with elongated bodies

sarcomere: one of the segments into which a fibril of striated muscle is divided by thin dark bands

scavengers: animals that feed on the remains of animals it did not kill

schizocoelous: the mesoderm originates from existing cell layers when the cells migrate



scleroblasts: cells that give rise to mineralized connective tissue

sedimentary rock: rock that forms when sediments are compacted and cemented together

semelparous: animals that only breed once and then die

serial homology: a rhythmic repetition

sessile: not mobile, attached

sexual reproduction: a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

sexual selection: selection based on secondary sex characteristics that leads to greater sexual dimorphism or differences between the sexes

sexual size dimorphism: a noticeable difference in size between the sexes

shoals: shallow waters

single-lens eyes: an eye that has a single lens for focusing the image

skeletal muscle: muscle attached to the bones and responsible for movement

smooth muscle: muscles of internal organs which is not under conscious control

somatic: having to do with the body

somatic nervous system: part of the nervous system that controls the voluntary movement of skeletal muscles

somatosensory information: sensory information from different parts of the body except for the eyes, tongue, ears, and other primary sense organs

somites: a block of mesoderm along each side of a chordate embryo

sonar: the bouncing of sound off distant objects as a method of navigation or finding food

spinal cord: thick, whitish bundle of nerve tissue that extends from the base of the brain to the body

splicing: splitting

spongocoel: the central cavity in a sponge

sporozoa: a group of parasitic protozoa

sporozoans: parasitic protozoans

sporozoite: an infective stage in the life cycle of sporozoans

stapes: innermost of the three bones found in the inner ear

stimuli: anything that excites the body or part of the body to produce a specific response

stimulus: anything that excites the body or part of the body to produce a specific response

strata: layers of sedimentary rock consisting of approximately the same kinds of material

striated muscle: a type of muscle with fibers of cross bands usually contracted by voluntary action

striated muscles: muscles with fibers of cross bands usually contracted by voluntary actions

superposition: the order in which sedimentary layers are found with the youngest being on top

symbiosis: any prolonged association or living together of two or more organisms of different species

symbiotic relationship: close, long-term relationship where two species live together in direct contact

symbiotic relationships: close, long-term relationships where two species live together in direct contact

symmetrical: a balance in body proportions

synapse: the space between nerve cells across which impulses are chemically transmitted

systematic: study of the diversity of life

tactile: the sense of touch

tapetum: a reflective layer in the eye of nocturnal animals

taxa: named taxonomic units at any given level

taxon: named taxonomic unit at any given level

taxonomy: the science of classifying living organisms

terraria: a small enclosure or closed container in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrariums: small enclosures or closed containers in which selected living plants and sometimes small land animals, such as turtles and lizards, are kept and observed

terrestrial: living on land

thoracic: the chest area

thromboplastin: a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

torpid: a hibernation strategy where the body temperature drops in relation to the external temperature

trachea: the tube in air-breathing vertebrates that extends from the larynx to the bronchi

transcription: process where enzymes are used to make an RNA copy of a strand of DNA



transgenic: an organism that contains genes from another species

transgenic organism: an organism that contains genes from another species

translation: process where the order of bases in messenger RNA codes for the order of amino acids in a protein

transverse plane: a plane perpendicular to the body

trilobites: an extinct class of arthropods

triploblasts: having three germ layers; ectoderm, mesoderm, and endoderm

trophic level: the division of species in an ecosystem by their main source of nutrition

trophic levels: divisions of species in an ecosystem by their main source of nutrition

ungulates: animals with hooves

urea: soluble form of nitrogenous waste excreted by many different types of animals

urethra: a tube that releases urine from the body

uric acid: insoluble form of nitrogenous waste excreted by many different types of animals

ventral: the belly surface of an animal with bilateral symmetry

vertebrates: animals with a backbone

viviparity: having young born alive after being nourished by a placenta between the mother and offspring

viviparous: having young born alive after being nourished by a placenta between the mother and offspring

vocalization: the sounds used for communications

voluntary muscles: a type of muscle with fibers of cross bands usually contracted by voluntary action

wavelength: distance between the peaks or crests of waves

zooplankton: small animals who float or weakly move through the water

zygote: a fertilized egg

zygotes: fertilized eggs

zymogens: inactive building-block of an enzyme

Topic Outline

ADAPTATIONS

Adaptation
Antlers and Horns
Aposematism
Biological Evolution
Biomechanics
Blood
Camouflage
Catadromous—Diadromous and Anadromous Fishes
Colonization
Communication
Community Ecology
Comparative Biology
Defense
Echolocation
Egg
Extremophile
Locomotion
Mimicry
Peppered Moth
Tool Use
Water Economy in Desert Organisms

