animal sciences

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VOLUME 1
A–Crep

Allan B. Cobb, Editor in Chief

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Macmillan Reference USA
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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.

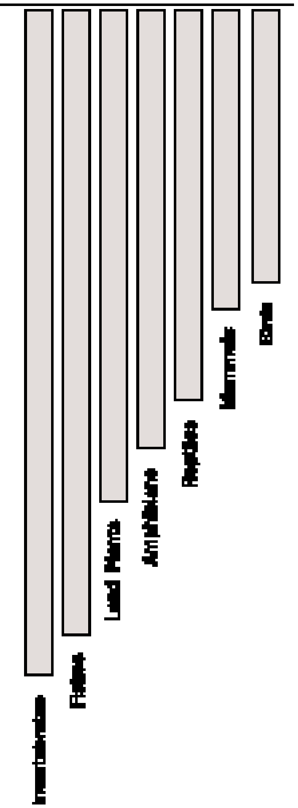
I wish to thank the staff at Macmillan Reference USA and the Gale Group for their hard work and attention to detail. In particular, I would like to thank Hélène Potter, Elly Dickason, Linda Hubbard, and Christa Brelin. I want to offer special thanks to Kate Millson for all her efforts and long hours 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

Geological Time Scale

Eon	Era	Period	Epoch	Significant Events	Million Years Before Present
Phanerozoic	Cenozoic	Quaternary	Holocene	recorded human history, rise and fall of civilizations, global warming, habitat destruction, pollution mass extinction	0.01
			Pleistocene	Homo sapiens, ice ages	1.6
		Tertiary	Pliocene	global cooling, savannahs, grazing mammals	5.3
			Miocene	global warming, grasslands, Chalicotherium	24
			Oligocene		37
			Eocene	modern mammals flourish, ungulates	58
			Paleocene		66
	Mesozoic	Cretaceous		last of age of dinosaurs, modern mammals appear, flowering plants, insects	144
		Jurassic		large plant-eating dinosaurs, carnivorous dinosaurs, first birds, breakup of Pangea	208
		Triassic		lycophytes, glossopterids, and dicynodonts, and the dinosaurs	245
	Paleozoic	Permian		Permian ends with largest mass extinction in history of Earth, most marine invertebrates extinct	286
		Pennsylvanian		vast coal swamps, evolution of amniote egg allowing exploitation of land	320
		Mississippian		shallow seas cover most of Earth	360
		Devonian		vascular plants, the first tetrapods, wingless insects, arachnids, brachiopods, corals, and ammonite were also common, many new kinds of fish appeared	408
		Silurian		Coral reefs, rapid spread of jawless fish, first freshwater fish, first fish with jaws, first good evidence of life on land, including relatives of spiders and centipedes	438
		Ordovician		most dry land collected into Gondwana, many marine invertebrates, including graptolites, trilobites, brachiopods, and the conodonts (early vertebrates), red and green algae, primitive fish, cephalopods, corals, crinoids, and gastropods, possibly first land plants	505
		Cambrian		most major groups of animals first appear, Cambrian explosion	570
Precambrian	Proterozoic			stable continents first appear, first abundant fossils of living organisms, mostly bacteria and archaeobacteria, first eukaryotes, first evidence of oxygen build-up	2500
	Archean			atmosphere of methane, ammonia, rocks and continental plates begin to form, oldest fossils consist of bacteria microfossils stromatolites, colonies of photosynthetic bacteria	3800
	Hadean			pre-geologic time, Earth in formation	4600

Time Range of Several Groups of Plants & Animals



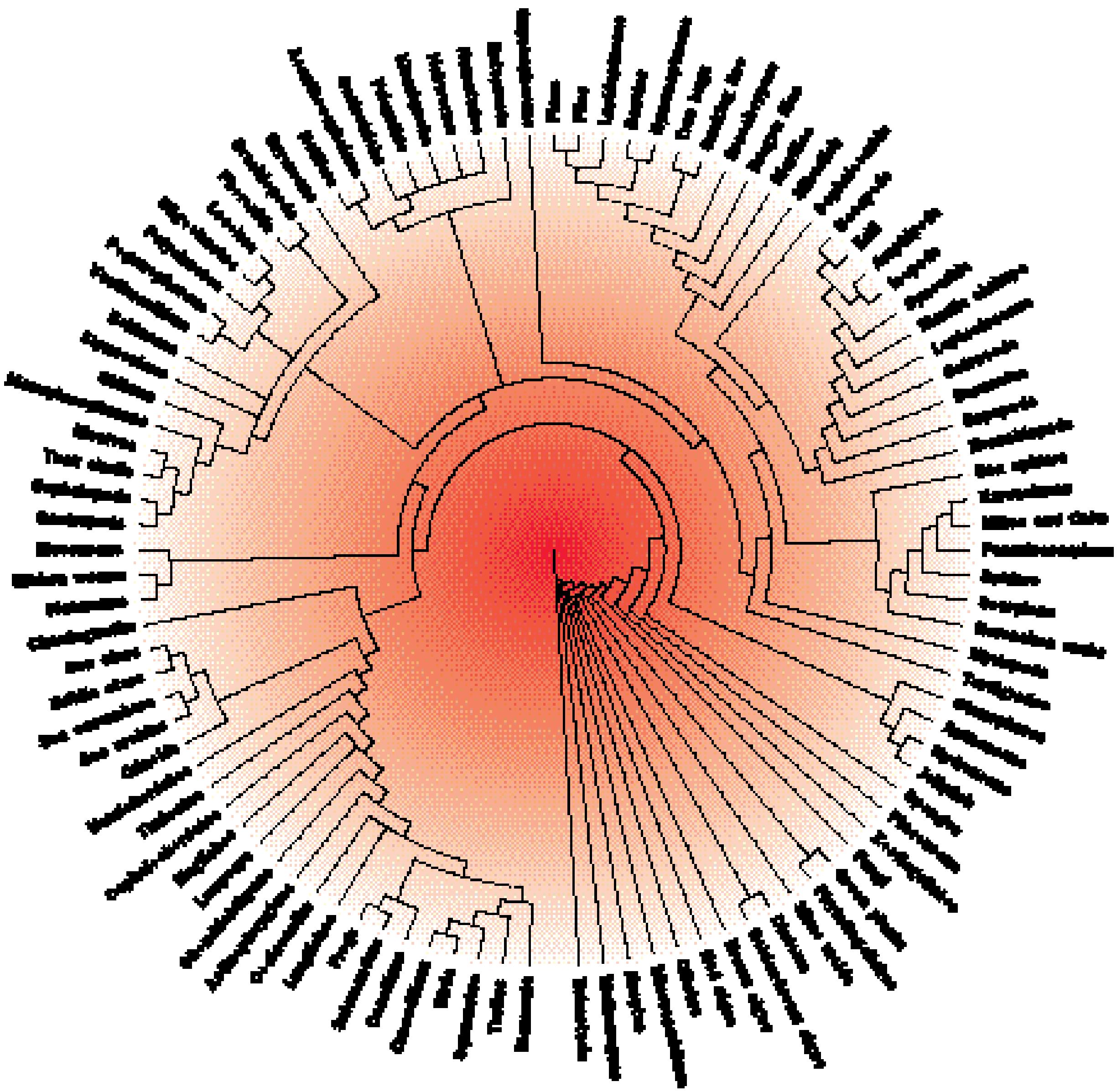
COMPARISON OF THE FIVE-KINGDOM AND SIX-KINGDOM CLASSIFICATION OF ORGANISMS

Five Kingdom	Six Kingdom
Kingdom: Monera Phylum: Bacteria Phylum: Blue-green algae (cyanobacteria)	Kingdom: Archaebacteria Kingdom: Eubacteria

- 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 liverworms
  - 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 (°F). 1°F = 1.8°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):
  °C = (°F-32)/(1.8)
- To change from Celsius (C) to Fahrenheit (F):
  °F = (°C x 1.8) + 32
- To change from Celsius (C) to Kelvin (K):
  K = °C + 273.15
- To change from Fahrenheit (F) to Kelvin (K):
  K = (°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	N m-2 =m-1 kg s-2
Energy, work, heat	Joule	J	N m =m2 kg s-2
Power, radiant flux	watt	W	J s-1 =m2 kg s-3
Electric charge	coulomb	C	A s
Electric potential, electromotive force	volt	V	J C-1 =m-2 kg s-3 A-1
Electric resistance	ohm	_	V A-1 =m2 kg s-3 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., angtsrom):

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

CONVERSIONS FOR STANDARD, DERIVED, AND CUSTOMARY MEASUREMENTS

Length

1 angstrom (Å)	0.1 nanometer (exactly) 0.000000004 inch
1 centimeter (cm)	0.3937 inches
1 foot (ft)	0.3048 meter (exactly)
1 inch (in)	2.54 centimeters (exactly)
1 kilometer (km)	0.621 mile
1 meter (m)	39.37 inches 1.094 yards
1 mile (mi)	5,280 feet (exactly) 1.609 kilometers
1 astronomical unit (AU)	1.495979 x 10^{13} cm
1 parsec (pc)	206,264.806 AU 3.085678 x 10^{18} cm 3.261633 light-years
1 light-year	9.460530 x 10^{17} cm

Area

1 acre	43,560 square feet (exactly) 0.405 hectare
1 hectare	2.471 acres
1 square centimeter (cm^2)	0.155 square inch
1 square foot (ft^2)	929.030 square centimeters
1 square inch (in^2)	6.4516 square centimeters (exactly)
1 square kilometer (km^2)	247.104 acres 0.386 square mile
1 square meter (m^2)	1.196 square yards 10.764 square feet
1 square mile (mi^2)	258.999 hectares

MEASUREMENTS AND ABBREVIATIONS

Volume

1 barrel (bbl)*, liquid	31 to 42 gallons
1 cubic centimeter (cm^3)	0.061 cubic inch
1 cubic foot (ft^3)	7.481 gallons 28.316 cubic decimeters
1 cubic inch (in^3)	0.554 fluid ounce
1 dram, fluid (or liquid)	1/8 fluid ounce (exactly) 0.226 cubic inch 3.697 milliliters
1 gallon (gal) (U.S.)	231 cubic inches (exactly) 3.785 liters 128 U.S. fluid ounces (exactly)
1 gallon (gal) (British Imperial)	277.42 cubic inches 1.201 U.S. gallons 4.546 liters
1 liter	1 cubic decimeter (exactly) 1.057 liquid quarts 0.908 dry quart 61.025 cubic inches
1 ounce, fluid (or liquid)	1.805 cubic inches 29.573 milliliters
1 ounce, fluid (fl oz) (British)	0.961 U.S. fluid ounce 1.734 cubic inches 28.412 milliliters
1 quart (qt), dry (U.S.)	67.201 cubic inches 1.101 liters
1 quart (qt), liquid (U.S.)	57.75 cubic inches (exactly) 0.946 liter

* There are a variety of "barrels" established by law or usage. For example, U.S. federal taxes on fermented liquors are based on a barrel of 31 gallons (141 liters); many state laws fix the "barrel for liquids" as 31½ gallons (119.2 liters); one state fixes a 36-gallon (160.5 liters) barrel for cistern measurement; federal law recognizes a 40-gallon (178 liters) barrel for "proof spirits"; by custom, 42 gallons (159 liters) comprise a barrel of crude oil or petroleum products for statistical purposes, and this equivalent is recognized "for liquids" by four states.

Units of mass

1 carat (ct)	200 milligrams (exactly) 3.086 grains
1 grain	64.79891 milligrams (exactly)
1 gram (g)	15.432 grains 0.035 ounce
1 kilogram (kg)	2.205 pounds
1 microgram (μg)	0.000001 gram (exactly)
1 milligram (mg)	0.015 grain
1 ounce (oz)	437.5 grains (exactly) 28.350 grams
1 pound (lb)	7,000 grains (exactly) 453.59237 grams (exactly)
1 ton, gross or long	2,240 pounds (exactly) 1.12 net tons (exactly) 1.016 metric tons
1 ton, metric (t)	2,204.623 pounds 0.984 gross ton 1.102 net tons
1 ton, net or short	2,000 pounds (exactly) 0.893 gross ton 0.907 metric ton

Pressure

1 kilogram/square centimeter (kg/cm^2)	0.96784 atmosphere (atm) 14.2233 pounds/square inch (lb/in^2) 0.98067 bar
1 bar	0.98692 atmosphere (atm) 1.02 kilograms/square centimeter (kg/cm^2)

Contributors

Allan B. Cobb
Austin, Texas
Jes Marie Creech
University of Texas, Austin
Emily H. DuVal
University of California, Berkeley
Andrew G. Gluesenkamp
University of Texas, Austin
Ann Guidry
Austin, Texas
Brook Ellen Hall
California State University, Sacramento
Laura A. Higgins
University of Texas, Austin
Ryan I. Hill
University of Texas, Austin
Alisha K. Holloway
University of Texas, Austin
Leslie Hutchinson
Flagstaff, Arizona
Jean Krejca
University of Texas, Austin
Stephanie A. Lanoue
Panama City Beach, Florida
Denise Prendergast
Austin, Texas
Ian Quigley
University of Texas, Austin
Elliot Richmond
Austin Community College
Karen Rogowski
University of Texas, Austin
Gil G. Rosenthal
University of California, San Diego
Todd A. Schlenke
University of Texas, Austin
Danielle Schnur
Austin, Texas
Judy P. Sheen
University of California, Berkeley
Kathrin F. Stanger-Hall
University of Texas, Austin
Rebecca M. Steinberg
University of Texas, Austin
Nancy Weaver
Driftwood, Texas
Brian R. West
University of Texas, Austin
Jennifer Yeh
University of Texas, Austin

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Absorption

A

The process by which substances are taken into the tissues of organisms is called absorption. It is essential to functions such as digestion, circulation, and respiration.

During digestion, valuable nutrients are absorbed across the **epithelial lining** of the digestive tract. Absorption occurs largely in the small intestine, which has developed a large surface area for this purpose. The walls of the small intestine contain numerous finger-like projections called villi, which are in turn covered by countless microvilli. Different nutrients are absorbed across the gut epithelium in different ways.

The methods of absorption include **active transport**, **facilitated diffusion**, and **passive diffusion**. Active transport requires energy in the form of **adenosine triphosphate** (**ATP**), as well as special carrier molecules that ferry nutrients, (their substrates), across the gut lining. Active transport is involved in the absorption of proteins, which have usually been processed into amino acids or other small peptides. Most ions are also absorbed through active transport, as are most carbohydrates.

Some carbohydrates, however, are absorbed in a process known as facilitated diffusion. Facilitated diffusion describes a situation in which special carrier molecules are necessary, but energy (ATP) is not. Fructose is an example of a carbohydrate that is absorbed through facilitated diffusion.

Other nutrients, such as **lipids**, are absorbed through passive diffusion. In passive diffusion, neither energy expenditure nor a special carrier molecule is required. Lipids interact with bile salts from the liver, combining with them to form structures known as micelles. Micelles are able to diffuse freely through cell membranes and so can pass directly across the gut lining. Water is another substance that diffuses passively across the gut walls.

The circulatory system transfers nutrients and other products throughout the body. Tissues absorb the products they need from tiny blood vessels called capillaries. Capillaries are characterized by very high surface areas and very low blood-flow rates, both of which facilitate absorption. The walls of capillaries are also very thin, consisting of only one or a few layers of flattened endothelial cells. Capillaries also possess small pores through which transport and absorption can occur.

epithelial lining sheets of tightly packed cells that cover organs and body cavities

active transport a process requiring energy where materials are moved from an area of lower concentration to an area of higher concentration

facilitated diffusion the spontaneous passing of molecules attached to a carrier protein across a membrane

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

adenosine triphosphate (ATP) an energy-storing molecule that releases energy when one of the phosphate bonds is broken; often referred to as ATP

lipids fats and oils; organic compounds that are insoluble in water

The absorption of materials from the capillaries occurs in one of several ways. Lipid-soluble substances are able to diffuse directly across the cell membranes of capillary cells into the tissues. Water diffuses directly as well, although it makes use of special pores in the cell membranes of capillary cells. Exchange via diffusion is comparatively rapid.

The absorption of other nutrients from the blood requires transportation through the capillary walls inside special vesicles. This process is called transcytosis. The vesicles are membrane-bound and are believed to be constructed by a cellular organelle known as the Golgi apparatus. Vesicles shuttle products repeatedly between the inner and outer walls of capillary cells. Because capillary beds in the brain are characterized by fewer transport vesicles, many substances cannot be absorbed into brain tissue, and the absorption of those that can be is slowed. This is often referred to as the blood-brain barrier.

integument a natural outer covering

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

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

trachea the tube in air-breathing vertebrates that extends from the larynx to the bronchi

erythrocytes red blood cells, containing hemoglobin that carry oxygen through the body

respiratory pigments any of the various proteins that carry oxygen

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

In the process of respiration, oxygen is absorbed by the **integument**, **lungs**, **gills**, or **trachea** from the air or water. As with the circulatory and digestive systems, large respiratory surface areas allow for efficient absorption.

Oxygen is absorbed from the environment by the red blood cells, or **erythrocytes**. Erythrocytes contain **respiratory pigments**, which bind oxygen and works to transport it to tissues. These specialized oxygen-binding molecules are called pigments because they are often brightly colored when carrying bound oxygen. Respiratory pigments have a high affinity for oxygen and are also able to dramatically increase the oxygen-carrying capacity of blood.

Hemoglobin is the respiratory pigment in vertebrate erythrocytes and is also common throughout the animal kingdom. Hemoglobin is a large molecule consisting of four polypeptide chains, each of which is capable of binding an oxygen molecule. The oxygen-binding part of the chain is called the heme group and includes an iron atom. Hemoglobin binds oxygen cooperatively, meaning that once it has bound a single oxygen molecule, it is more likely to bind additional oxygen molecules. Hemoglobin's oxygen affinity, or the degree to which oxygen binds to it, varies according to such external factors as pH. This plasticity (flexibility) of oxygen affinity allows hemoglobin simultaneously to bind oxygen in the oxygen-rich environment of the lungs and to release it in the oxygen-poor environments of the tissues.

Another respiratory pigment, myoglobin, is present in the muscles and is responsible for pulling oxygen molecules from the blood into the tissues. Myoglobin resembles hemoglobin but consists of only a single polypeptide chain. SEE ALSO DIGESTION; TRANSPORT.

Jennifer Yeh

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Acoustic Signals

Acoustic signals are noises that animals produce in response to a specific stimulus or situation, and that have a specific meaning. These may be vocal communications emitted from the animal's larynx, such as a wolf's howl; sounds produced by appendages, such as a cricket's chirp; or sounds created by an animal's interaction with its environment, such as a rabbit thumping the ground with its hind foot when it sights danger. The **physiological** characteristics of animals, such as throat shape or lung size, create constraints on the type of acoustic signals an animal produces. Similarly, the anatomical properties of the ear, and the processing capabilities of the auditory regions of the brain, can limit the range of sound that a species is capable of detecting. Compared with most mammals, humans have an abnormally complex system of **vocalization** that is supported by the expanded language centers of the brain, a dexterous tongue and throat, and powerful lungs. However, humans are unable to hear in the frequency range of animals that communicate at much higher pitches, such as voles, or animals that vocalize with lower pitches, such as certain species of whale.

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

vocalization the sounds used for communications

Signal Characteristics

Several features combine to create a meaningful auditory signal. The first of these is the frequency, or pitch, of a sound. Another variable is the amplitude, or loudness. Different combinations of these two features can drastically alter the meaning of a sound. For example, a dog that whines quietly is communicating pain with a high-frequency, low-amplitude sound; a dog that growls loudly is expressing anger with a low-frequency, high-amplitude sound. The repetition rate and duration of a particular sound are likewise important. Male frogs of certain species, such as the plains leopard frog, call during breeding season to attract females; females recognize the calls of their own species by the length of the call and its repetition rate (calls per minute). Other species of frog in the vicinity use the same frequency call but vary its length and repetition rate.

The circumstances that surround acoustic signals can also alter their meaning. These include the time of year, time of day, spatial location, weather conditions, and physiological state of the organism (such as reproductive state). A mating call presented to females outside of the mating season may have no effect—the females are not hormonally prepared to respond.

The Uses of Acoustic Signals

Animals use acoustic signals in several instances: conspecific communication, **sexual selection**, mother-young interactions, interspecies communication, orientation, and language.

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

Conspecific communication. This (intraspecies communication) occurs between animals of the same species. Although sexual selection, mother-young interactions, and language are included in the category of conspecific communication, they will be explained separately because of their ecological importance. Conspecific communication can be very complex. For example, black-tailed prairie dogs live in very structured colonies that can cover tens of acres. When a prairie dog recognizes danger, it gives a warning call to

A common tree frog calling. In some species, the male uses his call to attract females during the breeding season.

the rest of the colony. Their vocal abilities are so elaborate that these animals can communicate the size, shape, and behavior of a predator by varying the features of their call. For example, a prairie dog call signifying a running coyote would be different from one signifying a gliding eagle. Intraspecies communication can relate danger, sexual selection, state-of-being, or features of the environment. A fairly universal form of intraspecies communication is the call made by a sick or dying individual. This kind of acoustic signal refers to the animal's state-of-being.

Sexual selection. This is the process by which species evolve characteristics that improve the chances of successful reproduction. Two facets of sexual selection involve acoustic signaling: locating and recognizing a mate, and defending territory. Acoustic signaling can improve the likelihood that an animal will find a mate of its own species over large distances or in the darkness. Sound, which travels at a rate of 340 meters (372 yards) per second in air and 1,230 meters (1345 yards) per second in water, provides an excellent means for quick signal transmission. An animal's reproductive success—the number and health of its offspring—may be seriously compromised if it cannot locate a mate of the same species. As a result of this selective pressure, many species have come to rely upon intricate calls to locate one another.

Territoriality. Another reproductive strategy is a behavior known as territoriality, in which males guard a particular location from other males of their species. Territorial male songbirds, such as nightingale wrens, each have a unique song. They mark their territory by repeating their trademark song at the boundaries of their territory or at the nest. This warns other males away from the chosen female and the chosen tract of land, thereby increasing mating success for that male and assuring a food supply for the young. This strategy is so successful that it can be seen in such diverse animals as the midshipman fish. Males of this species growl, hum, and grunt to attract females to their nests. However, the importance of acoustic signaling to sexual selection varies widely across species.

Mother-young communication. This exists between many vertebrate mothers and their offspring. In some species, including several groups of primates, the mother is able to recognize the distinct vocalizations of her young. Baby bird vocalizations cannot distinguish one hatchling from another, yet a mother bird responds equally to the call of any hatchling of the same age as her own young. In species where the parents invest time and energy into raising their young, it is of the utmost importance for the mother to be able to recognize the acoustic signals of her young. If she cannot distinguish her young from the young of others, she will waste precious time and resources on other individuals while neglecting her offspring. The cuckoo bird takes advantage of this fact by laying its eggs in the nests of other species. The infant cuckoo bird hatches among the young from the other species, but then it pushes the legitimate chicks or unhatched eggs out of the nest. When the mother bird finds her young have disappeared, the infant cuckoo is given all the nourishment, and the mother bird's energy is wasted on an individual that will not carry on her **genes**. Usually the hypersensitivity of a mother to the call of her young diminishes as her offspring mature.

genes segments of DNA located on chromosomes that direct protein production

Interspecies communication. This occurs when the hallmark acoustic signal of one species is conveyed to another species and induces that species to react in a predictable manner. A common example of interspecies acoustic signaling is when a rattlesnake shakes its rattle-shaped tail tip before striking. In this case, the snake is warning offending animals of its presence and its impending strike. This type of acoustic signal is most often a warning, as in the case of the mother bear growling when an animal approaches her cubs too closely. Conversely, an unintentional form of interspecies communication occurs when a predator can track the acoustic emissions of its prey. Woodpeckers listen for the sounds of insects chewing through wood so that they know where to peck, and owls can hear the squeaking of mice in the darkness.

Orientation. Some animals use auditory signals as their primary means of orientation. These animals emit sounds and then listen for the echoes that rebound off objects in the environment. The arrival time of the echo, its amplitude, and its divergence from the original call all give clues about the animal's environment. The best-known example of this strategy is echolocation in New World bats of the suborder **Microchiroptera**. The echoes from their calls are such good indicators of the environment that bats are able to fly through complicated environments in complete darkness, even when they are blinded. They also use their high-frequency echolocation to forage for fruit or flowers and to capture prey such as insects, fish, and small animals.

Microchiroptera small bats that use echolocation

Language. Humans use auditory signals to communicate with each other through language. No other animal is considered to have a system of communication complex enough to be considered language. Language differs from other kinds of communication in four features: flexibility, form, abstraction, and essentiality. Humans do not learn how to speak by memorization, but rather by **learning** rules for forming meaningful speech. The flexibility of language assures that despite the infinite number of experiences that influence the way people speak, they can be readily understood. Rules of sound, word, and sentence combination comprise the framework for the form of language. People express emotional and philosophical abstractions when they speak, not just the physical necessities of life. Essentiality refers to the reliance of human society on the use of language. Language is not

learning modifications to behavior motivated by experience just a tool—it shapes thinking and speech patterns and constitutes an integral part of one's sense of identity. Aside from language, humans also communicate with sounds such as laughter, screaming, and applause.

terrestrial living on land

invertebrates animals without a backbone

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

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

sonar the bouncing of sound off distant objects as a method of navigation or finding food

The acoustic signals of marine and **terrestrial invertebrates** and vertebrates depend on the **physiology**, social structure, and ecological **niche** of the organism. They are so important that the success of a species may depend entirely on acoustic signals, whether for feeding, mating, or interacting with one another. Humans inhabit every environment on Earth, and it is possible that the noise of modern human civilization is interfering with the acoustic signals of other species. A dramatic example of this is the beaching of seven whales in the Bahamas near the site of a naval **sonar** research site in February 2001. All of the whales showed signs of inner ear damage, and scientists hypothesized that the high amplitude noises used at the research site deafened them, causing pain and confusion. Further research into the acoustic signals used by animals could help prevent such ecological disasters. SEE ALSO Communication; Vocalization.

Rebecca M. Steinberg

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Active Transport *See Transport.*

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

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

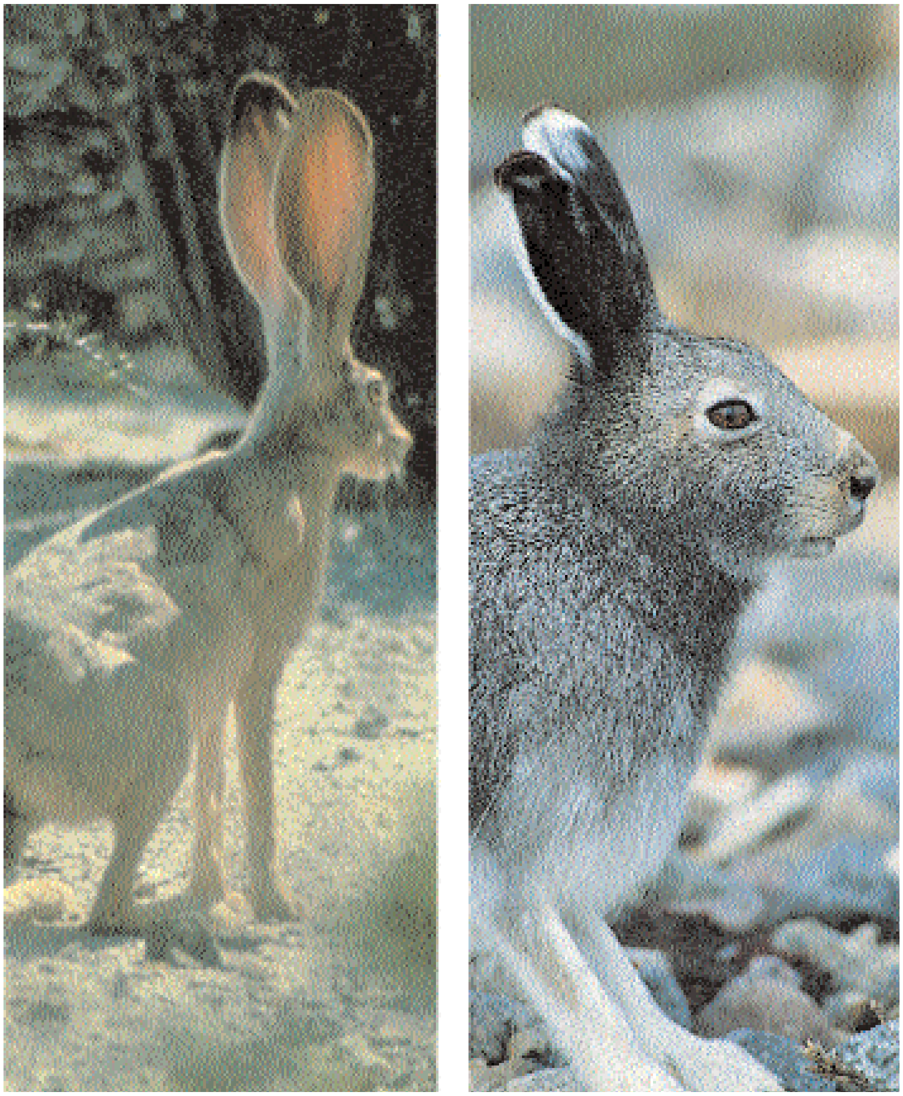
behavioral relating to actions or a series of actions as a response to stimuli

morphological adaptation an adaptation in form and function for specific conditions

Adaptation

Adaptations are the most important features of all organisms. An adaptation is a trait or characteristic that makes an animal survive or reproduce better in its environment. These traits can be **morphological**, **physiological**, or **behavioral**. Adaptations include almost all kinds of traits, such as what makes an organism blend into its surroundings, find food, mate with the correct species, and be able to survive.

An example of a **morphological adaptation** that increases the chance of survival is the coloration of an animal. Most animals that live in the arctic snow are white. Being white helps them blend in with the snow and hide from predators. An example of a physiological adaptation that increases the likelihood of survival is the kangaroo rat's metabolism. Kangaroo rats live



The different fur colors of the rural jackrabbit (left) and the arctic hare (right) allow them to blend into their environments, which helps them to evade predators, therefore increasing their chance of survival.

in the desert of the North American Southwest. It is extremely hot and dry there, and very little water is available. The kangaroo rat never needs to drink water because its metabolism has changed and adapted to conserve water; it gets all the water it needs from seeds it eats. Humans are the opposite; we must drink water daily because our metabolism uses lots of water. An example of a behavioral adaptation that increases reproduction is the croaking and calling of male frogs, which gets female frogs to come to the males for mating. Those frogs that call end up mating with more females and have more offspring than frogs that do not call.

Natural selection is the mechanism that produces adaptations. It is the difference in survival or reproduction between individuals with different traits. If an arctic hare, which lives in the snow, were gray rather than solid white, it would not survive as well as pure white hares. And if it does not live very long before it is killed by a predator such as a fox, then it will not produce as many offspring as a pure white hare, either. Natural selection increases the number of individuals in a **population** that actually has the adaptation; natural selection also maintains adaptations once animals have them.

natural selection the 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

All traits that are adaptations must have a genetic basis to them. That is to say, the trait must be produced in some way by **genes**, coded for by DNA. Genes enable an animal to pass on to its offspring the survival or reproductive advantage given by the adaptation.

genes segments of DNA located on chromosomes that direct protein production

There is one exception to the rule that adaptations need a genetic basis—traits that are learned within an organism's lifetime. Something that is learned does not have a genetic basis; it was not inherited from the parents. An example of a learned adaptation is that some male songbirds learn the songs of their neighbors. Neighborhoods of birds sing similar songs, and females prefer males that know more songs. A male that has learned more songs will reproduce more; **learning** songs is an adaptation. But learned traits are not completely free from genetics; there is a genetic basis to the ability to learn, even if the actual learning does not have a genetic basis. SEE ALSO Biological Evolution; Morphological Evolution in Whales; Morphology; Natural Selection.

learning modifications to behavior motivated by experience

Laura A. Higgins

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African Cichlid Fishes

The African cichlid fishes are well-known in the field of evolutionary biology as perhaps the most spectacular example of an **adaptive radiation**. An adaptive radiation describes a group of species that have rapidly diverged, or speciated, from a single ancestor, each of which occupies and is adapted to a distinct ecological niche. Other well-known adaptive radiations include those of two birds, the honeycreepers of Hawaii and Charles Darwin's finches, which occupy several islands in the Galapagos.

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

The African cichlids are found in the Great Lakes of the Rift Valley of Africa, including Lakes Victoria, Malawi, Tanganyika, Nabugabo, and others. In these lakes, cichlid fishes have undergone an unparalleled radiation. In all, over 1,500 species have evolved over the course of only ten million years, suggesting a truly remarkable rate of speciation.

Four separate genera and over 200 species occur in Lake Victoria alone. This is particularly impressive given that Lake Victoria is less than one million years old, having made a comparatively recent geological transition from flowing river to lake. When the Lake Victorian cichlids were initially discovered, the remarkably diverse species was initially confusing to biologists because the lake appeared to provide little opportunity for the ecological isolation of **populations**. Isolation is one of the factors generally believed to promote speciation.

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

habitats physical locations where organisms live in an ecosystem

The Reasons for Their Success

Why, then, have cichlid fishes been so successful in their African lake **habitats**? One reason is that the lakes provided a novel, underexploited habitat with few competing species. However, this cannot be the entire answer because several other species had the same opportunity to diversify in the new habitat soon after it formed. Why, among all the species present, was it the cichlids who underwent a remarkable radiation?

Feeding habits. The diversity of feeding habits is at the heart of the African cichlid radiation. The ancestral cichlid species was likely a generalist and an insect eater. However, extreme specialization now exists among the cichlid species, with each species specializing on a distinct, fairly narrow food niche.

There are, for example, cichlid species that specialize on algae, **plankton**, other fish species, mollusks, and insects, and there are even some species that eat only fish scales, or even fish eyes. This way of dividing up the available resources in a habitat is called trophic specialization ("trophic" refers to feeding). Because increased specialization allows for the coexistence of larger number of species, trophic specialization in cichlids is partly responsible for the great diversity of species.

Morphological specialization. In addition to using different food resources, the various species have also evolved different **morphological** specializations, or specializations of form, that are appropriate to their diet. For example, species exhibit a wide range of tooth shapes and sizes, as well as many different mouth and lip **morphologies**.

But how are individual cichlid species able to exploit such narrow food niches? One hypothesis is that cichlid success is related to their highly unusual anatomic characteristic of having two pairs of jaws. The outer jaws, also called the oral jaws, are **homologous** to the jaws of other vertebrates, and appear externally in the usual position.

The second pair of jaws are invisible externally and lie within the throat area. These are known as the **pharyngeal** jaws. Because the pharyngeal jaws are able to chew and process food, the outer jaws are free to become highly specialized for obtaining food.

Interestingly, trophic specialization is implicated in other instances of adaptive radiation, including those of the Hawaiian honeycreepers and of Darwin's finches. In both these radiations of birds, there is a great diversity in beak morphology, which is in turn related to differences in feeding. Among the Hawaiian honeycreepers, there are species that feed on seeds, insects, and nectar. Among Darwin's finches, as well, different species are specialized on different seed sizes.

Pharyngeal jaws, which characterize cichlids as well as a few other related families of fishes, can be described as the key innovation in the African cichlids that has allowed for the evolutionary success of the group. A key innovation is defined as a novel adaptation that allows a lineage to exploit resources that were previously unavailable. Key innovations are frequently associated with impressive species diversification. Other examples of key innovations include flight in birds, direct development in certain lineages of frogs (which bypasses the **aquatic** larval stage and allows for the occupation of more terrestrial habitats), incisors that grow constantly in rodents, and insect pollination by **angiosperms**.

In addition to the possession of pharyngeal jaws, cichlids appear to be highly adaptable both behaviorally and morphologically. Certain cichlid

The *Aulonocara nyassae* of Lake Nyassa, Africa, is only one species of thousands found throughout the Great Lakes of the Rift Valley. African cichlids are one of nature's best examples of adaptive radiation.

plankton microscopic organisms that float or swim weakly near the surface of ponds, lakes, and oceans

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

morphologies the forms and structures of an animal

homologous similar but not identical

pharyngeal having to do with the tube that connects the stomach and the esophagus

aquatic living in water

angiosperms a flowering plant that produces seeds within an ovary

species are able to alter their tooth and skull morphology depending on available food resources. The ability to change morphologically in response to cues from the environment is known as **phenotypic** plasticity.

phenotypic the physical and physiological traits of an animal

Plasticity allows cichlid species to take advantage of whatever resources become available. One cichlid species found in Lake Victoria, for example, specializes on snails and has the robust skull and teeth necessary to deal with snail shells. However, when introduced into a different habitat, the species switched to an insect-based diet and no longer developed the robust dentition.

Sexual selection. Another factor that may have played a role in the evolution of the African cichlids is sexual selection. **Sexual selection** describes a situation in which different individuals in a population have different reproductive success. Different reproductive success can result from any of several factors. In many animal species, however, including cichlids, sexual selection arises because the reproductive success of males depends on the number of female mates they are able to attract and convince to mate with them. Sexual selection can lead to the rapid evolution of male traits for the attraction of females and of female preferences for these traits.

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

Sexual selection has been hypothesized to have played a role in the rapid diversification of many other species-rich lineages, including the songbirds, where both plumage coloration and song are objects of selection; Hawaiian fruitflies of the genus *Drosophila;* ducks; and hummingbirds. All these groups are characterized by elaborate courtship displays. Cichlid fishes are also characterized by a complex courtship behavior in which males build elaborate nests, known as bowers, and females inspect them in order to decide which males to mate with. SEE ALSO HABITAT.

Jennifer Yeh

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Aggression

Because members of a population have a common niche, there is a strong potential for conflict. Agonistic behavior is displayed when there is a contest that will determine which competitor gains access to a particular resource—for example, food or a mate. The encounter involves both threatening and submissive behavior, and may also involve tests of strength. More often, the contestants engage in threat displays that make them look large or fierce, usually through exaggerated posturing and vocalizations. Eventually one animal will stop threatening and end with a display of submission or appeasement, in effect calling an end to the fight.

Much agonistic behavior includes ritual activity so that serious harm does not occur to either combatant. In many circumstances, escalated vio-

This badger's snarling is known as a "threat display." This badger uses this signal to defend its burrow.

lence over ownership of a mate or commodity is less an adaptive behavior than it is an exchange of signals, whether threatening or submissive. The agonistic signals provide information about the likely intentions and levels of commitment of the senders, as well as the relative fighting ability if escalation occurs. Any future interactions between the same two animals is usually settled much more quickly and in favor of the original victor.

Aggression can be used in a number of different interactions, such as those concerning territorial defense, potential mates, parent-offspring communication, social integration, and food. Conflict resolution usually occurs at short sender-receiver distances. The senders perform actions with tactical and signal functions, and the receivers make decisions based on all the information pooled from the cues and all secondary sources.

Intra– and Interspecific Competition

Conflicts usually arise between two more or less equal individuals who need the same resources to secure or increase their fitness. Both would like to obtain the resource with minimal fighting, so both want the other individual to back down. However, the two opponents are rarely of equal fighting ability or resource-holding potential. Each combatant wants to convey that it is the superior fighter and so uses displays of aggression. However, each one must also assess the other's fighting ability relative to its own. Thus both individuals are senders and receivers simultaneously. The number of signals and tactical acts, and the truthfulness in the information being conveyed, must have something to do with the resolution of the conflict.

Types of Conflict

Intraspecific competition. When the conflict is **intraspecific**, between members of the same species, **dominance hierarchies** come into consideration. For example, placing several hens together that are unfamiliar with each other results in pecking and skirmishing. Eventually, a **pecking order** is established in which the most dominant hen, the **alpha** hen, controls the behavior of all the other hens, mostly through threat rather than actual pecking. The beta (second-ranked) hen does the same and so on to the lowest hen, the omega. The advantage of the top hens is that they are

intraspecific involving members of the same species

dominance hierarchies the structure of the pecking order of a group of individuals where the multiple levels of dominance and submission occur

pecking order the position of individuals of a group wherein multiple levels of dominance and submission occur

alpha the dominant member of a group assured access to food resources. There is an advantage for the lower-ranked hens as well, because the system ensures that they will not waste energy or risk injury in futile combat.

Interspecific competition. In the event that two or more species in a community rely on similar resources, they may be subject to interspecific competition. Actual fighting between members of two different species is termed interference competition, whereas the use or consumption of the "shared" resources is called exploitative competition. As population densities increase and resources such as food or nesting sites decrease, there is bound to be an increase in competition between the species. The same tactics of agonistic signaling apply here despite the variation in numbers and types of signals among the different species.

Strategies for Victory

Individuals in conflict can employ a number of strategies when assessing their opponent and the minimal level of aggression necessary to be the victor.

Hawk vs. Dove. One theory, termed "hawk versus dove," helps explain why two animals do not always fight over the commodity that is sure to increase the fitness of the winner. Assuming the contestants are equal, there are two clear choices regarding the sought-after commodity: fight (as an aggressive hawk would do) or exhibit peaceable displays (as a dove would be more apt to do). When two hawks meet, they immediately fight over the commodity, with the loser suffering fight injuries as well as the cost of having lost the resource. Because the contest is assumed to be symmetric, each hawk wins half of its battles with other hawks. When a hawk meets a dove, the hawk becomes aggressive and the dove flees. Two doves will both use some costless exchange of displays to decide who gets the commodity and who leaves peacefully.

The take game. Another contest that has been observed is a take game, which again involves two strategies: to be passive or to cheat. The passive animal minds its own business. The cheat, however, increases its own fitness at the expense of the fitness of others. The fishing activity of gulls and terns offers a good example. Some (passive) birds will concentrate solely on catching their own fish. Others (the cheats) will give up some of their own fishing time to monitor the success of other birds. When another bird catches a fish, the cheat will chase after the bird until the fish is dropped and then steal the fish. There is an advantage to cheating only if the bird can steal more fish than it would catch on its own.

The significance of this game is that once any cheats appear, the population will become most stable once all the organisms cheat. Evolution will have therefore lowered the average fitness of the population, a nonintuitive outcome given the assumption that evolution generally improves the average fitness of populations. It is only where evolution models a more passive approach to the acquisition of resources that populations enjoy improvements in their average fitness. However, many evolutionary models lead to lower average fitness, and this simply reflects the costs of competition.

The war of attrition. Certain games employ strategies drawn from a continuous range of possibilities. A classic example is the war of attrition, in which two opponents compete by selecting an amount of strategic investment to be played during the particular confrontation. Neither opponent knows before the confrontation what level of investment the other has chosen. During the confrontation, the opponent that chose a larger investment wins. The investment might be the amount of time each is prepared to display to the other, or it might be how much energy the players put into the display.

It is unlikely that many animals meet the conditions for a symmetric war of attrition, where all players suffer the same cost of display and would obtain the same benefit in winning. Usually the rate at which costs accumulate will not be the same for any two players. Also, the commodity over which they are fighting is likely to have different fitness values for each player. The critical issue thus becomes which player stands to gain the most from the commodity and lose the least while trying to win it. If the two animals knew at the outset which one was on superior footing, then there would be no confrontation and the animal that stood to lose the most would leave immediately.

However, such complete and accurate information is rarely available as two opponents face each other. The "game" that is then played is called an asymmetric war of attrition. A player that suspects it has the winner role will likely select a higher investment, while a player that suspects it has the inferior role will likely select a lower investment. Of course, it is possible that both players will decide they occupy the same role. These considerations emphasize the uncertainty inherent in this game. Depending on the presumptions of both animals, the confrontation may brief—or it may prove to be a long and vigorous fight. SEE ALSO Behavior; Behavioral Ecology; Dominance Hierarchy; Social Animals.

Danielle Schnur

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Agnatha

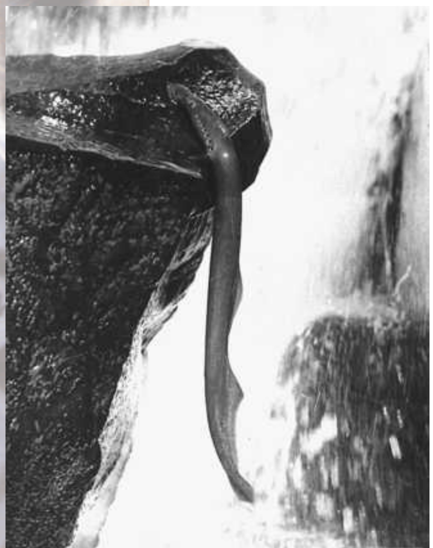
The group Agnatha consists of the jawless fishes, the most primitive group of **extant** vertebrates. While most agnathan species are now extinct, fossil evidence indicates that the group was once highly successful and extremely varied. Two lineages of agnathans have survived to the present, the lampreys and the hagfish.

extant still living

Characteristics of Agnathans

As the most primitive members of the vertebrates, agnathans differ from all others in several important respects. First, they lack hinged upper and lower jaws and instead have unhinged circular mouths. They also lack the paired appendages (fins or limbs) that are found in other vertebrates. In addition, the internal skeleton of agnathans is not bony but **cartilaginous**. However, many extinct agnathans had extensively developed bony plates

cartilaginous made of cartilage



Lampreys have suckerlike mouths which they use to attach to substrates, including the fish they parasitize.

directly under the skin. These were most often found in the region of the skull and served as a protective armor. Bony plates are not present in extant agnathan species.