AGRICULTURE

Apiculture
Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

ANIMAL DIVERSITY

Animal
Biodiversity
Biogeography
Biological Evolution
Cambrian Explosion
Camouflage
Cephalization
Coevolution
Colonization
Community Ecology
Constraints on Animal Development
Diversity of Major Groups
Extremophile
Functional Morphology
Kingdoms of Life
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Prokaryota
Sexual Dimorphism
Taxonomy

ANIMAL GROUPS

Agnatha
Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondrichthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata



Eukaryota	Cephalization
Mammalia	Comparative Biology
Metazoan	Echolocation
Mollusca	Embryology
Nematoda	Embryonic Development
Osteichthyes	Feeding
Platyhelminthes	Functional Morphology
Porifera	Gills
Primates	Growth And Differentiation of the Nervous System
Prokaryota	Homology
Reptilia	Keratin
Rotifera	Locomotion
Trematoda	Mouth, Pharynx, and Teeth
Turbellaria	Muscular System
Urochordata	Neuron
Vertebrata	Scales, Feathers, and Hair

ANIMAL HISTORY

African Cichlid Fishes
Animal
Burgess Shale and Ediacaran Faunas
Cambrian Explosion
Coevolution
Colonization
Constraints on Animal Development
Domestic Animals
Eukaryota
Extinction
Fossil Record
Horses
Kingdoms of Life
Living Fossils
Paleontologist
Paleontology
Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetrapods—From Water to Land
Xenopus

ANATOMY

Acoustic Signals
Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells

Cephalization
Comparative Biology
Echolocation
Embryology
Embryonic Development
Feeding
Functional Morphology
Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
Skeletons
Vision

BEHAVIOR

Acoustic Signals
Aggression
Altruism
Behavior
Behavioral Ecology
Circadian Rhythm
Courtship
Crepuscular
Diurnal
Dominance Hierarchy
Ethology
Homeostasis
Imprinting
Instinct
Learning
Migration
Nocturnal
Social Animals
Sociality
Sociobiology
Territoriality

BIOCHEMISTRY AND PHYSIOLOGY

Absorption
Allometry
Antibody



Blood
Cancer
Cell Division
Cells
Digestion
Egg
Homeostasis
Hormones
Keratin
Molecular Biologist
Molecular Biology
Molecular Systematics
Physiologist
Physiology
Respiration
Transport

BIODIVERSITY

Biodiversity
Biogeography
Biomass
Biomes
Colonization
Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

CAREERS IN ANIMAL SCIENCE

Ecologist
Environmental Lawyer
Farmer
Functional Morphologist
Geneticist
Horse Trainer
Human Evolution
Livestock Manager
Marine Biologist
Medical Doctor
Molecular Biologist
Museum Curator
Paleontologist
Physiologist
Scientific Illustrator

Service Animal Trainer
Systematist
Taxonomist
Veterinarian
Wild Game Manager
Wildlife Biologist
Wildlife Photographer
Zoologist

CELL BIOLOGY

Absorption
Blood
Cell Division
Cells
Viruses

ECOLOGY

African Cichlid Fishes
Behavioral Ecology
Biotic Factors
Camouflage
Community Ecology
Competition
Competitive Exclusion
Conservation Biology
DDT
Ecologist
Ecology
Ecosystem
Evolutionary Stable Strategy
Exotic Species
Expenditure per Progeny
Feeding Strategies
Fitness
Food Web
Foraging Strategies
Growth And Differentiation of the Nervous System
Habitat
Habitat Loss
Habitat Restoration
Home Range
Human Commensals and Mutual Organisms
Interspecies Interactions
Iteroparity and Semelparity
Keystone Species
Life History Strategies