Major Groups of Living Agnathans

There are two major groups of living agnathans, the lampreys and the hagfish. Both appear fishlike or eel-like.

Lampreys are parasitic species that use their suckerlike mouths to attach to a fish host. They use the many teeth in their mouths and on their tongues to rub at the flesh of their prey. Adult lampreys inhabit a saltwater marine environment but swim up rivers to reach freshwater breeding grounds. Lampreys breed only once in their lifetime, in a single tremendous reproductive bout, and die soon after. Lampreys pass through an immature larval stage before **metamorphosing** into adults. The larval lamprey is always in freshwater. It grows and matures for several years before undergoing metamorphosis and migrating to saltwater **habitats**. Before it was known that the larva was a larval lamprey, it was thought to be a separate species. The larva is of particular interest to biologists who study vertebrate evolution because it shares many features with the cephalochordate *Branchiostoma* (formerly called *Amphioxus*), which is the group believed to be most closely related to the vertebrates. The resemblance between *Branchiostoma* and the larval form of a very primitive vertebrate is striking, and supports the closeness of the relationship between the two groups.

metamorphosing changing drastically from a larva to an adult

habitats physical locations where organisms live in an ecosystem

fossil record a collection of all known fossils

The second group of living agnathans is the hagfish. Hagfish are scavenger species that feed off dead and wounded organisms in the ocean. They are also well-known for their defense mechanism; when threatened, hagfish ooze out great amounts of foul slime.

Evidence from the **fossil record** suggests that agnathans reached their peak of diversity between about 500 million and 340 million years ago. During this period, they were plentiful both in the seas and in freshwater habitats. More than 200 fossil species are known. The majority of these species were fairly small, perhaps a few inches long. The species that have survived to the present are but the remains of a group that was once considerably more diverse. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

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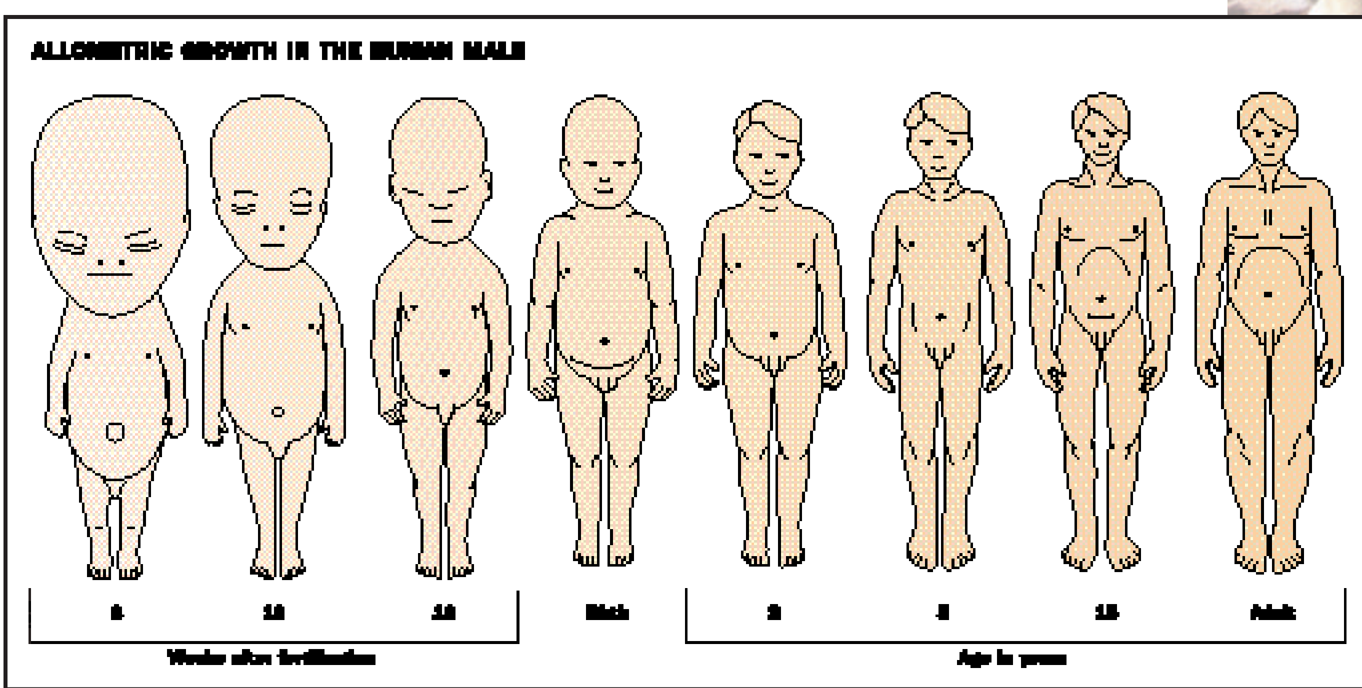
Allometry

The relationship of the growth of one part of an organism to the growth of another part or the growth of the whole organism is called allometry. The term also applies to the measure and study of such growth relationships. Allometry comes from the Greek word *allos*, which means "other," so allo-

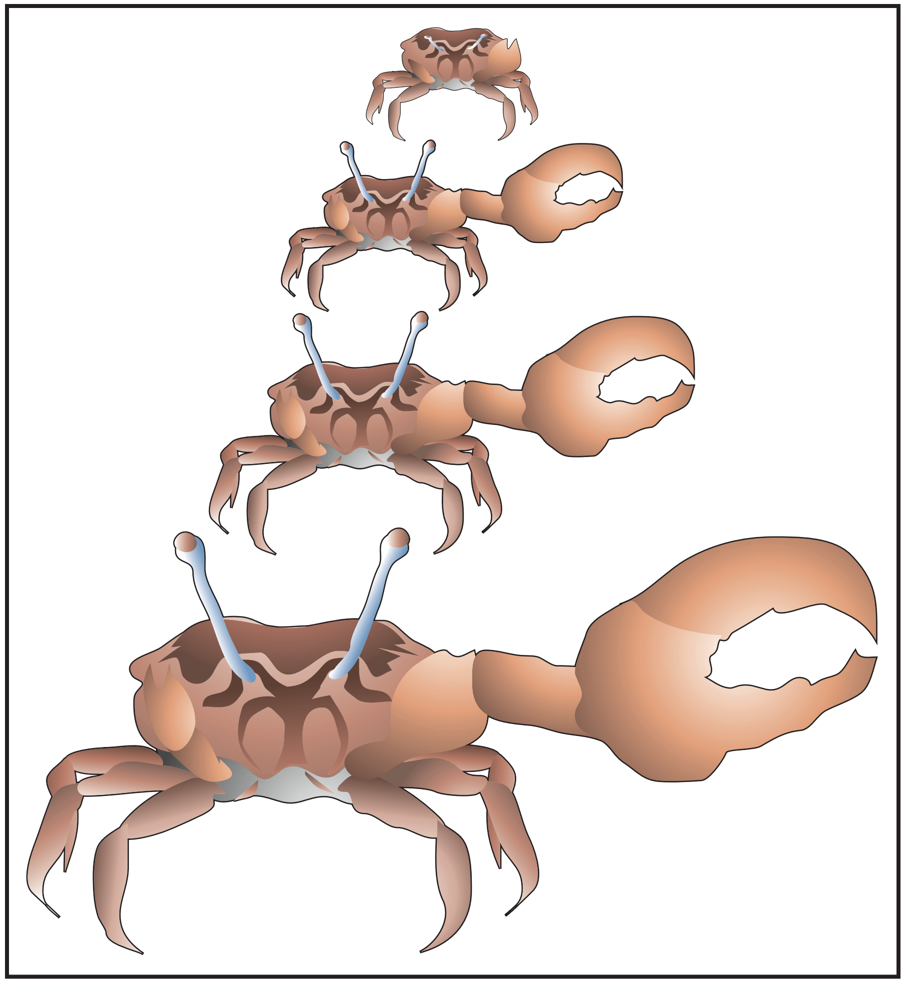


Allometric growth in the human male. Redrawn from Scott Gilbert, 1998.

metric means "other than metric." Isometric growth, where the various parts of an organism grow in one-to-one proportion, is rare in living organisms. If organisms grew isometrically, young would look just like adults, only smaller. In contrast, most organisms grow non-isometrically; the various parts and organisms do not increase in size in a one-to-one ratio. One of the best known examples of non-isometric growth is human growth. The relative proportions of a human body change dramatically as the human grows. Medieval and earlier painters sometimes did not realize this and drew children as tiny adults. But the bodies of tiny adults do not look like those of children. Children have proportionately larger heads and shorter legs than adults. The difference is even more dramatic when human embryos are compared to adults. The figure above shows the relative proportions of a human male at various stages of growth, scaled to the same total height.

A general equation expressing the fundamental relationship of allometric growth is $y = ax^k$ in which y is the size of one organ; x is the size of another; a is a constant; and k is known as the growth ratio. Mathematical tools developed by allometrists have allowed a thorough description of the differential growth of the different parts of an organism. Biologists expect that allometry will eventually improve our understanding of the biological processes that regulate the growth rate.

A change in form with increasing size is a response to increasing instability. For example, body weight increases with the cube of total height. But the strength of muscles and bone depends on cross-sectional area. Area is proportional to the square of a dimension, so the strength increases with the square of total body height. If muscle mass and bone mass did not increase more rapidly than the mass of the body as a whole, the human body would become unstable and unable to support its own weight. On the other hand, metabolic rates (and the heat produced by metabolism) increase less rapidly than total body height, since the larger volume-to-surface-area ratio means



Fiddler crabs (*Uca pugnax*) display allometric growth in their claws. Redrawn from Scott Gilbert, 1998.

that less heat is lost through the skin. In humans, a 100 percent increase in height produces a 73 percent increase in metabolic heat production.

Another example of allometric growth is seen in male fiddler crabs, *Uca pugnax*. These crabs are so named because of their one large claw and "pugnacious" attitude (*pugnare* means "to fight" in Latin). In small males, the two claws are of equal weight, each containing about one-twelfth of the total weight of the crab. However, the size of the large claw increases disproportionately to the growth of the rest of the animal, producing in larger males a claw that may contain two-fifths of the total weight of the crab.

Allometric growth is usually detected by graphing the growth data on a log-log plot. That is, the horizontal and vertical axes of the graph are both logarithmic scales. The general allometric growth equation has the form $y = ax^k$. Taking the logarithm of both sides produces the following equation: $\log(y) = k\log(x) + \log(a)$.

This equation has the basic form of a linear equation in slope-intercept form, $y = mx + b$. If the body mass of *Uca pugnax* is plotted on the x-axis and the claw mass is plotted on the y-axis of a log-log plot, then the result will be a straight line whose slope is the relative growth rate of claw mass to body mass. In the male *Uca pugnax*, the ratio is 6:1. This means that the mass of the big claw increases six times faster than the mass of the rest of the body. In females, the claw grows isometrically and remains about 8 percent of the body weight throughout growth. Allometric growth occurs only in males.

Allometric growth is also seen in nonhuman primates. For example, the jaw and other facial structures of baboons have a growth rate about four and one-quarter times that of the skull. As the baboon matures, the jaw protrudes further and further until it dominates the facial features. SEE ALSO Functional Morphology.

Elliot Richmond

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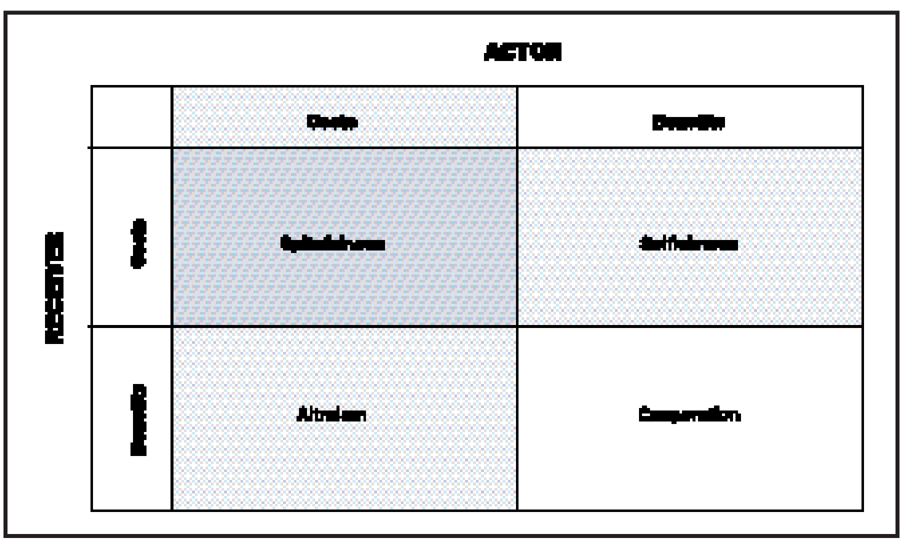
Altruism

Altruism, defined as an action that benefits the receiver but comes at some cost to the performer, is one of the four types of social interactions that can occur between animals of the same species. Figure 1 summarizes these four interactions. Cooperation, where both actor and receiver benefit, and selfishness, where the action benefits the actor at the expense of the receiver, are by far the most common of the four interactions in nature. Spite, where both actor and receiver are harmed, and altruism are very rare.

The prevalence of cooperation and selfishness over altruism and spite is explained by the rules of **natural selection**. The currency of natural selection is offspring. Any anatomical, physiological, or behavioral trait that enhances an individual's ability to produce more offspring will be favored, and the trait will be selected regardless of the effects on others. For example, seagulls sometimes steal food from nesting neighbors to feed themselves and their chicks. This behavior clearly increases the fitness of the actor while

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



Social Interactions that can occur between animals of the same species.

decreasing the fitness of the receiver; it is selfish. Imagine an altruistic seagull that willingly provided food for its neighbors. This trait would not last very long in the population because the helpful gull would not be able to feed many of its own offspring.

Within the social structure of the meerkats' community, there is always a sentry "on duty" keeping watch for any predators.

Reciprocal Altruism and Kin Selection

Despite the odds against altruism evolving, it does exist in nature. Some biologists, however, consider these instances to be examples of pseudoaltruism, and insist that true altruism has yet to be found. Pseudoaltruistic acts appear to be altruistic, but "in the long run" are actually beneficial to the actor. There are two types of pseudoaltruism—reciprocal altruism and kin selection.

Reciprocal altruism. This occurs when the actor acts altruistically in expectation of having the same done in return at a later time. Many animals that live in groups will post sentinels to watch for predators while the rest forage for food. The sentinel changes several times daily, so the animal "on duty" is assured of being protected later when it is his turn to forage. Vampire bats provide another example. If, when the group returns from hunting, one individual has not found food, a neighbor will regurgitate a portion of its meal for the hungry one. The next evening, the helpful bat may be the hungry one and need the favor returned.

Kin selection. This other type of pseudoaltruism, kin selection, was proposed by British scientist W. D. Hamilton in 1964. He realized that an individual could not only increase his fitness by having its own offspring, but it could also help a close relative raise its offspring, since they share genes. The combination of individual fitness and fitness through kin selection is inclusive fitness. Hamilton argued that if the benefits the actor receives by helping its relatives outweighs the cost of the action, then altruism can evolve. This concept can be expressed mathematically through **Hamilton's Rule**: $br > c$, where b is the benefit to the actor, r is the relatedness of the actor to the receiver, and c is the cost to the actor. Relatedness is measured by the proportion of genes that are identical between two individuals. Because of Mendelian inheritance, half of a diploid individual's genes are shared with each of its parents, siblings, and children. Diploid grandparents share one-quarter of their genes with their grandchildren, and cousins share one-eighth of their genes with each other. An individual who helps two of its siblings, four of its grandchildren, or eight of its cousins is just as fit as the individual who helps only itself.

Hamilton's Rule individuals show less aggression to closely related kin than to a more distantly related kin

Kenyan bee-eaters of the bird genus *Merops*, have evolved behaviors by kin selection. Male bee-eaters will typically forgo reproducing when they are young, instead opting to help more mature birds raise their young. These young males help relatives more often than nonrelatives, thus raising their inclusive fitness. Young males that attempt to have their own offspring actually fare worse than helpers because their territories are too poor to raise more than one chick.

eusocial animals that show a true social organization

haplodiploidy the sharing of half the chromosomes between a parent and an offspring

Conclusion

The classic example of altruism occurs in the **eusocial** bees. Honeybee workers rarely reproduce, letting the queen provide all the offspring. An unusual chromosome condition, called **haplodiploidy**, produces unusual relatedness among the bees in a hive. Workers are actually more related to their sisters (eggs laid by the queen) than their own offspring! Although honeybees are considered the classic example of altruism, they really practice a form of kin selection. True altruism has not yet been found in nature, and some scientists believe that true altruism can be found only in human populations. SEE ALSO Social Animals.

Jes Marie Creech

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Amphibia

Amphibia is one of the five major classes of vertebrates. There are three orders in the amphibia group, two of which are widely familiar, frogs (Anura) and **salamanders** (Caudata), and one of which is less well-known, the tropical caecilians (Gymnophiona). The name "amphibian" refers to the use of both aquatic and terrestrial habitats, and the life history patterns of species in the group.

salamander a four-legged amphibian with an elongated body

Amphibian Characteristics and Life History

The earliest tetrapods (four-legged, terrestrial vertebrates) were amphibians, and living amphibian species retain some of the primitive characteristics of the first terrestrial vertebrates, which invaded land habitats during the geologic period known as the Devonian, which was approximately 408 million years ago. For example, unlike other terrestrial vertebrates, amphibians lack scales and claws, and are instead characterized by a moist, glandular skin composed of living cells. The skin is involved in respiration to some degree in most amphibians. Certain lungless salamanders rely largely on the skin for gas exchange. In many species, skin glands secrete noxious, or sometimes highly poisonous, substances that serve as deterrents to predators. This is sometimes associated with a warning coloration that advertises toxicity, and some species have even evolved specific defensive postures to show off effectively their warning coloration. One example of this is the "unken reflex," in which the animal throws back its forelimbs to display the bright warning colors on its belly. The possession of skin with living cells limits many amphibian species to fairly moist habitats, although certain species have drier skins and are able to tolerate drier habitats. Amphibian eggs also require moist environments. These lack the water-conserving eggshells found in other terrestrial vertebrate groups and are instead covered with a gelatinous capsule.

Many amphibian species make use of both aquatic and terrestrial habitats, either simultaneously or sequentially during different life stages. A typical amphibian life cycle involves semiterrestrial adults that breed and lay eggs in water. Eggs then develop into aquatic larvae. After a period of

This tree frog belongs to the Anura order of the amphibian group.

growth, the larvae undergo metamorphosis, or transformation, and become semiterrestrial adults. Metamorphosis is triggered by changes in concentrations of circulating **hormones**. Numerous anatomical changes occur during metamorphosis. These include the loss of gills; the development of lungs; the development of eyelids; the loss of aquatic sensory systems such as the **lateral line,** which is responsible for underwater "hearing"; tongue development; maturation of the kidneys and **gonads**; and changes in the skin, which becomes thicker and develops dermal glands. Of the three amphibian **clades**, or orders, metamorphosis is most extreme among frogs, where there is a striking difference between the larva (the tadpole) and the adult. Particularly striking is the rapid development of fore- and hindlimbs and the loss of the tail. In addition, there are anatomical changes associated with the transition from an **herbivorous** tadpole to a **carnivorous** adult. These include reshapings of the jaws and mouthparts, as well as a shortening of the digestive tract. The rapid and extreme nature of metamorphosis in frogs results in unusually high mortality levels during this period. Locomotion is difficult both in the water and on land because of the simultaneous presence of limbs and a tail.

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

lateral line a row of pressure sensitive sensory cells in a line on both sides of a fish

gonads the male and female sex organs that produce sex cells

clades a branching diagram that shows evolutionary relationships of organisms

Although aquatic larvae, metamorphosis, and semiterrestrial adults make up a typical amphibian life history, it is important to remember that there are numerous exceptions to this pattern. These include egg laying in drier habitats, including trees, rather than in aquatic habitats; bypassing the larval stage via direct development of eggs into miniature versions of adults; and even live-bearing in select species. In fact, the diversity of reproductive modes is greater among amphibians than other vertebrate groups.

All amphibians are carnivorous, with the exception of larval frogs (tadpoles), which are primarily herbivorous. Most amphibians are generalists, and will eat anything they can capture and ingest. Frogs and salamanders capture prey with their tongues, which are highly developed. Certain salamander species have specialized projectile tongues that they fire with impressive accuracy to capture prey.

herbivorous describes animals that eat plants

carnivorous describes animals that eat other animals

Major Amphibian Groups

The three orders of amphibians are salamanders, frogs, and caecilians.

Salamanders. There are approximately 400 species of salamanders worldwide. Salamanders retain a fairly primitive vertebrate **body plan**, with slender bodies, four limbs, and tails. Some species have undergone limb reduction, and a few species lack hindlimbs, possessing only two front limbs. Although a few species of salamanders are characterized by external **fertilization** of eggs, the majority use internal fertilization via spermatophore. After an often extensive courtship, in which mating pairs swim or walk together, the male releases a spermatophore that consists of a gelatinous pedestal capped with a ball of sperm. The female walks over the spermatophore and picks it up with the lips of her cloaca, the common chamber into which digestive, urinary, and reproductive tracts discharge. Sperm are then stored internally in the spemathecae, where they are used to fertilize eggs that are laid later. A large number of salamander species are actually direct developing, with eggs hatching directly into miniature adults. In this way, the aquatic larval stage is bypassed. Other species are perrenibranchiate, and never **metamorphose**. These species retain the larval morphology their entire lives. Among amphibians, only salamanders include perrenibranchiate species. The axolotl, a well-studied organism, is perrenibranchiate. There are also a small number of live-bearing salamanders, with development taking place in the oviduct of the female.

body plan the overall organization of an animal's body

fertilization the fusion of male and female gametes

metamorphose to change from a larva to an adult

Frogs. There are over 4000 species of frogs, making it the most diverse of the amphibian orders. Frogs have made striking modifications in the ancestral amphibian body plan, many of these associated with their saltatory (jumping) mode of locomotion. These include the loss of the tail, a shortened vertebral column, and the fusion of many bones of the forelimbs and hindlimbs. Frogs are ecologically diverse, and have adapted to a wide variety of habitats. Some species are highly aquatic, with adults never making use of terrestrial habitats. Highly aquatic species are characterized by streamlined bodies and extensively webbed hindfeet. They swim by kicking their hindlimbs simultaneously, which essentially represents the use of saltatory motions in the water. Several separate lineages of frogs have adapted to **arboreal** habitats. These species are characterized by adaptations such as expanded toe pads and opposable thumbs. They also tend to locomote by

arboreal living in trees

walking hand over hand rather than jumping. A few arboreal species are even able to parachute from tree to tree. These "flying frogs" have extensive webbing between their fingers and toes, which they extend as they parachute. Finally, some frogs are fossorial and live underground. These species often possess digging specializations such as muscular forearms or hard, keratinized spade-shaped digging tools on the hindfeet. Certain fossorial frogs are even able to survive in desert environments. Individuals remain **torpid** in burrows much of the time, but come out once a year during heavy rains to reproduce.

torpid a hibernation strategy where the body temperature drops in relation to the external temperature

Frogs are unique among amphibians in that courtship in most species involves vocal calling by males. Calls are species specific, and considerable research has been done on sexual selection in certain species. Mating typically involves amplexus, in which the male clasps the female either at the shoulders or at the hindlegs. Fertilization is most commonly external, although certain species use internal fertilization.

Caecilians. The third group of amphibians is the caecilians, which are found only in tropical regions. There are approximately 200 species. Caecilians are wormlike amphibians that lack limbs. They have rings on the outside of the body that cause them to appear segmented. Many species lack a tail, and the cloaca is at the end of the body. They vary in size, with the largest species attaining lengths of up to three feet. Caecilians are fossorial or aquatic, and eyes are smaller than in the other two groups. In certain species the eyes are buried beneath the skin or even beneath skull bones. Caecilians also possess a unique sense organ called the tentacle, which is found between the nostril and the eye. It functions as a chemical sensor (detector). Caecilians feed primarily on earthworms and other invertebrates. Unlike frogs and salamanders, caecilians do not use tongue projection to capture prey. Rather, they catch a worm with their jaws, spin it lengthwise in order to remove and ingest a piece, and then try to catch the worm again.

Also in contrast to frogs and salamanders, more than half of caecilian species are **viviparous**, or live bearing. Fertilization is internal, via a male organ called the phalloideum. Free-swimming larvae hatch within the maternal oviduct, where they live and feed until birth. Caecilian larvae are characterized by special larval teeth that they use to scrape the walls of the oviduct. This stimulates maternal glands to secrete a fatty milk on which the larvae feed. The adult teeth develop prior to birth. Larvae in viviparous species also possess large gills that they flatten against the wall of the oviduct to obtain oxygen.

viviparous producing living young (instead of eggs) that were nourished by a placenta between the mother and offspring

Recent Amphibian Declines

In the last few decades of the twentieth century, scientists began observing a rapid and alarming global decline in numerous species of amphibians. This is particularly disturbing in that certain previously abundant species have apparently gone extinct in relatively undisturbed pristine habitats. Many causes have been suggested as possibly being involved in the declines, including increased levels of ultraviolet radiation due to destruction of the ozone layer through human activities; declining pH levels from **acid rain**; parasites; disease; and **habitat loss**. It is quite possible that a combination

acid rain rain that is more acidic than non-polluted rain

habitat loss the destruction of habitats through natural or artificial means of these factors is responsible. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

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Animal

Animals are multicellular, **heterotrophic eukaryotes**. Because animals are unable to make their own food, they must have some means of ingesting food. They do this by consuming plants, other animals, or decomposing organic matter, or by absorbing nutrients directly from a host. Animals typically store food reserves in their body as glycogen. Animals have nerve tissues to gain information about the environment and muscle tissue to allow them to move. They have membrane-bound cells that lack rigid walls. Most animals reproduce sexually and spend most of their life cycle as diploid organisms. These are the characteristics that generally separate animals from other groups.

heterotrophic eukaryotes organisms containing a membrane-bound nucleus and membrane-bound organelles that do not make their own food

PLANTS	ANIMALS
Multicellular	Multicellular
Cell wall and cell membrane	Cell membrane
Autotrophs—make their own food	Heterotrophs—must ingest food
Store excess food as starch	Store excess food as glycogen
No form of locomotion	Most animals have a form of locomotion

Comparison of basic characteristics of plants and animals.

By this definition the first animals appeared on Earth in the Precambrian oceans over 500 million years ago. Since that time animals have evolved into many diverse forms. Some of those forms have become extinct while others continue to thrive. At the start of the twenty-first century, more than one million species of animals are known on Earth, with more being discovered all the time. Animals are grouped into about thirty-five **phyla**. Over 95 percent of the animal species lack a vertebral column and are called invertebrates.

phyla broad, principal divisions of a kingdom

Animals are found in nearly all environments on Earth. The oceans are home to the largest number of animal phyla. Freshwater environments are home to a large number of phyla, but those environments are not as

terrestrial living on land

diverse as the oceans. **Terrestrial** environments have the smallest number of animal phyla.

Allan B. Cobb

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Animal Rights

The opinions regarding animals and their rights greatly vary. To some, animals have no rights and are merely a form of property that exists only to fulfill human needs. To others, they are creatures that can be used or owned by people, but which also have feelings and are not to be subjected to needless suffering or pain. (Some would say that people with this belief are animal welfare, as opposed to animal rights, advocates.) Finally, there are those who believe that at least certain animals, such as those with sophisticated levels of intelligence and emotions (including nonhuman primates such as monkeys and chimpanzees), are not property at all nor meant to be utilized by man in any way. Such people believe that these animals are entitled to fundamental moral and legal rights that are currently accorded only to humans.

The animal rights movement includes many different organizations. In the United States alone, more than 100 groups are interested in the welfare of animals, and the focus of their activities and their tactics vary widely. For example, the Humane Society uses public education to promote responsible pet ownership, eliminate pain and cruelty in hunting and animal research, and advance similar causes. In contrast, the Animal Liberation Front commits illegal acts such as break-ins, the destruction of property, and the releasing of animals in its efforts to end all forms of what it considers to be animal exploitation.

Opponents to the animal rights movement also vary. Some see it as a group of do-gooders who are interfering with their right to treat or use their property as they wish. Others believe that the movement (or at least a part of it) consists of extremists who threaten the economic, political, and religious institutions in our country. Virtually every other country has one or more anticruelty statutes that prohibits the mistreatment of animals, but the provisions and effectiveness of those laws vary greatly. Many nations also have organizations that are interested in protecting the welfare of animals. Aside from the United States, the animal rights movement is most active in Canada, Western Europe, Australia, and New Zealand.

Historical Groundwork

Humans have long used animals for a variety of purposes. For hundreds of thousands of years, people have hunted for food and clothing. Between 10,000 and 18,000 years ago, humans began to domesticate animals such as dogs, goats, sheep, and chickens as beasts of burden and as food. For at least 2,500 years, animals have been used in circuses and other forms of entertainment. In the second century C.E., the Greek scientist Galen conducted some of the first medical experiments on living animals.

Animal rights activists gathered on the steps of the statehouse in Boston, Massachusetts (1999), with their greyhound dogs to protest the treatment of animals still used in dog racing.

Antiquity. The ancient Greeks believed that nonhuman creatures were created by the gods to be used however people wished. According to the Bible, God gave man dominion "over the fish of the sea, over the birds of the air, and over the cattle, over all the Earth and over every creeping things that creeps on the Earth" (Gen. 9.1–3). This statement reflects the understanding of the ancient Israelites of how the world began, of why humankind hunted and domesticated the animals for food and clothing, and of how God provided for the human race which He made in His image. These same principles were in the laws of the ancient Greeks and Romans, which then evolved into or influenced the laws of the various western European countries (including England's common law) and those nations in the New World that were settled by western Europeans. For hundreds of years, no act committed upon an animal was prohibited, no matter how cruel or unnecessary.

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

New ideas. The concept that animals have rights is relatively new. The first animal-protection law in western civilization was adopted in 1641 by the Massachusetts Bay Colony. This law made it illegal to "exercise any Tirranny or Crueltie towards any bruite Creature which are usuallie kept for man's use." However, the rest of the western world continued as before. Indeed, during most of the seventeenth and eighteenth centuries, many experiments were conducted using living animals. This was largely because of the new idea that scientific conclusions had to be based on observable facts and because the dissection of human bodies and the use of living people in medical experiments were illegal. This meant that scientists had to experiment with animals to learn more about **physiology** and anatomy. There were no controls on how these experiments were conducted, but there were few qualms because most believed that animals had no souls and, thus, felt no pain.

> Since the days of ancient Greece, the common belief for centuries was that animals were nothing more than living machines that had no consciousness. Without consciousness, the animals could not reason or think nor could they suffer or feel pain. Later, with the establishment of Christianity, this consciousness, which the animals supposedly did not have, became known as a "soul."

Ironically, these very experiments proved that animals do experience pain. By the end of the eighteenth century, many argued that animal abuse

contributed to a person's cruelty. Others said that the mistreatment of animals was a misuse of a gift from God. In 1789, the English philosopher Jeremy Bentham became the first to say that animals have rights. According to Bentham, animals suffer pain just as humans and thus deserve the same freedom from pain.

Modern Movements

Slowly, most people came to accept Bentham's idea. Maine adopted the first modern anticruelty law in the United States in 1821, and every other state eventually enacted similar legislation. To encourage the police to enforce these laws, private organizations such as the American Society for the Prevention of Cruelty to Animals (ASPCA) were created throughout the last third of the nineteenth century. In addition, since World War II, a number of federal animal-rights laws have been adopted. These laws regulate animal experimentation and the treatment of animals by medical research facilities, slaughterhouses, and circuses, as well as people such as animal dealers who use animals as a source of livelihood.

Protection of animals. Many groups concerned with the treatment and welfare of animals still believe in the superiority of humans and the right to use other living creatures to meet human needs. However, in 1975, the Australian philosopher Peter Singer argued that animals are entitled to live free from the infliction of pain and suffering, whether from animal experimentation, the raising of animals for food, or other causes.

Eight years later, the American philosopher Thomas Regan argued that every individual animal has an inherent value and thus has moral rights that should not be violated even if to do so benefits society. The ideas of both Singer and Regan provide the basis for those who argue that animals have rights that must be observed and protected as opposed to those who believe that it is all right to use animals so long as it is done without cruelty.

State and Federal Statutes

The provisions of anticruelty statutes vary state to state. In addition, the effectiveness of these laws depends to a large degree on whether one believes animals are property and whether there should be limits on how to use animals to meet human needs. Many of these laws were written about 100 years ago and have rarely been amended. Some are only a few paragraphs long. Most statutes contain broad exemptions that usually include agricultural practices (e.g., dehorning, castration, docking, and limiting feed) as well as hunting and scientific experiments.

Even when an anticruelty law does not have exemptions, the courts have often created them by ruling that the statutes do not prohibit the infliction of pain, suffering, or death so long as it is not outside the traditionally accepted use of animals. In addition, while some laws define "animals" as all living creatures other than man, some laws apply only to warm-blooded vertebrate animals. Others list specific animals or types of animals that the provisions do or do not protect.

In a few states, persons are guilty of violating the anticruelty statutes if they are criminally or unreasonably negligent in their treatment of an animal. Most states, however, require that the defendant have some form of

POLIO

Polio was once one of the world's most dreaded diseases. Between 1948 and 1952 alone, 11,000 people in the United States died of polio and another 200,000 became partially or completely paralyzed.

In 1953, Dr. Jonas Salk announced the development of a vaccine. Salk and his colleagues developed the vaccine by growing three strains of the polio virus in monkey tissue and then killing the viruses with formaldehyde. This vaccine is between 80 percent and 90 percent effective and has saved millions of lives.

intent before a conviction can be obtained. For instance, if a jurisdiction requires willful intent, then the prosecutor must prove not only that the defendant acted intentionally and voluntarily, but also that the defendant acted without just cause or reason. In one case in North Carolina, two dog trainers were found not guilty of violating the local anticruelty law when they beat a dog and submersed its head under water because they did it to teach the animal not to dig holes.

In most states, violations of anticruelty laws are considered as summary offenses, which only involve a fine, or as misdemeanors with penalties that do not exceed a year in jail and a fine. Some states have recently made the violation of these laws a felony, but it is not yet known if this will make any substantial difference in the obedience to, or the enforcement of, the statutes. Most police and prosecutors are not very concerned about crimes against animals and are reluctant to spend the time or the money to make arrests or to take the cases to court. As a result, the enforcement of the anticruelty laws is frequently left to such organizations as the Humane Society and the ASPCA.

Animals and science. Since World War II, the number of scientific experiments involving animals has increased dramatically. Although the number of animals used in these experiments is just a small percentage of the millions killed every year for the benefit of humans for food and other reasons (such as clothing and the use of animal fats, oils, bones, and other byproducts in the manufacture of commercial goods), much of the recent focus of the animal rights movement has been on attempts to prohibit experimentation on live animals.

In addition to the state anticruelty statutes, animal experimentation is governed by the federal Animal Welfare Act which was enacted in 1966 and substantially amended in 1985. This law and its accompanying administrative regulations prohibit the use of animals in a scientific experiment if a nonanimal alternative is readily available. Scientists are also required to keep an animal's pain to a minimum, and to consider alternatives to any procedure that causes pain or distress. However, the law does not apply to rats or mice, the animals used most often in experiments, nor does it limit the type of experiments that may be conducted.

In the last decade of the 20th century, groups such as the Animal Liberation Front have used illegal means to fight what they believe is animal exploitation. In response, many states have adopted laws that specifically target these activities. The federal government has also enacted the Animal Enterprise Protection Act (1992). This law makes it a crime to cross a state border with the intent to physically disrupt zoos, aquariums, or similar public attractions, as well as to physically disrupt commercial or academic facilities that use animals for food production, research, or testing. SEE ALSO Animal Testing; Bioethics.

Mark A. Thorburn

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Animal Testing

In order to more completely understand biology, researchers sometimes conduct experiments on animals. Animal experimentation has a lengthy and productive history in biological research, especially in biomedicine. For example, the organ transplant pioneer Thomas E. Starzl conducted his early surgical transplantation experiments on dogs in the 1960s before successfully attempting them on humans. Psychiatrist John Cade made the discovery that lithium aids manic-depressive patients by experimenting with guinea pigs in the 1940s. Today, many animals are used for a variety of purposes in experimental science. While some studies use primates or other animals, over 90 percent of studies involve mice and rats, for experiments from immunological projects to cancer research. While animal research is enormously important to the advancement of biomedical science, some activists feel that animals should not be used as experimental subjects.

The Animal Welfare Act (1966)

To ease undue suffering inflicted on these experimental subjects, scientists William Russell and Rex Burch published *The Principles of Humane Experimental Technique* in 1959, wherein they described the three Rs: Reduce animal experiments, Refine them to make the experiments less unpleasant, and Replacement of animals by different techniques. Their concern over the "distress" suffered by animals, along with more general feelings of humaneness, led to the creation of the Animal Welfare Act by the federal government in 1966. The act was designed to protect animals that might be test subjects by requiring proper care of them, and it sets forth a list of guidelines researchers must comply with. For example, it stipulated that the animals must receive adequate veterinary care. In 1970, the act expanded from protecting dogs, cats, primates, guinea pigs, rabbits, and hamsters to "all warm-blooded animals." Significantly, the act exempts mice, rats, and birds from the protection it confers on other species. The act originally applied largely to pet dealers but with subsequent amendments grew to include, and even focus on, scientific research animals.

As the act forced scientists to care more properly for their test subjects (and with consistently healthy animals, enjoy more predictable and complete experimental results), a movement began in the 1970s to stop the use of animals in experimental science altogether. In 1975, philosopher Peter

Singer published *Animal Liberation*, in which he argued that all animals capable of perceiving pain were moral equals to human beings. In subsequent years, some animal rights activists (who, willing to cede moral rights to animals, must be differentiated from animal welfare activists, who only wish to see animals treated humanely) have taken increasingly severe stances on the subject of animal research. In 1986, the then-director of People for the Ethical Treatment of Animals, Ingrid Newkirk, asserted to the *Washingtonian* that "animal liberationists do not separate out the human animal, so there is no rational basis for saying that a human being has special rights. A rat is a pig is a dog is a boy. They're all mammals." She also likened the deaths of broilerhouse chickens to those of Jews during the Holocaust. Extreme animal rights activists have targeted scientists with terrorist or destructive acts in an effort to stop research. In particular, behavioral scientists and addiction researchers receive a lot of attention from activists because of the use of live primates in these fields.

Electrodes, used to detect neurological activity, protrude from the brain of a Japanese macaque who is immobilized in a laboratory cage.

Ethics vs. Research Imperatives: Finding a Compromise

Many activists protest cosmetics research rather than biomedicine, as some consider makeup to be less crucial to human existence than, say, cancer research. Additionally, not all animal rights activists are terrorists or extremists. For example, the Johns Hopkins Center for Alternatives to Animal Testing promotes the 3 Rs wherever it can. While many alternative suggestions for scientists may not be feasible, no scientist is so cruel as to want animals to suffer unnecessarily. However, for certain experiments, there are many advantages to using animals over other methods. The creation and maintenance of tissue and/or organ cultures in a test tube to simulate biological systems is extremely difficult, and using a live animal instead makes studying such systems possible. For addiction research, it is impossible to gain behavioral data without working with some sort of living animal. Many drug studies require the observation of treated animals, as do experiments on blood vessels (such as angioplasty research) and immune system tolerance (for investigations of transplantation biology). While many activists call for the use of computer simulations as an alternative to animal research, such simulations rarely work or reflect reality.

This is not to say that animals are required for every study. There are plenty of in vitro (test-tube) tests for the toxicity of certain compounds. Using human cells grown in culture has proved to be particularly accurate in this regard. For educational purposes, computer simulations can be as effective as real-life dissections. Only 70 percent of agents that cause cancer in mice will cause it in rats, suggesting that comparisons across species are not always valid: conclusions reached by studying animals may not be true for humans. In 1990, David Wiebers and colleagues from the Mayo Clinic reported that of twenty-five drugs found to reduce damage following strokes in animals, none proved effective in human trials. There are many instances in which animal studies may not work, simply because animal organ systems and cellular structure differ from humans.

Knowledge can be gleaned from epidemiological studies, or studies that follow the spread of disease, as an alternative. Clinical study, or the investigation of disease and how it manifests itself in a human population, can also offer insights to biological questions that cannot be answered with the use of animals. Some diseases, like HIV, rely heavily on these tactics because the animal simulations are too different or unwieldy. While studies of the transmission of Simian Immunodeficiency Virus (SIV), a close relative of HIV, in nonhuman primates can be useful, SIV is still a different disease.

It is worth noting that the animal rights movement has gained momentum at a time when there are far fewer Americans living on farms. A familiarity of animals as house pets, and not dinner, may have contributed to the movement. Animals may prove invaluable to certain studies. Moral considerations aside, the practical constraints of a given study might dictate that the use of animal subjects will not answer the question. Explorations of alternatives can be a good idea, because they may produce experiments that more closely mimic the human response to a treatment. And, after all, a more perfect model system is good news for everybody. SEE ALSO Animal Rights; Bioethics.

Ian Quigley

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Annelida

ecosystems self-sustaining collections of organisms and their environments

coelom a body cavity

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

chitin a complex carbohydrate found in the exoskeleton of some animals

exoskeletons hard outer protective coverings common in invertebrates such as insects

mesoderm the middle layer of cells in embryonic cells

hydrostatic skeleton a pressurized, fluid-filled skeleton

The phylum Annelida includes three main groups: the earthworms, the leeches, and the bristleworms. Annelids are found worldwide, and inhabit terrestrial, freshwater, and marine **ecosystems**. There are over 15,000 described species.

Characteristics of Annelids

All annelids are segmented. Segments, also called metameres, are structures that occur repeatedly along the body of the animal. Each annelid segment contains units of the circulatory, nervous, and excretory systems. In the earthworms and bristleworms, but not the leeches, segmentation extends to the interior of the body, and includes the **coelom**, which is partially divided into units by structures called septa.

The annelid body is covered by a moist outer cuticle that is secreted by the **epidermis**. Both earthworms and bristleworms also possess hairlike setae, composed of **chitin**, the hard material that also forms the **exoskeletons** of insects. These are absent in leeches.

Annelids have a true coelom, that is, one that is lined with cells originating from the embryonic **mesoderm**. The coelom is fluid-filled, which creates hydrostatic (water) pressure and acts as a **hydrostatic skeleton**. Annelids have a well-developed, closed circulatory system (one in which blood is limited to vessels) that is segmentally arranged. They also have a complete, one-way digestive tract with a mouth and anus. The digestive tract is not segmented.

Respiration in annelids occurs primarily through their moist skin, although certain species have evolved specialized gills or use paired projections called parapodia in gas exchange. The annelid excretory system consists of paired nephridia found in each segment which function in excreting nitrogenous waste. In terms of nervous system structure, annelids possess a pair of ganglia (masses of nerve tissue) at the front end of the body; this serves as their brain. A double nerve cord runs along the **ventral** (belly) side of the body, and sends branches into each segment. Annelids have many types of sensory receptors, including **tactile** (touch) receptors, **chemoreceptors** (smell or taste), and **photoreceptors** for light. Some have well-developed eyes.

Annelids possess both circular and lengthwise muscle fibers. These, combined with their segmentation and hydrostatic skeleton, allow for great flexibility in movement. One part of the body is able to contract, or change its diameter and length, without affecting the rest of the body. It is believed that the need for elaborate mechanisms to control motion led to the development of the comparatively complex nervous system of annelids.

Some annelids are **hermaphroditic** while others are **dioecious**, that is, the sexes are separate. Some species have direct development, in which eggs develop directly into miniature versions of the adult. In other species, there is a larval stage. The annelid larval form is called the trochophore larva. Some annelid species can also reproduce asexually by **budding**.

ventral the belly surface of an animal with bilateral symmetry

tactile the sense of touch

chemoreceptors a receptor that responds to a specific type of chemical molecule

photoreceptors specialized cells that detect the presence or absence of light

hermaphroditic having both male and female sex organs

dioecious having members of the species that are either male or female

budding a type of asexual reproduction where the offspring grow off the parent

filter feeders animals that strain small food particles out of water

gametes reproductive cells that have only one set of chromosomes

Classes of Annelids

Annelids have been divided into three classes. The Polychaeta is exclusively composed of the bristleworms, the Oligochaeta the earthworms, and the Hirudinea include the leeches.