Malthus, Thomas Robert
Parasitism
Plankton
Population Dynamics
Populations
Predation
Territoriality
Trophic Level
Zooplankton

ENVIRONMENT

Biological Pest Control
Biomass
Biomes
Biotic Factors
Carson, Rachel
DDT
Ecosystem
Endangered Species
Environment
Environmental Degradation
Environmental Impact
Environmental Lawyer
Fossil Fuels
Global Warming
Human Populations
Natural Resources
Pesticide
Pollution
Silent Spring
Threatened Species

ETHICS

Animal Rights
Animal Testing
Bioethics

EVOLUTION

Adaptation
African Cichlid Fishes
Aposematism
Biological Evolution
Camouflage
Coevolution
Constraints on Animal Development
Continental Drift
Convergence

Darwin, Charles
Genetic Variation in a Population
Heterochrony
Homology
Human Evolution
Lamarck
Leakey, Louis and Mary
Modern Synthesis
Morphological Evolution in Whales
Morphology
Natural Selection
Peppered Moth
Sexual Dimorphism
Sexual Selection
Spontaneous Generation

FORM AND FUNCTION

Acoustic Signals
Adaptation
African Cichlid Fishes
Antlers and Horns
Aposematism
Biomechanics
Blood
Body Cavities
Body Plan
Bone
Burgess Shale and Ediacaran Faunas
Camouflage
Cell Division
Cells
Cephalization
Chitin
Circulatory System
Communication
Defense
Digestion
Digestive System
Echolocation
Endocrine System
Excretory and Reproductive Systems
Feeding
Flight
Gills
Gliding and Parachuting
Locomotion
Mimicry



Nervous System
Respiratory System
Sexual Selection
Shells
Vision
Vocalization

GENETICS

Drosophila
Genes
Genetic Engineering
Genetic Variation in a Population
Genetically Engineered Foods
Geneticist
Genetics
Mendel, Gregor
Modern Synthesis
PCR
Viruses

GEOLOGIC HISTORY

Cambrian Period
Carboniferous
Continental Drift
Cretaceous
Devonian
Geological Time Scale
Jurassic
K/T Boundary
Oligocene
Ordovician
Permian
Pleistocene
Quaternary
Silurian
Tertiary
Triassic

GROWTH AND DEVELOPMENT

Allometry
Antlers and Horns
Body Cavities
Body Plan
Bone
Cartilage
Cell Division
Cells

Comparative Biology
Constraints on Animal Development
Egg
Embryology
Embryonic Development
Haeckel's Law of Recapitulation
Heterochrony
Mesenchyme
Metamorphosis
Molting
Ontogeny
Serial Homology
Von Baer's Law

HISTORICAL FIGURES IN SCIENCE

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Bailey, Florence Augusta Merriam
Bates, Henry Walter
Carson, Rachel
Darwin, Charles
Diamond, Jared
Elton, Charles Sutherland
Fausto-Sterling, Anne
Fossey, Dian
Goodall, Jane
Gould, Steven Jay
Haldane, J. B. S.
Lamarck, Jean-Baptiste
Leakey, Louis and Mary
Linnaeus, Carolus
Lorenz, Konrad
Malthus, Thomas Robert
Mayr, Ernst
McArthur, Robert
Mendel, Gregor
Montalcini, Rita Levi
Pasteur, Louis
Simpson, George Gaylord
Stevens, Nettie Maria
Wallace, Alfred Russel
Wilson, E. O.

HUMANS AND THE ANIMAL WORLD

Cultures and Animals
Human Commensals and Mutual Organisms
Human Populations
Human–Animal Conflicts

Hunter-Gatherers
Hunting
Malaria

LIFE CYCLES

Catadromous—Diadromous and Anadromous Fishes
Cell Division
Colonization
Courtship
Endosymbiosis
Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

REPRODUCTION

Antlers and Horns
Asexual And Sexual Reproduction
Cell Division

Excretory and Reproductive Systems
Fertilization

SCIENTIFIC FIELDS OF STUDY

Behavioral Ecology
Community Ecology
Comparative Biology
Conservation Biology
Ecology
Embryology
Entomology
Functional Morphology
Herpetology
Ichthyology
Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
Paleontology
Physiology
Sociobiology
Taxonomy