Polychaeta. The Polychaeta, or bristleworms, are a large and diverse group that includes polychaete worms, lugworms, ragworms, and sandworms, among other groups. It is the largest annelid class, with over 10,000 species, most of which are marine. Bristleworms are found in a wide variety of habitats and employ various feeding strategies. There are active burrowers whose habitat is at the bottom of the water, that which live within tubes they secrete, and pelagic (open ocean-dwelling) forms. Some are sedentary **filter feeders** that extract small food particles from the water while others process sediment. Also, some species are active predators; these generally prey on small invertebrates.

Various species of earthworms typically feed on organic debris and are capable of passing large quantities of soil through their guts.

Bristleworms are characterized by paired paddle-like appendages called parapodia, used for gas exchange. These are covered with setae ("polychaete" means "many hairs"). Bristleworms have a well-developed head region, often with tentacles, and well-developed sense organs, including paired eyes, antennae, and sensory palps (projections). They are unusual among annelids because their reproductive organs are developed only during the breeding season; afterward, they wither away. The sexes are separate. **Gametes** (eggs and sperm) are shed into the water, and fertilization is external. Development is indirect, via a trochophore larval stage.

The polychaetes are believed to be the most primitive of the annelid classes. Some species, however, are highly specialized.

Oligochaeta. The class Oligochaeta includes the familiar terrestrial earthworms, found just about everywhere, as well as some freshwater annelid species. Approximately 3,000 oligochaete species have been described.

"Oligochaete" means "few hairs," and oligochaete species generally have fewer setae than bristleworms. Oligochaetes lack parapodia, eyes, and tentacles. Many aquatic oligochaete species have gills to aid in gas exchange. Species typically feed on debris and algae. Earthworms are critical components of land-based ecosystems. By passing large quantities of soil through their guts, they speed the rate of nutrient turnover. Their burrowing activity also supplies the soil with air.

Most oligochaete species are hermaphroditic, with each individual producing both eggs and sperm. Earthworms, however, generally do not self-fertilize. During mating, two worms line up next to each other, with swollen regions called clitella placed next to each other. Sperm is released through grooves in the skin by both individuals, and these are passed to sperm receptacles in the other worm. The clitellum of each then secretes a ring of mucus that carries eggs from the oviduct (a tube for transporting eggs) and collects sperm from the sperm receptacles. This ring slides over the head of the worm, drops into the soil, and closes off, forming a cocoon. Fertilization takes place within the cocoon and a few eggs hatch two weeks later. Development in earthworms, as well as in the other oligochaetes, is direct, without a larval stage.

Hirudinea. The Class Hirudinea consists of the leeches. Leeches differ from other annelids in that most have a fixed number of segments. Leeches lack the hairlike setae of the other annelids and their bodies are somewhat dorsoventrally flattened (i.e., in such a way that the back and belly are close together). As with the oligochaetes, leeches are primarily hermaphroditic and exhibit direct development. There are about 500 described species.

Most leeches are aquatic, and of these, nearly all are found in freshwater environments. A few species are terrestrial, but are found only in fairly warm, moist habitats. Leeches are almost all **ectoparasites**, which attach to the external surface of the host (as opposed to **endoparasites**, which live within their hosts). Segments at the front end of the animal are specialized to form suckers, while back-end segments are specialized for attaching to the host. The mouth contains teeth that are used to make an incision in the host. Leeches secrete an anticoagulant that keeps the blood of their host from coagulating, or clotting. They have been put to medical uses for thousands of years. In fact, bloodletting was extremely common as a standard prescription for a wide variety of ailments. The anticoagulants produced by leeches are still of great interest to medical scientists. SEE ALSO Phylogenetic Relationships of Major Groups.

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

Jennifer Yeh

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Antibody

Antibodies are protein molecules that function in the body's immune response. They are present throughout the circulatory and lymph systems, and are therefore exposed to all tissues in the body. An antibody is able to recognize and bind to a particular offending **antigen**. Antigens stimulate immune responses because they are recognized to be foreign, or "non-self." Invaders such as bacteria, viruses, fungi, toxins, and other foreign substances generally carry a variety of antigens on their surfaces.

antigen foreign substances that stimulate the production of antibodies in the blood

The antibody for a particular antigen functions by binding to that antigen. This results in one of two possibilities. The antibody may deactivate the antigen by either blocking its active site or otherwise changing it so that it can no longer harm host cells. Alternatively, an antibody may label the antigen-carrying object for destruction. In this case, one part of the antibody binds to the antigen while another part binds to immune system cells that are specialized to destroy antigens, cells such as **macrophages** or neutrophils.

macrophages a type of white blood cells that attacks anything foreign such as microbes

Foreign organisms such as bacteria or viruses typically possess numerous antigens on their surfaces. In addition, any particular antigen can usually be recognized by numerous antibodies, each of which binds to a slightly different site on the antigen. Each part of an antigen that can be bound by an antibody is called an **epitope**. With multiple epitopes on each antigen, and multiple antigens for any foreign invader, numerous antibodies can potentially be involved in an immune response.

epitope a localized region on a antigen that is recognized chemically by antibodies

Antibodies are made by immune system cells known as **B-lymphocytes**. B-lymphocytes are produced in the red marrow of bones. After they mature, the cells move to lymph nodes and begin to secrete antibodies into the lymph and blood. Each B-lymphocyte cell produces a unique antibody that targets a specific antigen.

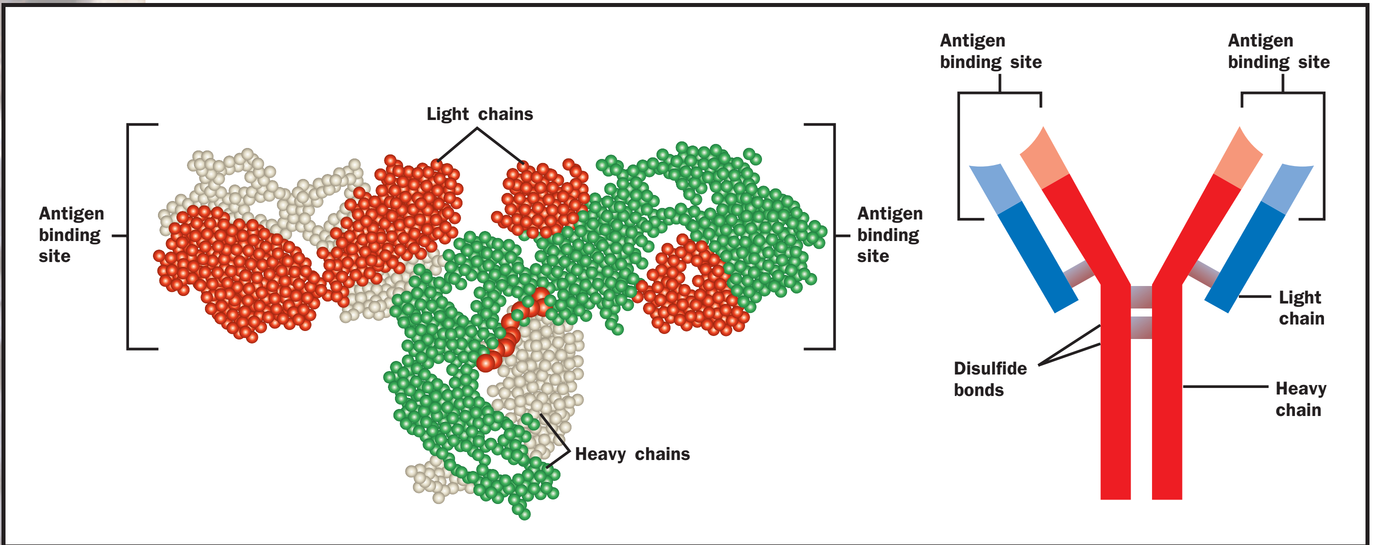
B-lymphocytes specialized cells produced from stem cells in the bone marrow that secrete antibodies that bind with antigens to form a pathogen fighting complex

Antibodies are Y-shaped proteins with binding sites at the tips of the branches of the Y. The antibody binds to an antigen in a way similar to how a key fits into a lock. The site on the antibody that binds to the antigen is known as the Fab region.

The antibody protein bundle contains two pairs of chains of proteins held together by disulfide bonds. The two identical longer chains, called heavy chains, form the base of the Y and one-half of each branch of the Y. The two identical shorter chains, called light chains, form the other halves of the branches of the Y. The ends of the branches of the Y contain a variable region on both the heavy and light chains. These are the Fab regions.

There is great diversity in Fab regions, which is essential to the body's ability to respond to a wide range of antigens. High diversity is possible because each heavy and light chain consists initially of numerous different segments, which can be spliced and combined in a variety of different ways. Consequently, there are thousands of possible heavy chains and light chains, with each giving rise to a slightly different binding site.

Antibodies are divided into five different classes. IgA antibodies function at mucous-producing surfaces such as the bronchioles, nasal passages, vagina, and intestine. They are also present in saliva, tears, and breast milk.



Antibodies are made by immune system cells known as B-lymphocytes. Redrawn from Hans and Cassady.

The function of antibodies of the IgD group is unclear. Most of these antibodies are not secreted into the bloodstream but, rather, are associated with B-lymphocytes.

IgE antibodies are found at mucous-producing surfaces, as well as in blood and tissues. They are responsible for many hypersensitive, or allergic, responses, in which the immune reaction to a relatively unharmful antigen is disproportionately intense. IgG antibodies are abundant in the bloodstream. They are able to cross the **placenta** and therefore provide the only protection for babies until their own immune systems mature. IgG antibodies are a very active antibody group that also plays a role in neutralizing toxins. IgM antibodies are largely found on B-lymphocytes.

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

Medical Uses of Antibodies

Vaccinations against various diseases are often made using antigens isolated from bacteria or viruses. Removed from their carriers, these antigens are in and of themselves harmless. However, they still trigger an immune response, after which antibodies specific for those antigens continue to circulate in the bloodstream. This allows those antibodies to be produced quickly and in great quantity in case of a future invasion by the entire pathogen.

Antibody-binding activity can also be used to diagnose disease. That is how HIV infections are identified.

In addition, attempts have also been made to produce antibody-related therapies for cancer. These aim to take advantage of the great specificity of antibodies to fight tumors. Some scientists are optimistic about the use of monoclonal antibodies in cancer therapy. These are antibodies that are specifically designed to recognize molecules present in tumor cells but not in healthy cells.

These antibodies can then be used to target antigens that are present only in small quantities, as is the case with many cancer cells. Monoclonal antibodies can function on their own by tagging cancerous cells for destruction, or can be attached to toxins or radioisotopes that help to destroy cancer cells.

Cancer cells do not typically induce an immune response in the host because they are not foreign. However, they can be transplanted to another organism, such as a mouse, where an immune response can be induced. After antibodies are harvested from the reaction, monoclonal antibodies can be isolated and cloned.

Jennifer Yeh

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Antlers and Horns

Antlers and horns are two kinds of ornamentation present on the front of the heads of mammals. Antlers consist of pure **bone tissue** and are shed and regrown annually, whereas horns consist of a bony knob and an exterior horn sheath and typically grow throughout life. Both structures were first seen in fossils from about 25 million years ago. Most even-toed **ungulates** (Artiodactyla) have head ornaments, such as deer, reindeer (antlers), antelopes, oxen, cows, and giraffes (horns). Some odd-toed ungulates (Perissodactyla), such as rhinoceroses, have horns. In most species, only males have antlers, but both females and males can have horns.

The number of branches, or "points" on a set of antlers can be used to indicate an individual's age and/or social status.

Antlers stem from the upper part of the frontal bone processes, called burrs. They grow by the accumulation of a **cartilage**-like bone **matrix**. The development of antlers begins in the spring with small nubs covered with "velvet," a layer of skin with oil and scent glands and nerves, as well as the sparse coating of hair that gives the velvet its name. Nutrients are supplied from the diet to the underlying bone through the velvet, and the antlers grow quickly throughout the summer. Not uncommonly in urban areas where the animal is malnourished or overpopulated the antlers are deformed, twisted and assymetrical because of inadequate nutrients. Toward the end of the velvet stage, growth slows and mineralization begins to increase. The velvet begins in spring and ends in the fall. During this period the interior of the bone becomes more dense, increasing the final weight from the beginning of mineralization process by about 70 percent. The velvet dies in the fall, and the animal rubs its antlers against tree trunks and branches to get the dead velvet off. Mating occurs later in the fall and in early winter when the antlers are at their peak size and weight, afterward the antlers are shed. Over a lifetime, the antlers usually grow more branches, or "points," so that an individual's approximate age can be estimated based on the number of points its antlers have.

bone tissue dense, hardened cells that make up bones

ungulates animals with hooves

cartilage a flexible connective tissue

matrix the nonliving component of connective tissue

Horns arise from an independent horn bone (the *os cornu*) that forms in the mesoderm (deep skin layers) of the forehead during fetal development, and the frontal bone fuses with the horn bones after birth. As the animal matures, the horn bones grow longer and wider, and the skin around the bone (the ectoderm) forms a horny outer covering, with the growth originating from the base. As it grows, the horn accumulates layers, and the horns of many species have grooves around them, the rings of which can be counted to determine the age of the animal. Although the structure of a horn is a single shaft, there are variations such as spirals and hooks or horn parts that are greatly broadened like those of the African buffalo, whose horn bases meet at the center of the head, and are broad and flat to form a giant shield over the top of the skull before curving up and outward.

Antlers and horns can be used as a defense against predators, but scientists believe that their primary function is to establish an individual's ranking within its species. Many animals point the ends of their horns or antlers away from their target during an advance, and adaptations such as branches, rings, and grooves facilitate direct, nonlethal combat with similarly adorned individuals. Antlers and horns are also used in ritual fights among individuals of the same species. Their size and scent indicate to other members of the same species an individual's rank and maturity, and this information often avoids the need to fight to establish the same ranking.

Jean K. Krejca

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Apiculture

Apiculture is the science of beekeeping. Humans have collected honey from wild bee hives for more than 8,000 years, as shown in Mesolithic rock paintings dating from 6000 B.C.E. By 2500 B.C.E., Egyptians were keeping bees in artificial hives. Hives exploit the honeybees' natural tendency to build nests in cavities, and allow apiculturalists to easily move (via boat, wagon, truck) and manipulate bee colonies. This mobility has allowed beekeepers to introduce honeybees around the world: The first hives were brought to the New World in the 1620s by European settlers.

Primitive hives were made of hollow logs, holes built in mud walls, or cones of mud, earthenware, or thatch. A modern apiary hive is a series of stacked boxes. The bottom box serves as the brood chamber where larvae develop; the upper boxes provide a space to store honey. Each box contains eight to twelve frames, which are set so they approximate the distance between combs in a natural hive. Bees then build their comb on the frames, which can be removed individually. Beekeepers remove the wax caps that cover each cell of the comb and let the cells' contents drip out by gravity, or use a specialized machine to spin the frames and draw the comb contents out by centrifugal force. The honey is then filtered and stored. Honey quality is determined by its flavor, clarity, and color.

The Products of Apiculture

The most widely cultivated and economically important bee species is the European honeybee (*Apis mellifera*), but beekeepers also keep a range of other species from the subfamilies Apidae (honeybees) and Meliponinae (stingless bees). Honeybees gather large amounts of flower nectar and pollen.

This beekeeper is holding one of the eight to twelve frames that the apiary box would contain.

They transform nectar into honey by evaporating water through fanning the nectar with their wings, and by adding **enzymes** produced by specialized glands on their bodies. Finally, the bees usually seal the finished honey in the hexagonal cells of their comb. Pollen is a source of protein, fats, and vitamins for the bees; carbohydrates from honey provide vital energy. While gathering pollen and nectar, bees cross-pollinate flowers and allow or improve the production of seeds and fruit. Economically, honeybees are more valuable as pollinators than as honey producers. Farmers rent more than one million colonies each year to pollinate crops valued at more than $10 billion. Unlike other pollinating insects, bees can be easily moved to agricultural fields where crops need to be pollinated.

enzymes proteins that act as catalysts to start biochemical reactions

Most beekeepers maintain hives for honey, but bees also produce other useful products. Beeswax from cell caps and old combs is used for high-quality candles, pharmaceuticals, lotions, and friction-reducing waxes for skis and surfboards. As well as honey, several other bee products are sources of food for humans. Bee brood (young bees that are housed in the brood comb of a hive) is consumed as a form of meat in many non-European countries. Food additives for humans and domestic animals are made from bee-collected pollen and from royal jelly, which bees produce as food for their larvae. Several bee products are also used as medicines. Since the 1930s, researchers have been refining extraction techniques to collect bee venom, because bee stings can relieve the symptoms of arthritis, rheumatism, and other diseases. Propolis, a gluelike plant resin that bees use to maintain the comb, is used in cosmetics and healing creams and may have antibiotic or anesthetic properties. Propolis was formerly an ingredient in some varnish, including the varnish on Stradivarius violins.

Threats to Apiculture

Cultivated bee colonies are susceptible to a number of diseases, parasites, and insect predators. Honeybee populations declined dramatically across the United States during the 1990s, when tracheal and *Varroa* mites destroyed up to 90 percent of hive populations in some areas. Another recent and widely publicized threat to apiculture comes from Africanized bees, *Apis mellifera suctellata*. This subspecies of the European honeybee commonly takes over the hives of its more docile European relatives. Africanized bees were imported from Africa to Brazil in 1957 with the hopes that their hardiness in tropical conditions would improve the Brazilian apiculture business. Unfortunately, some colonies escaped captivity and founded populations in the wild or took over other cultivated hives. The bees steadily spread northward into the United States, reaching Texas in 1990 and continuing to move up both coasts. The presence of Africanized bees in a hive makes beekeeping difficult because they are aggressive toward handlers, tend to swarm and leave the hive, and produce less honey than European honeybees. These bees are famous for their easily provoked mass stinging, which can be lethal to humans and other animals and has caused the deaths of several people. Public concern over Africanized bees has led to increased insurance liability for beekeepers, since they have had to pay more insurance because of the risk of keeping hives that may be taken over by Africanized bees, hence posing a threat to humans and animals in the area. Beekeepers in regions of Venezuela where people have been killed by Africanized bees have had their hives burned and been physically attacked by other citizens, regardless of whether their hives housed the Africanized bees that caused the problem. Many beekeepers also voluntarily destroyed their hives because they were unable to handle the more aggressive bees. SEE ALSO FARMING.

Emily H. DuVal

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Aposematism

The term "aposematism" is commonly used as a synonym for warning coloration (i.e., something that is aposematic is warningly colored). The word literally means "away signal." Aposematism is the combination of a conspicuous signal and an unprofitable trait in a prey species.

Conspicuous signals are most often bright colors presented in banded or contrasting patterns. The banding pattern of coral snakes or the contrasting colors of Heliconius butterflies are obvious examples. These signals are easily seen over large distances. Auditory signals are also used. For example, some arctiid moths **emit** ultrasonic clicks upon approach of a bat predator. Rattlesnakes, with their caudal rattle, warn of their venomous bite.

emit to send out or give off

The rattle of the rattlesnake is an aposematic signal that warns its predators of its venom.

An additional possibility is the use of offensive or unpleasant odors to signal unprofitable traits.

Unprofitable traits include anything that harms the predator or reduces its efficiency. Some examples are the distastefulness (unpalatability) of butterflies and other insects, the stings of wasps, the bites of snakes, the skin toxins of some tropical tree frogs and **salamanders**, or perhaps even an exhaustive chase between a bird and butterfly that ends with wasted energy for the bird.

salamanders four-legged amphibians with elongated bodies

Aposematism works by advertising to potential predators, rather than by hiding or escaping from them. Advertising to predators seems dangerous, but the obvious signals allow predators to quickly learn which prey are unprofitable. Predators encountering aposematic animals will have an unpleasant experience. This interaction may be so unpleasant that the predator immediately associates the visual or auditory characteristics of the prey with the experience. When the predator subsequently encounters the same signal, it will be more cautious and may avoid the prey. Not all unprofitable traits are so unpleasant. Some are only mildly deterrent and require frequent resampling by predators in order to reinforce the avoidance response.

Benefits and Costs of Aposematism

Aposematism has benefits for predator and prey. Efficient interactions between predator and prey in this context allow each to pursue other activities such as mating, care for offspring, and feeding. The prey benefit by avoiding death or injury because trained predators will not attack them as frequently as naive predators. Predators benefit by not expending energy on suboptimal prey.

There can also be costs for prey that have unprofitable traits. For example, unprofitable traits such as unpalatability require special chemicals to be manufactured or sequestered from host plants and these chemicals may be expensive to produce or detoxify.

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

Established aposematic signals may give rise to further interactions among species. Unprotected prey species could benefit by appearing the same as an aposematic species if they share the same predators. Predators might mistakenly avoid an unprotected prey if it closely resembles a well-established signal. This type of interaction is known as **Batesian mimicry**. Müllerian mimicry can also arise between two similar signals. In that case, two aposematic species converge on a common signal. In effect, each species contributes to the work of training the predators. In times of prey scarcity, predators may be forced to consume relatively unprofitable prey. This may lead to predator specialization on such unprofitable prey. For example, in Mexico, black-headed grosbeaks and black-backed orioles both consume large numbers of distasteful monarch butterflies when the butterflies are overwintering.

Adopting an aposematic lifestyle may alter prey behavior and lead to changes in other aspects of prey biology. This is because aposematic prey no longer require other defenses such as escape behaviors. For example, Heliconius butterflies have evolved differences from their palatable relatives that allow them to live longer, fly in more microhabitats, invest more energy in reproduction, and be more selective about where they lay their eggs.

Aposematism and Evolution

Evolutionary biologists have pointed out that it is paradoxical that an association between conspicuous signals and unprofitability could evolve. It would be difficult for a conspicuous signal to evolve in prey with unprofitable traits because predators will quickly sample the prey and kill it. Thus, any genes for the conspicuous signal are eliminated from the population. An alternative scenario is for unprofitability to evolve in prey with conspicuous coloration. However, this is not likely because being conspicuous without a defense offers no protection and simply makes the prey more visible to predators. Of course, evolution need not follow such mutually exclusive pathways, and unprofitability and conspicuous signals could evolve together.

A debate has developed over whether individual selection is sufficient for aposematism to evolve. Individual selection works by aposematic individuals training their own predators and passing on more genes than non-aposematic individuals. Evolutionary biologists have questioned whether aposematic individuals are able to survive the predator's attacks. Some experimental evidence suggests that aposematic animals, especially insects, are durable and can survive sampling by the predator. This means that one unprofitable individual with a newly evolved conspicuous signal could train predators in the area to avoid its own color pattern. Assuming this individual does not suffer damage and can reproduce normally, it will pass on genes for the conspicuous signal. However, if the individual dies or has fewer offspring than nonaposematic individuals because of predator sampling, then individual selection might not be sufficient by itself to cause aposematism to evolve. In this case, sharing genes for the aposematic traits with other individuals could aid in the evolution of aposematism.

Research on aposematism is ongoing and resolving the debate over how aposematism evolves will require experiments and observations of predation on aposematic species in the wild. SEE ALSO MIMICRY; PEPPERED MOTH.

Ryan I. Hill

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Aquaculture

Aquaculture is the rough equivalent of agriculture on land. Aquaculture is the raising of fish, shellfish, or aquatic plants to supplement the natural supply. Although aquaculture includes the growing of aquatic plants, most people use the term to mean fish and shellfish farming. Fish and shellfish are raised as food under controlled conditions all over the world. The goal of fish and shellfish culture is to increase the yield of useful products, including increased food production.

While most aquacultural production is in food items such as fish, **mollusks**, and **crustaceans**, some marine algae, kelp, and other aquatic plants are raised commercially. Cultured pearls are created by placing small bits of material in the shells of young oysters. Various types of floating algae and phytoplankton are also grown, primarily as food for animals.

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

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

Aquatic animal husbandry includes all of the activities terrestrial farmers and ranchers have used, such as selective breeding, care of the young, feeding, sanitation, environmental modifications, and harvesting. Species having characteristics that make them suitable and practical for culturing are selected for extensive cultivation. This includes considerations of con-

Aquaculture worker sorts salmon as they come down a water-filled chute in Anacortes, Washington.

sumer choice. Aquaculture is relatively expensive, so most aquacultural products are luxury items such as trout, oysters, and shrimp. Some less expensive fish species, such as carp and tilapia, are successfully cultured in China, India, and southeast Asian countries.

History of Aquaculture

Aquaculture has been practiced for thousands of years. Chinese in the fifth century C.E. practiced aquaculture, and temple friezes (ornamented bands on a building) dating from the Middle Kingdom of Egypt (2052–1786 B.C.E.) depict what appear to have been intensive fish farming. The ancient Romans are known to have cultivated oysters.

Commercial Importance

As suitable arable land diminishes and the world's population increases, aquaculture is expected to become increasingly important. Aquaculture is an environmentally friendly source of high-quality animal protein. Many countries with limited arable land, such as Japan, are actively developing an aquaculture industry.

Problems of Aquaculture

Aquacultural practices are not as efficient as they could be. Lack of capitalization in developing countries, inefficient and outdated techniques, and poor marketing all contribute to the lack of commercial success in aquaculture. Another factor limiting production is the lack of suitable domesticated species. Only a few aquatic animals are used, and much of the life cycle of these animals is not controlled. Research into new species, development of commercially viable **hybrids**, and new techniques of breeding should improve the efficiency of commercial aquaculture. Continued research and the dissemination of new skills and techniques holds promise for substantially increased aquacultural production, perhaps exceeding 30 million metric tons (33 million short tons) per year.

hybrids offspring resulting from the cross of two different species

Selection of Suitable Species

In order to be aquaculturally useful, species must be able to reproduce in captivity, have robust eggs and larvae, feed on inexpensive food, and grow quickly to harvestable size. For example, trout and carp have large, hardy eggs; mullet fry are easily collected; and young oysters are easily collected and grown. So these were the species of choice for aquaculture. The feeding habits of species also limit suitability. Wide-ranging plankton feeders, such as herring, are not suitable. **Sessile** animals, such as oysters and mussels, which filter the water for their food, can be cultured extensively but still must be supplied with a rich food supply if they are to grow rapidly.

sessile immobile, attached

Selective Breeding

Aquaculturists, like their terrestrial counterparts, selectively breed for desirable traits in captive organisms. Since the traits that enhance success in a wild population are often inconsistent with a successful captive population, these traits must be eliminated through breeding. Desirable characteristics include fast growth and a body shape that provides more edible tissue. Since captive populations are usually held at a higher density than wild populations, disease is a problem. So resistance to disease is desirable. Since aquatic animals usually produce many offspring per generation, selective breeding is somewhat easier than with terrestrial animals.

One desirable characteristic of captive populations is an accelerated onset of sexual maturity. This event is triggered in the wild by a combination of factors, including water temperature, length of daylight hours, and salinity. These factors in turn act on the animal's pituitary gland, which controls the output of sexual hormones. Attempts to control environmental factors to accelerate spawning have been largely unsuccessful, except in the cases of oysters and shrimp. A more generally successful method involves the injection of pituitary hormones. This is expensive and labor intensive so alternatives are being sought.

Evolving Technologies

Large-scale fish culture projects, if properly managed, have the potential to produce thousands of tons of fish. Community ponds and reservoirs created by the damming of tropical rivers are often designed to include large-scale fish farming. When a new reservoir is created, nutrients from the soil trigger the growth of abundant algae and aquatic plants. So herbivorous fish must be included in the plans. These fish can provide the first harvested "crops."

Fish "ranching" is also widely practiced. For example, salmon are raised in hatcheries then released into wild streams. This allows the establishment of new salmon runs, the reintroduction of salmon into previously used streams, and the replenishment of depleted stocks. This form of aquaculture also helps alleviate losses due to human-induced environmental degradation.

Hybridization is another technique coming into use in aquaculture. Crossing one trout with another trout having seagoing tendencies enables breeders to send fish to new oceanic pastures and then to harvest them when they return to freshwater to spawn. Promising crossbreeding experiments with tilapia have also resulted in species exhibiting hybrid vigor.

Both coal-fired and nuclear power plants use water for cooling. This water is generally discharged into a reservoir of evenly warmed water. This water has significant potential to be used in aquacultural programs. Many aquatic animals grow more rapidly in somewhat warmer water. Other species, such as carp and catfish, prefer warmer water. Many of the farm-raised catfish available in supermarkets are grown in ponds warmed by water from power plants.

Pelagic (open ocean) fish have not been raised in captivity with any great success. They are desirable species because they grow fast. But they require huge quantities of food fish or other pelagic organisms, which are also hard to raise in captivity. As research continues, it is likely that new aquacultural techniques will be developed that will permit the farming of many new species such as spiny lobsters, crayfish, octopus, and others not presently husbanded. Improved techniques will increase the yield of existing aquacultural species. As demand continues to increase for world food supplies, aquaculture promises to grow into a thriving and productive industry. SEE ALSO FARMING.

Elliot Richmond

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Aristotle

Philosopher
384 B.C.E.–322 B.C.E.

Aristotle, Greek philosopher and scientist, was born in 384 B.C.E. in Stagira, northern Greece. He died in 322 B.C.E. He is considered one of the most influential thinkers in history.

Aristotle's father was the physician to the king of Macedonia. Being a doctor's son most likely influenced his strong interest in science. Upon the death of his father in 367 B.C.E., Aristotle was sent to the Academy of Plato in Athens. He remained there for twenty years, first as a student, then as a teacher. He studied a wide variety of subjects, earning the nickname "the reader." After Plato's death, Aristotle left Athens and traveled about for twelve years. For a number of years during this time, he tutored Alexander the Great, the son of Phillip II of Macedonia. Aristotle married once or twice and had two children. At the age of fifty, he returned to Athens and founded his own school, the Lyceum. There, for twelve years, Aristotle studied a wide range of subjects, especially nature. When Alexander the Great died in 323 B.C.E., Aristotle feared political persecution, so he left Athens. He moved to Chalcis in central Greece, where he lived for a year until his death.

Aristotle, philosopher and biologist.

Aristotle made many important contributions to biology. He was the first to classify animals. He grouped animals as having blood or not in his most basic classification. His observations led to the knowledge that mammals are warm-blooded, have lungs, breathe air, and suckle their young. In classifying animals, Aristotle realized that they should not be grouped based only on their external parts. Instead, he understood that even animals that appeared very different could be related. Aristotle identified four means of reproduction: the **abiogenetic** origin of life from nonliving mud; **budding** (**asexual reproduction**); **sexual reproduction** without **copulation**; and sexual reproduction with copulation. Aristotle did not believe in natural selection, or survival of the fittest. Instead, he believed in teleology, that plants and animals have natural goals. Their form could be fully understood only when those goals were known. Aristotle believed that all organisms are perfectly adapted to their surroundings. His observations led to the principle that general structures appear before specialized ones, and that tissue forms before organs.

budding a type of asexual reproduction where the offspring grow off the parent

asexual reproduction a reproduction method with only one parent, resulting in offspring that are genetically identical to the parent

abiogenetic pertaining to a nonliving organism

sexual reproduction a reproduction method where two parents give rise to an offspring with a different genetic makeup from either parent

copulation the act of sexual reproduction

mutations abrupt changes in the genes of an organism

Aristotle's theory is in opposition to Charles Darwin's "theory of evolution by natural selection." Darwin argued that random genetic **mutations** produced slightly different characteristics in members of a species. Those individuals with advantageous traits would reproduce more successfully than those without them, resulting in a constantly evolving population. Darwin's ideas of constant change, chance, and chaos are in contrast with Aristotle's explanation of biology through order and purpose.

Although it is known that Aristotle wrote a huge amount of material, most of it has been lost. The few documents that remain appear to be notes he used for teaching. Also, it is not certain whether some of the books attributed to him were actually written by him or by others who were summarizing his writings and teachings.

Aristotle made lasting contributions in fields other than the natural sciences. These were philosophy, logic, ethics, and psychology.

Denise Prendergast

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Arthropoda

The phylum Arthropoda is the largest and most varied in the animal kingdom. It includes well over one million described species. This represents approximately three-quarters of all known biological organisms, living or extinct. Countless arthropods remain undescribed (not yet named and studied), and the actual number of living species could be as high as ten million or more. Some of the more well-known arthropods include insects, crustaceans, and spiders, as well as the fossil **trilobites**. Arthropods are found in virtually every known marine (ocean-based), freshwater, and terrestrial (land-based) ecosystem, and vary tremendously in their habitats, life histories, and dietary preferences.

trilobites an extinct class of arthropods

Characteristics of Arthropods

Despite the remarkable variety of arthropod species, all share aspects of a single basic body plan. All arthropods possess a stiff **exoskeleton** (external skeleton) composed primarily of **chitin**. In some species, lipids, proteins, and calcium carbonate may also contribute to the exoskeleton. The external skeleton offers organisms protection as well as support for the body. Its walls provide anchors for the attachment of muscles. The exoskeleton is incapable of growth, and is **molted** (shed) repeatedly during the growth of the animal. This process is called ecdysis. Molting allows for rapid growth until the newly secreted exoskeleton hardens.

exoskeleton a hard outer protective covering common in invertebrates such as insects

chitin a complex carbohydrate found in the exoskeleton of some animals

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

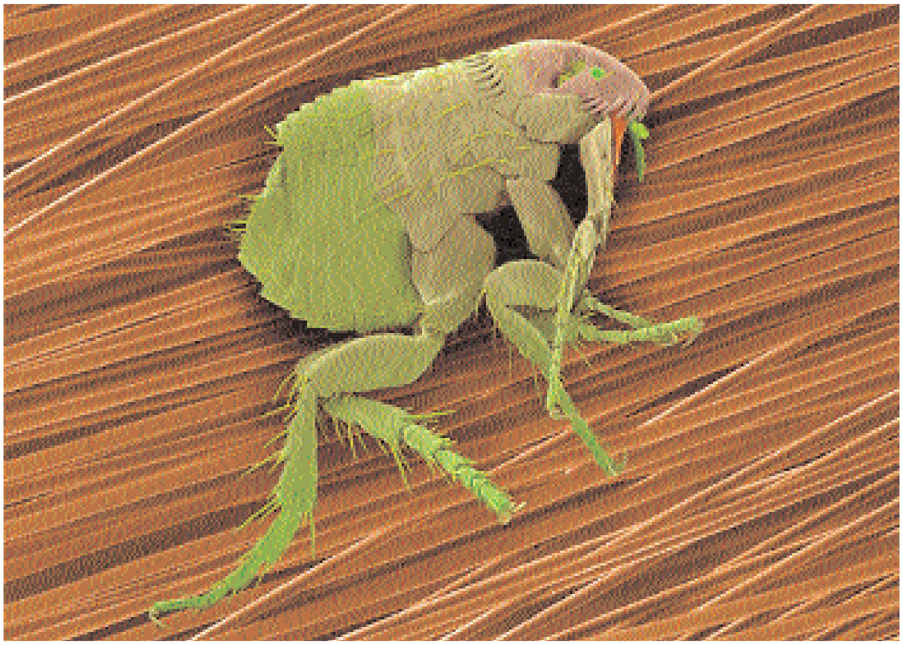
Arthropod bodies are divided into segments. However, a number of segments are sometimes fused to form integrated body parts known as tagmata. This process of fusion is called tagmosis. The head, thorax, and abdomen are examples of tagmata. Arthropods also have appendages with joints (the word "arthropod" means "jointed feet"). In early, primitive anthropods, each body segment was associated with a single pair of appendages (attachments). However, in most species some appendages have been modified to form other structures, such as mouthparts, antennae, or reproductive organs. Arthropod appendages may be either biramous (branched) or uniramous (unbranched).

Some arthropods have highly developed sense organs. Most species have paired **compound eyes**, and many also have a number of simpler eyes called ocelli. Arthropods have an open circulatory system (without blood vessels) that consists of a tube that is the heart and an open **hemocoel**, the coelom of the animal, in which blood pools. Arthropods also have a complete gut with two openings, the mouth and the anus.

compound eyes multifaceted eyes that are made up of thousands of simple eyes

hemocoel cavity between organs in arthropods and mollusks through which blood circulates

Gas exchange in the phylum occurs in various ways. Some species have gills, while others employ tracheae, or book lungs. The tracheal respiratory system consists of external openings called spiracles that are linked to a system of branched tubules which allow respiratory gases to reach internal tissues. Arthropods are characterized by a brain as well as a nerve ring around the area of the pharynx, in the oral cavity. A double nerve cord extends back-



This scanning electron micrograph of a dog flea reveals the structure of its rigid exoskeleton, a characteristic of arthropoda, in detail.

wards along the **ventral** surface of the body, and each body segment is associated with its own ganglion, or mass of nerve cells. In most arthropod species, the sexes are separate. Fertilization usually occurs internally, and most species are egg laying. While some species exhibit direct development, in which eggs hatch as miniature versions of adults, other species pass through an immature larval stage and undergo a dramatic metamorphosis before reaching adult form.

ventral the belly surface of an animal with bilateral symmetry

Major Groups of Arthropods

Arthropods are divided into four subphyla. These are the Chelicerata, the Crustacea, the Uniramia, and the Trilobita. The last consists exclusively of extinct forms.

Subphylum Chelicerata. The chelicerates include the **horseshoe crabs**, scorpions, spiders, ticks, mites, sea spiders, and other related species. They are characterized by the presence of two tagmata (fused segments), a cephalothorax (fused head and thorax), and an abdomen. They possess six pairs of unbranched appendages. These include a pair of **chelicerae**, a pair of pedipals, and four pairs of legs.

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

chelicerae the biting appendages of arachnids

The class Arachnida includes scorpions, spiders, ticks, and mites. There are over 100,000 described species in this class. The majority are land-based and most are found in fairly warm, dry habitats. Like other chelicerates, arachnids have six pairs of appendages. The first pair, the chelicerae, is typically adapted for killing and consuming prey. The second pair, pedipals, have a sensory function, and may include both receptors sensitive to touch and receptors sensitive to chemical changes. The final four pairs of appendages are walking legs. Arachnids have fairly simple eyes that register only changes in light levels. Of the arachnids, spiders (which make up the Order Araneae) are the most diverse. All spiders are able to spin webs using modified appendages called spinnerets. These are located in the rear abdomen. Webs are used for a variety of purposes in different species. In many, they are used to catch prey and to build nests. Spiderwebs can even be used for movement, as in those species that create parachutes to catch the air, enabling them to descend safely. Many spiders have toxic poisons to immobilize prey or to use in self-defense; perhaps the most famous of these is the black widow. Spiders prey primarily on insects, and are often ecologically important for this reason. Scorpions (order Scorpiones) are arachnids characterized by a pair of claws and a long, jointed tail with a poisonous sting at the end. Ticks and mites (order Acari) are ectoparasites. They embed themselves in the skin of vertebrate animals and feed on blood. Certain tick species carry diseases such as Lyme disease and Rocky Mountain spotted fever.

The class Merostomata includes the horseshoe crabs. Horseshoe crabs are an extremely ancient marine lineage. Only five species have survived to the present. They are characterized by a long appendage called a telson that projects from the rear end of the body, which is used in flipping the animal over when it is lying on its carapace. They use book gills to breathe and generally feed on small invertebrates.

The class Pycnogonida consists of the sea spiders. There are 2,000 described species, all of which are marine. Most species are fairly small. Like spiders, they have small bodies with long legs. They use an extensible proboscis to suck nutrients from the bodies of soft invertebrates.

Subphylum Crustacea. The subphylum Crustacea includes lobsters, crabs, shrimp, barnacles, and other related organisms. There are approximately 40,000 described species. The majority are marine, but there are freshwater and land-based representatives as well. Unlike other arthropods, the crustacean exoskeleton often includes calcium carbonate, which offers added rigidity. Crustaceans generally have three tagmata: a head, a thorax, and an abdomen. There are two pairs of antennae, complicated mouthparts consisting of two pairs of maxillae (upper jaws) and one pair of mandibles (lower jaws) used in food processing, and a series of branched appendages. These appendages are associated with the thorax. Some function as walking legs while others may be specialized for capturing prey. The abdomen is sometimes equipped with swimmerets (small swimming legs that are also used for other purposes, including as copulatory organs in males and for egg carrying in females) and a tail that is composed of modified appendages in addition to a telson. Some crustacean species have well-developed sensory systems, including highly sensitive compound eyes on stalks, ears, chemoreceptors for taste and/or smell, telson and hairs or bristles that function as touch receptors. Crustaceans have a wide variety of ways to capture food. Some are **filter feeders**, while others are **scavengers** or predators. In most species, the sexes are separate. Some species pass through what is called a nauplius larval stage prior to metamorphosing into adults, while others have direct development and bypass the larval stage. Crustaceans use gills to inhale and exhale air.

filter feeders animals that strain small food particles out of water

scavengers animals that feed on the remains of animals that they did not kill

The class Branchiopoda include the brine shrimp, water fleas, and other related groups. Species in this class are generally small and tend to live in freshwater habitats or in salty lakes. Most species have a large number of segments with minimal fusing of segments, or tagmiosis. The majority are filter feeders.

The class Maxillopoda includes the barnacles and related groups. Maxillopods have a head, thorax, and abdomen along with a telson projecting from the back end of their bodies. Most species are small and feed using their maxillae. Barnacles, however, are sessile (immobile) filter feeders. They are often seen in large numbers, anchored to structures such as ship bottoms or piers.

The class Malacostraca has over 20,000 species and is the largest group within the Crustacea. Most species are marine, but others are freshwater or terrestrial. The largest order, Decapoda, includes shrimp, crabs, crayfish, and lobsters. Other well-known malacostracans include **krill** as well as a terrestrial group, the sowbugs. The malacostracans exhibit a variety of feeding strategies. The more primitive species tend to be filter feeders. Others are scavengers. Crabs and lobsters are active predators. They have a pair of chelipeds, also known as claws or pincers, which are used to capture and carry prey. Pincers have evolved to serve other functions as well, however, and in various species are used for digging, defense from predators, or in courtship rituals. Some malacostracan species are parasites. Many malacostracans, including many of the larval forms, are critical components of oceanic plankton, a critical component of oceanic food webs.

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

Subphylum Uniramia. Uniramia is the largest subphylum within the arthropods. It includes the centipedes, the millipedes, and the insects, as well as a few smaller related groups. The name Uniramia comes from the unbranched appendages that characterize members of the group. Species generally have two or three tagmata. There are one pair of antennae and two pairs of maxillae. Respiration occurs via tracheae. Uniramians generally have separate sexes.

The class Chilopoda includes the centipedes, a diverse group of over 5,000 species. These terrestrial organisms are characterized by a very large number of segments, often well over 100. The largest centipedes reach lengths of up to 25 centimeters (10 inches). Each centipede body segment, aside from a few at the head and tail of the organism, is associated with a single pair of legs. All centipedes are carnivorous, and the appendages that are frontmost have been modified to form large poisonous fangs that are used to immobilize prey. Centipedes feed primarily on earthworms and insects. Species of centipedes are generally egg laying, and in some, the female remains to guard the eggs. Development is direct—there is no larval stage. In some species, juveniles hatch with the same number of segments as an adult, while in others, individuals add segments with each molt.

The class Diplopoda consists of the millipedes, a group that includes over 8,000 described species. Like centipedes, millipedes have a large number of segments. However, they differ from centipedes in that each segment has two pairs of legs rather than just one. Millipedes do not have fangs, and in fact, most species are either herbivorous or scavengers. Many millipedes do, however, exude (ooze) poisonous or noxious substances as a defense against potential predators. Millipedes are often found in decaying organic matter or in moist soils. They are effective burrowers. Like some species of centipedes, they lay eggs in nests that are attended by the female. Millipedes add body segments as they grow and molt.

This chewing louse belongs to the order Mallophaga. Its head is wider than its thorax in order to accommodate its complex mouthparts. Most lice are host-specific, and feed on their hosts' hair, feather, and skin scales.

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

The class Insecta is the largest class in the animal kingdom. There are nearly one million described species, and no doubt countless others that have yet to be named. Insects are found in a wide variety of terrestrial and freshwater habitats, and there are even a few marine forms.

Insects have three tagmata, or fused segments: a head, a thorax, and an abdomen. They have a pair of antennae; a series of complex, highly variable mouthparts, which vary greatly from species to species; and three pairs of legs. Both the antennae and mouthparts are evolved from modified appendages (walking legs, most likely). Most insect species also have two pairs of wings, although these are absent in a few very primitive species and have been reduced in others, becoming nonfunctional or adapted for a different purpose. Insect legs and wings are associated with the thorax, not the abdomen, which does not usually carry appendages except for appendages that are evolved into reproductive organs. A theory of the origin of insect flight maintains that wings evolved from external gills that were present in certain primitive groups. Aside from their breathing function, these gills served as flaps that assisted insects in leaping and jumping, and were advantageous because they made escape from predators more likely. Gradual increases in wing size allowed for gliding movement, and ultimately for flapping flight.

Insects have highly elaborated sense organs. For example, they may possess a pair of compound eyes as well as several cranial ocelli, or simple eyes. The compound eye is made up of hundreds of individual facets, or parts. Each facet points in a different direction. An individual facet provides information regarding the color and intensity of light but does not provide a complete image. Together, however, the numerous facets create a combined, mosaic image of the world. Compound eyes are particularly effective for seeing nearby objects; distance vision is not as good. The greatest advantage of compound eyes is that they are able to register changes in the visual field much more quickly than eyes with lenses. This is particularly important for detecting motion, as well as for the rapid maneuvering required during flight. Many insects also have well-developed ears. Some species also have an extraordinary ability to detect chemicals. This is especially true in species that use chemical signals called **pheromones** for detection of a sexual partner. The pheromones are emitted by receptive females and picked up by males, which use them to locate potential mates.

Insects breathe through the tracheal system, described earlier. Because of limits on the spread of gas in the trachea, insects are restricted to a comparatively small size. The excretory system of insects consists of structures known as Malpighian tubules. The sexes are separate in insects, and fertilization occurs internally in most species.

The variety in patterns of insect development is exceptionally high. Most insects pass through several stages before reaching the final adult form. Insects may be described as either hemimetabolous or holometabolous. In hemimetabolous forms, the hatched young resemble adults reasonably closely, although they may be sexually immature and may lack wings. In holometabolous insects, on the other hand, there is a distinct larval stage that is dramatically different from the adult stage in almost all ways: morphology (form and structure), diet, and habitat. In holometabolous insects, there are usually several different larval stages separated by molts. After a period in which the larva grows, it then enters a sessile pupal phase during which a dramatic metamorphosis occurs, and the insect emerges from the pupa with its adult form.

Certain insect groups are highly social. Termites and many species of Hymenoptera (ants, wasps, and bees) are **eusocial**, meaning that their colonies include a caste (a segment of the population) that reproduces as well as a large number of individuals that do not. The evolution of nonreproductive species seems to pose a problem because it appears to defy natural selection, which emphasizes the production of offspring. However, direct reproduction is not the only way for an individual to pass on its genes. For example, because an individual's siblings share some of its genes, contribution to the production of a large number of siblings will also result in an individual's genes being represented in the population. This is what occurs in the eusocial insects. In addition, unusual behaviors in termites (repeated cycles of inbreeding) and unusual genetic systems in hymenopterans (haplodiploidy, in which males of the species are haploid while females are diploid) increase the proportion of genes shared by siblings.

eusocial animals that show a true social organization

Insects play many vital roles in maintaining ecological systems. Many insects act as pollinators to higher plants. Others are important in decomposition. Many species are agricultural pests or parasites, and have a dramatic impact on humans. The fruit fly *Drosophila melanogaster* is one of the most well-studied biological organisms and serves as a model species for studies of **genetics**, development, and evolution.

genetics the branch of biology that studies heredity

Some well-known insect groups include the Thysanura (silverfish), Ephemeroptera (mayflies), Odonata (dragonflies), Orthoptera (grasshoppers, crickets, katydids), Blattaria (cockroaches), Isoptera (termites), Heteroptera (true bugs), Homoptera (cicadas and aphids), Coleoptera (beetles), Siphonaptera (fleas), Diptera (flies), Lepidoptera (butterflies and moths), and Hymenoptera (ants, bees, and wasps).

Subphylum Trilobita. The subphylum Trilobita includes only extinct species found in fossil form. The trilobites were a primitive group of marine species that was particularly abundant during the Cambrian (570 million years ago) and Ordovician (505 million years ago) periods. The group became extinct at the end of the Permian (286 million years ago). Trilobites had flattened, oval-shaped bodies. Most were a few inches long, although one species is known to have attained a length of 0.6 meters (2 feet). SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

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Aves

Eggs and poultry make up a significant part of peoples' diets. Similarly, products made from feathers such as pillows, comforters, or down-lined coats are widely used. There is an increasing awareness and heightened passion for our feathered friends sweeping the nation. The popularity of feeding wild birds has actually changed the ranges of several common songbirds. Additionally, because of the low fat content of turkey and chicken meat and America's fascination with losing weight, the poultry industry is booming. And what other animal has a day dedicated to it like the tradition of roast turkey at Thanksgiving? Clearly, birds are a relevant and special part of our lives.

But what makes them so unique? How are they different from animals in the other major classes of organisms? And most importantly, how are they different from us?

Position in the Animal Kingdom

Birds make up the class Aves of the subphylum Vertebrata, phylum Chordata. Class Aves contains 28 orders, 163 families, 1,975 genera, and nearly 10,000 species. Their distribution is worldwide, including open oceans. While the majority of the world's bird species are known to science, a handful of new birds are still discovered each year. Most of these rare birds are found in remote regions of the world.

It is widely believed that birds descended from two-footed, lizard-like reptiles that lived in the Jurassic period some 208 million years ago. Birds still have many resemblances to reptiles, such as their habit of laying eggs, the possession of scales on their beaks and legs, and the arrangement of many internal structures.

The three highest classes of vertebrates—reptiles, birds, and mammals—have adapted their reproduction to terrestrial life, largely through the evolution of an egg whose embryo is enveloped in a protective membrane called the **amnion**. Hence these three classes are grouped under the term "amniota," or "**amniotes**." Among all animals, only birds and mammals have evolved the high, constant temperature or **homeothermism** that makes energetic activity possible in all habitats and at all seasons. This,

amnion the membrane that forms a sac around an embryo

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

homeothermism maintainenance of body temperature

The yellow warbler's bright feathers provide warmth, protection, and the ability to fly.

more than any other advance, is what makes these two classes the dominant vertebrates.

Birds have numerous characteristics that make them distinct from all other classes of organisms. While not all birds fly, a large number of these characteristics complement their amazing adaptation for flight.

Feathers

All birds have feathers, which no other animals living or extinct are known to have had. The number of feathers is relatively constant within a species, although birds tend to have more feathers in the winter than in the summer. Smaller birds tend to have more feathers per square surface inch than larger birds, although fewer total feathers. For example, a ruby-throated hummingbird, with a relatively small surface area, has approximately 940 feathers, while a Canada goose, with a much larger surface area, has 33,000.

Feathers serve many purposes, including warmth, protection, flight, attractive adornment for courtship, and sex recognition. The heat-insulating value of feathers is so extraordinarily effective that it permits birds to live in parts of the Antarctic too cold for any other animal.

For their weight, it is estimated that feathers are as strong as the best human-made materials used in the aerospace industry today. Their flexibility allows the broad-trailing edge of each large wing feather to bend upward with each downstroke of the wing. This produces the equivalent of pitch in a propeller blade, so that each wingbeat provides both lift and forward propulsion.

There are well-documented stories of birds deliberately swallowing their feathers. Grebes, for example, consume feathers by the hundreds. Fifty percent of the stomach contents of horned or pied-billed grebes may be feathers. This odd behavior seems to have a purpose. Scientists believe the action

gizzard the muscular part of the stomach of some animals where food is ground

of the **gizzard** in these primarily fish-eating birds is insufficient to crush the bones that are swallowed. The feathers are thought to protect the stomach by padding the sharp fish bones and slowing down the process of digestion so that the bones dissolve rather than pass into the intestine. This belief is supported by the observation that the least grebe, which, of all the grebes consumes the fewest fish, also accumulates the smallest amount of feathers in its stomach. Additional studies are needed to test this hypothesis.

Fusion and Reduction of Bones

pectoral of, in, or on the chest

fusion coming together

Bird bones are extensively fused and thus reduced in number. Birds have no teeth or heavy jaws. Unlike mammals, which have a single bone, the lower jaw of birds is made up of five small fused bones. Additionally, the bones in the **pectoral**, pelvic girdle, and spinal column are fused, which serves as a rigid framework for flight muscles, limbs, and major flight feathers of the wing and tail. Birds have no tail vertebrae. The upper limbs show extensive **fusion** in the carpal and metacarpal bones. The finger bones are reduced in both size and number; two of them are completely missing and two of the other three are fused together. The ankle and foot bones in birds have also been fused and reduced in number.

Hollow, Thin Bones

The major bones of most birds' bodies are thin and hollow, while most other animals possess denser, more solid bones. The skeleton of the pigeon, for example, accounts for a mere 4 percent of its total body weight, while the skeleton of a mammal of comparable size, such as a rat, amounts to almost 6 percent of its total body weight.

Although the bird skeleton is thin and lightweight, it is also very strong and elastic. This is very helpful, since most birds' skeletons are subject to great and sudden stresses of aerial acrobatics. Interestingly, the wing, leg, and skull bones in some large, soaring birds have internal, trusslike reinforcements much like the struts inside airplane wings.

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

Not all birds have such hollow bones. To decrease their **buoyancy** and make diving easier, some diving birds, such as loons and auklets, have relatively solid bones.

Air Sacs

In addition to lungs, birds possess an accessory system of air sacs connected with the lungs. These air sacs often branch throughout their bodies, frequently entering the larger bones of the body to occupy their hollow interiors. While this system of air sacs certainly contributes to weight reduction, it is believed that they have a more important contribution. The air sac system appears to supplement the lungs as a supercharger, increasing the utilization of oxygen.

thoracic the chest area

In addition, air sacs provide buoyancy for aquatic birds. Swimming species have particularly large abdominal and **thoracic** air sacs whose volume can be controlled for swimming or diving.

Air sacs also serve as a cooling system for the bird's speedy, hot metabolism. It has been estimated, for example, that a flying pigeon uses one-fourth of its air intake for breathing and three-fourths for cooling.

Nervous System and Sense Organs

Birds have a very high metabolism. They may consume thirty times the amount of energy as reptiles of similar size. Several factors contribute to their metabolism level. Of all the million or so animals on Earth, birds have evolved the highest operating temperatures. Their average body temperatures range between 104°F and 110°F (42°–43.5°C). Birds live intense lives and their metabolic "engine" is always warm and ready for action.

Behind the high temperature in birds lie some interesting anatomical and physiological refinements. Besides eating an energy-rich diet, birds possess digestive equipment that processes their food rapidly, efficiently, and in large amounts. Fruit fed to young cedar waxwings passes through their digestive tracts in as little as sixteen minutes. Other perching birds may take from one-half to two hours to pass food through their bodies.

The excretory system of birds is also extremely efficient and fast. Their kidneys are roughly twice as large as those of comparable mammals. Except in ostriches, there is no urinary bladder. Its absence further assists flight by reducing weight, since there is no stored urine. Birds do not have a **urethra** to discharge urine.

urethra a tube that releases urine from the body

Avian cardiovascular systems are extremely efficient, enabling birds to withstand **cardiopulmonary** stresses far beyond what mammals can tolerate. Like mammals, birds have a four-chambered heart. Relative to their size, however, it is large, powerful, and very rapid in beat. The world altitude record for birds is held by a Rüppell's griffin, which was pulled into the jet engine of an airliner at nearly 11,000 meters (36,000 feet). Although the vulture was undoubtedly soaring passively, no mammal of equivalent size could breathe enough air even to remain conscious at that altitude.

cardiopulmonary of or relating to the heart and lungs

Birds also have blood sugar concentrations averaging about twice that found in mammals. This elevated blood sugar supports a greater amount of activity.

The respiratory system of birds is a complex network of lungs and specialized air sacs. This unique system acts as a supercharger for their fast metabolism by supplying large amounts of oxygen. While the lungs of humans constitute about 5 percent of body volume, the respiratory system of a duck makes up about 20 percent of its body volume (2% lungs and 18% air sacs).

Birds have no sweat glands and lose heat through their respiratory system and exposed skin. To cool off, most birds pant, which is an important form of heat loss. Additionally, many if not all birds flutter the throat area during heat exposure, resulting in heat loss from the mucous membranes of the throat. This throat flutter may account for 35 percent of heat loss in chickens, for example.

Finally, birds have a highly developed central nervous system and rapid nerve impulses. Birds are highly visual animals; they must be in order to fly. The importance of birds' eyes is implied by their size; of all animals, theirs are the largest relative to the body. Some hawks and owls have eyes as large as human eyes. In some owls, the eyes comprise up to one-third of the total weight of the head. In starlings the eyes comprise 15 percent of the head weight; in humans it is only one percent. In most aspects, the avian eye structure resembles that of mammals. The eyes of birds are able to adjust to light about two times as well as those of a twenty-year-old person.

There has been a lot of debate regarding the acuteness of avian vision. Generally, it appears that it is better than human vision, but there are exceptions. A vulture sees about as sharply as humans, whereas a chicken appears to see only about one twenty-fifth as well as humans. Hawks and songbirds see about two and one-half times as sharply. Birds also appear to see in dim light better than humans because of the density of receptor cells in the **retina**. Barn owls can see an object at two meters with an illumination of 0.00000073 foot candles. This is the equivalent to a person seeing an object by the light of a match a mile away.

retina a layer of rods and cones that line the inner surface of the eye

The brain of a small perching bird weighs about ten times that of a lizard of the same body weight. The cerebral hemispheres in birds are large and well developed, as in mammals, but the location of the complex behavior in the cerebrum is different in the two. The brain of a mammal is dominated by the top layer of the cerebral hemispheres, which have a high capacity for learning. The bird brain is dominated by the middle of the cerebral hemisphere, which lacks learning capacity. So mammals, in general, learn behavior, while bird behavior tends to be instinctive and stereotyped. This is probably the basis for the well-known phrase “bird brain.”

Laying of Eggs

All birds lay shelled eggs and incubate them outside of their body. Eggs range in size from 25 centimeters (10 inches) long for ostriches to only 8.5 millimeters (0.3 inch) long for hummingbirds. Smaller birds lay eggs that weigh more in proportion to body weight than do the eggs of larger birds. Hummingbirds lay eggs that are 15 percent of their body weight, while ostriches lay eggs that are only 2 percent of their body weight. Flightless kiwis lay only one huge egg that can be 25 percent of their body weight. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Stephanie A. Lanoue

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Bailey, Florence Augusta Merriam

American Ornithologist
1863–1948

Florence Augusta Merriam Bailey was born in Locust Grove, New York. Bailey was an important ornithologist, who spent nearly fifty years observing, protecting, and writing about birds.

The natural setting of her home in the country inspired Bailey's love of nature. Her interest in wildlife was encouraged by her family who also loved natural history. Bailey was educated in private school and then attended Smith College from 1882 to 1886. Although she did not follow a degree course at Smith, she was later awarded a bachelor's of arts degree by Smith in 1921. While at Smith, Bailey organized one of the nation's first Audubon Societies and worked to end the era's fashion craze of decorating women's hats with bird feathers and even entire birds. She wrote many articles on birds for *Audubon Magazine*, and these articles formed the basis for her first book about birds, *Birds through an Opera Glass* (1889).

After college, Bailey traveled and dabbled in social work. However, contracting tuberculosis led her to travel west in 1893 to find a better **climate** in which to recover. She traveled and studied birds throughout Utah, California, and Arizona. Her first major western bird book was *A Birding on a Bronco* (1896). This book was aimed at beginners in ornithology and became one of the first popular American bird guides. She went on to write ten books altogether. In 1899 she married Vernon Bailey, a biologist who also studied animals, especially mammals. They traveled the country together, studying wildlife and helping each other write magazine articles and books that are considered classics on western natural history. Florence Bailey's book *Handbook of the Birds of the Western United States* (1902) became a standard reference book, documenting hundreds of species of birds. She became the first woman associate member of the American Ornithologist's Union in 1885, and its first woman fellow in 1929. In 1931 Bailey was the first woman recipient of the organization's Brewster Medal for her book *Birds of New Mexico* (1928).

climate long-term weather patterns for a particular region

naturalists scientists who study nature and the relationships among the organisms

When not traveling, the Baileys entertained amateur and professional **naturalists** in their home in Washington, D.C. Florence Bailey helped organize the Audubon Society of Washington D.C. and frequently taught its classes in basic ornithology. Although childless, Bailey spent her life educating young people about the value of birds. In 1908 a California mountain chickadee, *Parus gambeli baileyae*, was named in her honor.

Denise Prendergast

Florence Augusta Merriam Bailey committed her life to educating others on the basic principles of ornithology through her prolific writing and teaching.

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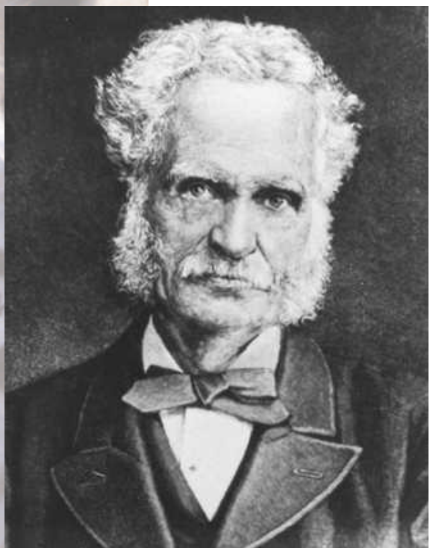
Baüplan

See Body Plan.



A prominent entomologist, Henry Walter Bates developed the "Batesian mimicry" theory following his research in the Amazon.

Bates, Henry Walter

British Naturalist

1825–1892

Henry Walter Bates was born in Leicester, England. Bates was a **naturalist** who specialized in the study of insects.

Bates left school at the age of thirteen and worked in his father's stocking factory. He was an amateur botanist and entomologist. In 1844 Bates met Alfred Russel Wallace, who along with Charles Darwin originated the theory of evolution by natural selection. In 1847 Wallace suggested Bates accompany him on a trip to tropical jungles to study natural history. They would pay for their trip by collecting animal specimens and selling them in Europe. In 1848 Bates and Wallace arrived in Brazil at the mouth of the Amazon River. Wallace stayed for four years, and Bates for eleven years. During this time, Bates explored the entire valley of the Amazon and collected nearly 15,000 species, mostly insects. Of these species, 8,000 were previously unknown. Many of the specimens were sent back to museums and collectors in Europe to raise funds to pay for the trip.

After returning to England in 1859, Bates worked on his huge collections, classifying and describing the various species. He wrote a famous paper entitled "Contributions to an Insect **Fauna** of the Amazon Valley" and presented it to the scientific community in 1861. Bates also proposed a hypothesis about a certain type of mimicry which is now called **Batesian mimicry**. While in the Amazon valley, Bates observed that certain harmless butterflies looked very similar to other butterflies that were poisonous or distasteful to predators. Bates theorized that the harmless butterflies had evolved to look like the toxic butterflies. In this way, he believed that the harmless butterflies increased their chances of survival by taking advantage of the defenses of the toxic butterfly. A classic example of Batesian mimicry is the viceroy butterfly which looks very similar to the foul-tasting monarch butterfly. Bates was a strong supporter of evolution by natural selection, and his findings about mimicry supported this theory.

In 1864 Bates was appointed as the assistant secretary of the Royal Geographical Society in London. He held this position for twenty-eight years until his death. Bates is recognized among scientists for his contribution to the classification of scarabs, a type of beetle. He described over 700 new species of scarabs. Bates wrote *The Naturalist on the River Amazons* (1863) and many scientific papers on insects.

naturalist a scientist who studies nature and the relationships among organisms

fauna animals

Batesian mimicry a type of mimicry in which a harmless species looks like a different species that is poisonous or otherwise harmful to predators

Denise Prendergast

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Behavior

Animal behavior includes the actions and reactions of animals to external stimuli. The study of animal behavior involves two main approaches: answering questions about how an animal does something (proximate questions) and why an animal does something (ultimate questions). Though humans have always observed animals behave, animal behavior did not become a field of study until the 1930s, when it was called **ethology**.

ethology animal behavior

Behavior is determined by both genetics and environmental factors, and is controlled by neural mechanisms. Thus, all animals with nervous systems are capable of behavior, including extremely simple ones such as the flatworm, *Caenorhabditis elegans*, which responds to light. The study of animal behavior is expanding rapidly and includes **taxa** and subjects too numerous to list here. Major divisions of the field include learning, cognition, and social behavior.

taxa named taxonomic units at any given level

Founders of animal behavior studies include scientists Karl von Frisch, Konrad Lorenz, and Niko Tinbergen, whose work in the 1930s won them a shared Nobel Prize in 1973. Their work focused on how animals can do things they have never before seen done, which is a proximate question relating to the genetics that determine some of an animal's makeup and the physiology that allows the animal to perform the feat.

Their work also included elements of ultimate questions, and it is the answers to these "why" questions that lead us to fully understand the driving force behind the evolution of the behavior. Using the *C. elegans* example given above, questions about how the flatworm avoids light will be answered by geneticists and physiologists studying light sensors and locomotion capabilities. Why the flatworm avoids light relates to things like evolution (its ancestors avoided light, and it increases an individual's fitness for survival to do so) and environment (predators can detect flatworms better in the light). These ultimate questions helped link the fairly new study of behavior to established disciplines of evolution and **ecology**, and gave birth to the field we know today as behavioral ecology.

ecology the study of how organisms interact with their environment

Behavior is a **phenotypic trait**, and, as with other such traits, an individual's behavior is determined through both genetics and environment. There are few examples of a trait that is strictly determined through just one of these routes, though through rigorous study we can tease apart the genetic and environmental components that determine a behavior.

phenotypic traits the physical and physiological variations within a population

For example, when a gene for a complex behavior such as alcoholism is reported, it usually means that there has been an abnormal allele of a gene found in some large percentage of alcoholics tested, and that the presence of this allele may somehow make the individuals with it more likely to be alcoholics. It does not indicate, however, that all people with that allele are alcoholics or that all alcoholics have that allele. There are many social factors such as depression and stress that contribute to alcoholism.

Behavior is controlled by the nervous system. Nerve cells acquire sensory cues from the environment, such as light in the case of *C. elegans*, and convert them to electrical signals that are transported to a central decision-making location, such as a nerve ganglion in *C. elegans* or the brain in a higher animal. There it will be determined whether the received stimulus

Worker bees surround their queen honeybee. The workers will feed and care for their queen, therefore helping to preserve their family's genetic information.

demands a reaction. From there, another electrical signal will be sent back out to the target where the response will occur, such as a muscle that controls locomotion and performs the actual behavior.

Learning

One loosely defined category of animal behavior is learning, and this includes imprinting, kin recognition, associative learning, and play. During learning, behaviors are changed based on what an individual sees or experiences.

Imprinting is irreversible learning that occurs during a specific time in an individual's development. Documented in both mammals and birds, one type of imprinting is the recognition and bond that develops between the parent and child in the first few days after birth. A famous example of this occurred when Konrad Lorenz divided a clutch of goose eggs in half, and allowed half of them to incubate with their mother and the other half in an incubation chamber. Those in the first half displayed normal behavior, following their mother around and ultimately interacting and mating with other geese. Those in the second half spent their first few hours with Lorenz and the baby geese imprinted on him. Even when these geese were later reintroduced to their mother and siblings, they showed no recognition but instead always followed Lorenz around and even later showed courtship behavior toward humans. This experiment shows the importance of the **critical period** in which imprinting occurs (the first few hours of life in this case) and the irreversibility of what is learned, even when the species that is imprinted (a human in this case) is incorrect.

critical period a limited time in which learning can occur

Another example of imprinting includes recognition of kin. At an early age, odors of the nest and early companions are used as cues that let animals recognize who their kin are. Documented even in insects, this kin recognition can be used to explain interactions later in life (significantly after separation from the nest) in which an animal treats another one like a relative if it smells like the nest from which it originated. This may be an important part of kin selection, which is discussed in the final, social behavior paragraph of this entry.

Other types of learning, such as associative learning, are not dependent on a critical period, though the learning may happen most efficiently if taught at a certain time. Associative learning is simply the ability to associate one stimulus with another. One example is trial-and-error learning, where as a result of a certain behavior and its outcome, a good or bad association is learned. Whether an association is positive or negative ultimately leads to the repetition or avoidance of the behavior. Food choices may fall under this category, where the sampling of different food types may lead to satisfaction and nourishment or bad taste and sickness.

Finally, play can be viewed as a type of learning in which capturing prey and social behavior are practiced. Though play is usually done with siblings and without the actual goals of hunting to kill or establishing social and mating hierarchies, the actions practiced in play allow these skills to be practiced for use later on.

Play time for these young lions teaches them essential survival skills. The hitting, biting, and roaring learned through playing may help these cubs in their later courtships of possible mates.

Cognitive Behaviors

A second group of behaviors that can be loosely gathered together are cognitive behaviors. These are complex behaviors that involve the perception, storing, processing, and use of information.

Long-distance travel is an example of this complex process. Whales, butterflies, and birds travel thousands of kilometers to return to the exact same spot they were the year before. Migrating animals use several mechanisms including orientation, piloting, and navigation. Orientation involves moving in a certain compass direction, which can be known from cues like stars and the Sun, although some animals can detect magnetic north without these cues.

Piloting is employed for short distances. It involves moving between landmarks such as rivers and mountains that are familiar from past migrations.

Navigation is the most complex. It involves both determining present location in relation to other known locations and using orientation to get to the next destination. This means the animal must create a mental map that is spatially correct in order to plot out the next course.

Social Behaviors

aural related to hearing

olfactory related to smell

tactile related to touch

A third group of behaviors is related to social living. Examples include communication, cooperation, and competition. Communication can be between species, such as when a dog snarls to expose its teeth to warn a potential attacker what may be in store. Frequently, communication occurs among species and can be **aural** such as bird song or cricket chirp; **olfactory**, such as a spot where an animal urinates; visual; or **tactile**.

Communication serves a myriad of purposes, including defining territories, attracting mates, telling where a food source is, or warning of impending danger. Cooperation is when two or more individuals work to perform a single task. Many times this task may seem more beneficial to one individual than the other, in which case the individual getting less or no benefit is termed altruistic. Examples of cooperation are in food finding, child rearing, and standing watch for predators.

genomes the sum of all genes in a set of chromosomes

In many cases of apparent altruism, it is found that the individual receiving the benefit is related to the one giving, such that the one giving is actually helping to preserve a genetically related line. This phenomenon is called kin selection and serves to propagate related **genomes**, an act that is not purely altruistic.

Competition occurs when a limited resource needs to be divided among individuals. An example of a resource to be divided is territory. Frequently, males must establish a territory that has good food or is a good mating or nesting spot so that they are preferentially chosen by females for mating. Those males who accomplish this are the most successful in passing on their genes. Competition for territory can take the form of violent contests with other males, and even after the territory is won it may need vigilant guarding to keep intruders out. SEE ALSO Acoustic Signals; Behavioral Ecology; Communication; Courtship; Social Animals; Sociobiology.

Jean K. Krejca

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Behavioral Ecology

Behavior is what animals do and why they do it. Behavioral ecology examines the evolution of behaviors that allow animals to adapt to and thrive in their habitats.

There are two broad categories of behavior—learned and instinctive. Instinctive behavior is a pattern passed genetically from one generation to the next. A spider, for example, never needs to see another spider weave a web to know exactly how, where, and when to do it. This information is carried innately with the spider and allows it to carry out many of its life processes without ever having to think about them. The disadvantage to instinct is that is inflexible and does not allow the animal to change when the behavior is no longer appropriate. The armadillo's instinctive upward leap when threatened worked fine until the animal encountered a new environmental hazard—the automobile. **Learned behavior**, in contrast, is the result of experience accumulated and assimilated throughout a lifetime that allows the animal to adapt to unpredictable changes.

learned behavior behavior that develops with influence from the environment

A behavioral ecologist studies patterns of behavior that fall somewhere between instinctive and learned. They include:

- Reflex: A rapid automatic response to a stimulus. Hedgehogs automatically curl into a ball when threatened.
- Conditioned reflex: An instinctive reflex that can be trained to occur under different conditions. A racehorse will go faster when flicked with a whip because it associates the whip with its traditional predator, a large cat, clawing at its back.
- Migration: A seasonal movement to a more favorable summer or winter environment. One of the most phenomenal migrations is that of the monarch butterfly, which spans thousands of miles and two generations. The young are genetically programmed to return to the fields their parents left.
- Hibernation and estivation: A state of torpor, or lowered metabolic rate resembling sleep, entered into by some animals in order to survive severely cold winters or hot, dry summers.
- Imprinting: Memorization by a young animal of the shape, sound, or smell of their parents or birthplace during a very brief period following birth. If the parent is absent, the baby will imprint on the first object it senses, giving rise to the sight of ducklings that think humans are their parents or kittens that have imprinted on dogs.
- Courtship: The special signals and complicated rituals that allow male-female bonds to occur for mating purposes. These behaviors assure the intentions and, consequently, the safety of both partners, who might attack or devour an approaching mate if the signals are unclear.
- Mimicry: The evolution of a harmless animal to look or behave like a dangerous animal. The viceroy butterfly mimics the coloration of the poisonous monarch, which most birds are genetically programmed to avoid.
- Preadaptation: A mixture of instinctive and learned behavior. Purple martins who once nested on cliffs have learned to use human-built structures to extend their ranges.

Behavioral ecologists who study animals closely in natural settings report numerous incidents of watching them encounter a new situation and think out a new response. Harvard biologist E. O. Wilson describes watching several beavers whose dam had been vandalized come up with a solution to the problem. Because the water flow was too strong to be stopped by their instinctive techniques, the beavers came up with a new and successful idea of patching the dam with gooey underwater mud and debris. Wilson is convinced that this showed the beavers' ability to evaluate a problem and solve it with reasoning.

For many years it has been taboo for scientists to propose the idea that animals consciously reason. As biologist Jane Goodall explained, "If you admit that animals have sentience and emotion, you have to take a long, hard look at how we abuse them." SEE ALSO Acoustic Signals; Behavior; Communication; Courtship; Social Animals; Sociobiology.

Nancy Weaver

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Binomial (Linnaean System)

Despite the overwhelming diversity of life that exists (and once existed) on this planet, it is clear that some organisms are more similar to each other than to others. Thus, organisms can be assigned to groups based on their overall similarity to other organisms. For example, humans belong to the group "mammals" as do all other organisms that possess mammary glands and hair. The grouping of organisms provides a convenient means of classification; that is, an organism can be described by the groups to which it belongs.

Carolus Linnaeus (1707–1778) is the naturalist responsible for developing the system still used in the twenty-first century for classifying animals.

The classification system that is used today is called the Linnaean System after its inventor, the Swedish naturalist Carolus Linnaeus (1707–1778). In his 1758 book, *Systema Naturae*, Linnaeus categorized all organisms into seven hierarchical groupings arranged from most inclusive to least inclusive. They are kingdom, phylum, class, order, family, genus, and species. Humans belong to the kingdom Animalia, the phylum Chordata, the class Mammalia, the order Primates, and the family Hominidae, and have been given the generic name (genus) *Homo* and the specific name (species) *sapiens.* The Linnaean System is hierarchical because there may be many species per genus, many genera (plural of genus) per family, and so on.

Because specific names are not unique (i.e., there may exist a plant with the specific name *sapiens*), the name of a species always includes both the generic name and the specific name, for example, *Homo sapiens*. This method of giving every species a unique combination of two names is called "binomial nomenclature," and is part of Linnaeus's classification system. By convention, these scientific names for organisms, as opposed to the common names, are always italicized. Furthermore, the generic name is capitalized while the specific name is not. Biologists prefer scientific names to common names because of their uniqueness, stability, and universality. Common names, on the other hand, often refer to more than one species and vary over time and from place to place. Biologists follow a certain Code of Nomenclature when deciding what to name a newly discovered species.

The practice of naming and classifying organisms is termed "**taxonomy**." Linnaeus classified organisms mainly by their physical (morphological) characteristics. He believed that his groups held theological significance, that is, that they revealed God's plan in creating life. However, with the recognition that species evolve, which led to Charles Darwin's *On the Origin of Species* in 1859, it became apparent that Linnaeus's classification system held biological significance as well. Organisms that are morphologically similar and consequently grouped together are usually similar because they share a common ancestry. The Linnaean System thus reflects evolutionary relationships among organisms. For example, humans are grouped with gorillas and chimpanzees in the order Primates because we are more closely related to gorillas and chimpanzees then we are to other mammals. Likewise, Primates are grouped with Rodentia in the class Mammalia because primates and rodents are more closely related to each other than they are to other organisms in the phylum Chordata, such as reptiles and fish. SEE ALSO LINNAEUS, CAROLUS.

taxonomy the science of classifying living organisms

Todd A. Schlenke

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Biodiversity

Biodiversity is the term applied to the variety of organisms that occupy a given region. This includes all organisms that live in the region, from microscopic protists to large mammals. The region can be a political unit such as a country, a geographic feature such as a mountain range, or the entire world.

The term "biodiversity" is a combination of two words, "biology" and "diversity." The union of these two words is fairly recent, being inspired by the growing realization that the number of species in the world is seriously declining. Used in this context, it has taken on a greater meaning than just the variety of species, having grown to include three closely related levels: genetic diversity, taxonomic diversity, and **ecosystem** diversity. Biodiversity is created by complex physical and biological environments (ecosystem diversity) that allow organisms to evolve specializations, and genetic barriers (genetic diversity) that allow them to speciate (taxonomic diversity).

ecosystem a self-sustaining collection of organisms and their environment

The importance of biodiversity has been recognized by people of many cultures and backgrounds who understand the multitude of functions it serves for humans, from providing food to filtering waste. Threats to biodiversity include direct killing of species by hunting, contaminating the environment with toxins, and **habitat loss**. The loss of biodiversity through extinction must ultimately be overcome by drastic changes of human behavior. Otherwise, humans will destroy the very environment that supports them.

habitat loss the destruction of habitats through natural or artificial means

Levels of Biodiversity

Genetic Diversity. The first level of biodiversity, genetic diversity, is the level at which we can most clearly observe the evolution of diversity. Genetic diversity includes the many kinds of genes that are available for given members of a species, such as a family, a population, or the entire species. This variety of genes allows the species to have many kinds of heritable traits that allow it to survive through changing environments.

For example, in a particularly cold winter, many individuals of a species may die from lack of insulation, but if the population as a whole has genetic diversity for a trait such as fat storage, then at least some members of the population will survive and the species will not become extinct. The next year, more offspring will have the valuable trait and the species will evolve to tolerate the cooler environment.

Species with little genetic diversity, such as farm hybrids (special breeds of crops or livestock that are all closely related), have limited ability to adapt to changing weather conditions or insect pests. Species lacking genetic diversity cannot adapt to a changing environment and may become extinct without help like the careful maintenance that goes into farm crops and animals.

At the opposite extreme, characteristics of genetically healthy populations are a high population size that includes many individuals that are unrelated to each other. Often, the existence of disjunct populations, those separated by some geographic barrier that only occasionally lets migrants through, ensures that there are always unrelated individuals.

Taxonomic Diversity. The next level of biodiversity, taxonomic diversity, refers to the variety of individuals at a given hierarchical level in the scientific naming system. This could be the number of different species, genera, families, or kingdoms. For example, a cornfield may have hundreds of birds living in it, but they may represent only three species that are all in one family, meaning that there is low taxonomic diversity. A similar-sized area in a nearby forest may also have hundreds of birds living in it, but these birds may be from twenty different species that belong to eight families and three orders, representing a higher level of diversity. Around the world, crops and livestock typically consist of only one species. These **monocultures** support a low level of biodiversity.

monocultures cultivation of single crops over large areas

habitat the physical location where organisms live in an ecosystem

Ecological Diversity. Ecological diversity is the variety of **habitat** types that are available in a given area. These habitats can have different physical characteristics such as temperature and soil type, as well as different organisms inhabiting them. When the habitat with all its organisms and their complex interactions are considered together, it is termed an ecosystem. Ecosystem diversity is typically the level that is discussed in relation to biodiversity.

Beyond ecosystems is a division termed "landscape" that consists of all of the ecosystems in a defined region, such as a drainage basin. **Biomes** are groups of similar landscapes, such as all the mountain ranges in the world. Finally, the largest division is the biosphere, which refers to all life on Earth.

biomes major types of ecological communities

A mountain range is as an example of ecological diversity that illustrates the evolution and patterns of biodiversity. Because of the latitude of the range selected as an example here, the temperatures are warm and plants grow throughout the year. The topography and weather patterns typically make one side of the mountain moist while the other is dry, meaning that each side grows its own kinds of plants. There will also be variation in soil type, as the soils are made from dead plants, and variation in insects because many insects can eat only certain species of plants.

Soil type will determine what kind of ground-dwelling invertebrates and other decomposers can live there, as well as providing habitat for reptiles, amphibians, and small mammals that build their burrows in the soil and feed on the invertebrates. This kind of variation at the base of the food chain determines that there will be variation at all the higher levels as well, including predators.

Another major habitat characteristic is elevation. Higher elevation means colder temperatures and less oxygen, which also dictates that tougher, scrubbier plants will live near the top and that there will be less soil and fewer species at high elevations. Barriers that are inhospitable to some taxa, such as a mountaintop, a river, or a deep canyon, add complexity to the habitat that consequentially creates separate populations that do not communicate very often. These separated populations allow for greater genetic, and ultimately taxonomic, diversity.

From these examples we can make the generalization that biomes in warmer **climates**, with greater energy from primary **producers** and with more varied and complex habitat types, have a higher biodiversity than those without those traits. For example, a mountain range of the same overall characteristics at a higher latitude will have less soil and less energy because there is less primary production from the plants, which go dormant for much of the year. This will cause the overall number of species and biodiversity to be lower.

climates long-term weather patterns within particular regions

producers organisms which make up the level of an ecosystem that all other organisms ultimately depend on; usually these are plants

The Importance of Biodiversity

The value of biodiversity has been argued by many different people for a variety of reasons, but they all point to a unified ideal of conservation. Aldo Leopold is known as the father of environmental ethics in the United States. In books such as *Sand County Almanac and Sketches Here and There* (1949), he stressed that humans must change their role from consumer of the natural world to cohabitator of it. This change is needed to preserve biodiversity, which would ensure that natural resources are available for future generations.

The value of biodiversity is also recognized by various groups and organizations in modern society. They include waste managers who use wetlands to clean runoff; pharmacists who search for new drugs in rare species; a food industry that interbreeds wild species to improve domestic ones; a pet industry that imports and breeds rare animals; hobbyists who bird-watch, camp, and photograph in search of new species; hunters and fishermen who selectively harvest to eat and teach their families about the wilderness; scientists who use species to study evolution; and, finally, conservationists interested in preserving biodiversity not only for what it can do for them, but for its inherent value in that it lives and breathes as we do.

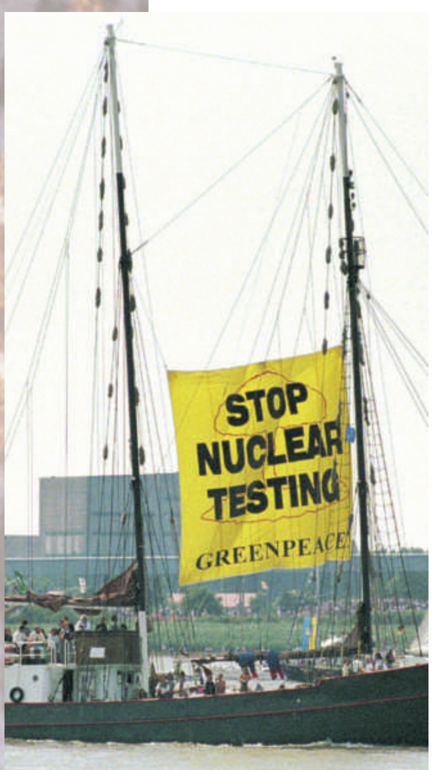
The Decline of Biodiversity

The decline of biodiversity is documented for prehistoric times and can be the result of natural events that may or may not be related to the fitness of the species that become extinct. A constant level of background extinction has always existed, but it is mass extinction events that cause concern about the future of biodiversity.

Extinction. The largest extinction event recorded occurred 250 million years ago, when 95 percent of marine species died in response to an uplift of the species-rich continental shelf that was caused by **plate tectonics**. Another famous example of mass extinction is the impact of the Chicxulub meteorite, which is thought to have left a dense cloud over the sky worldwide for a decade, causing a decrease in primary production (plant activity) and a subsequent extinction of many taxa. This impact coincides with the end of the dinosaur age and probably contributed to the extinction of many of those lines.

plate tectonics the theory that Earth's surface is divided into plates that move

Extinction rates at the beginning of the twenty-first century are undeniably higher than background rates, but the exact rate calculated depends on what method of calculation is employed. Using estimates from recent past extinction rates based on fossils, mammal extinctions were once one per two hundred years, and most recently were twenty species in the twentieth century. At the turn of the twenty-first century, the rate of bird extinction is 1,000 times the average over the past 2,000 years. Combining the two calculations provides an estimate of a 1 percent loss of species diversity over the twentieth century, a number much greater than any prehuman impact. Using habitat loss as a predictor of species loss, it is estimated that between 2 and 25 percent of biodiversity will be lost over the twenty-first century.



Greenpeace, responsible for hoisting this large banner on this boat's masts, is one of the best-known organizations working to publicize and educate the public on current environmental challenges.

Causes of extinction. Biodiversity decline can result from excessive hunting, environmental contamination, or habitat loss and there are a variety of ways to combat these sources of decline. Excessive hunting typically impacts large species that come into frequent contact with humans, usually because the humans are moving into the animal's habitat. These species are killed out of ignorance, because they are seen as a safety threat, or because they are desired for their fur or meat or as trophies. Many times these species are top predators, so their loss is felt throughout the food chain as populations of prey items go unchecked, which causes subsequent problems for the ecosystem and humans. The regulation of hunting, however, involves innumerable complications when impoverished people rely on hunting for their livelihood and when regulation is not well-funded.

Contamination of the air, land, and water results largely from the generation of energy and the use of machines such as the automobile. Power plants and cars produce huge amounts of pollution that have far-reaching impacts because the pollution is spread by wind and river to formerly pristine areas. Contamination of soils and waters also results from the use of

pesticides and fertilizers associated with farming as well as from human waste generated in large urban centers. However, the major threat to biodiversity is habitat loss. Human activities alter the environment to the degree that it can no longer sustain species where they once lived.

pesticides substances that control the spread of harmful or destructive organisms

The solution to these problems must start with global recognition of the importance of conservation. Biodiversity will need to be maintained in those places where it still exists by creating and managing large protected areas. Some species will need to be helped along artificially by maintaining them in captivity and creating seed banks. Previously destroyed habitat will need to be restored by revegetating and repairing the damage that has been done. Management strategies will have to be created that allow for the conservation of land in concert with human goals. To support all of these strategies, a financial, legal, and political infrastructure will need to be created.

It is important to recognize that Earth's declining biodiversity is a serious global problem. It will be up to educators and future generations to stress the importance of conservation and find means to preserve biodiversity, the immense variety of organisms and interactions that support life on Earth. SEE ALSO Ecology; Habitat; Habitat Loss.

Jean K. Krejca

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Bioethics

The term "bioethics" is derived from the Greek words *bios*, meaning life, and the Greek word *ethos*, meaning character. The meaning is essentially "life character." Today, ethics might be better described as applied morals or the philosophy of being moral, with bioethics being the discussion or application of morals within the diverse fields of the life sciences.

The quest for better health has guided scientists and researchers to develop many tools for analysis including organic chemical synthesis and improved genetic engineering. A significant aspect of contemporary medical research is the use of animals as test subjects. Many advances in personal care products, pharmaceutical drugs, and life-saving medical treatments have come about through the use of animals for testing and research. However, this practice is controversial.

Many people feel that animals are abused and mistreated for unnecessary research. The use of animals to test the safety of household or personal care products angers those who feel that humans are unfairly abusing animals for commercial gain. In contrast, scientists point out that animals are the most reliable indicators of potential human response to certain diseases and treatments, and that many successful, life-saving treatments and medical breakthroughs have emerged only because it is possible to test treatment options using animals, rather than human beings.

Unfortunately, some of these discoveries have come at the cost of the natural or induced death of test animals. So the ethical situation arises: Does the benefit of the new data outweigh the risk to the organism, or is the risk greater than the benefits? What may be considered unacceptable to one person may be an acceptable trade-off to another. To address this dilemma, bioethicists attempt to set reasonable restrictions and limits on experimentation so as to maintain a balance between the suffering of experimental animals and the research benefits that may be derived from animal experimentation.

During PETA's (People for the Ethical Treatment of Animals) worldwide campaign to educate the public about the treatment of animals on fur farms, many protestors posed dramatically in front of stores selling fur-trimmed products.

Ethics itself has long been coupled to philosophy and religion. Each person's moral viewpoint is constructed from a host of factors, including education, family background, religion, personal experiences, social level, economic standing, and profession. So if every researcher and every consumer can, hypothetically, hold different views about the relationship between risk and benefit, who is responsible for setting guidelines? And what is the foundation for such guidelines?

Bioethics and Research Institutions

A first step toward establishing ethical guidelines for animal testing has been taken by institutions in the United States that fund research, such as the National Institute for Health, the Food and Drug Administration, and the Agriculture Department. Their policies are primarily set by the public in the form of political action initiated by their elected representatives. The directors and boards of these institutions consider the opinions of their constituents when deciding what types of research to support.

Private institutions such as the Howard Hughes Foundation and Rockefeller Foundations set their policies through committee discussion groups and professional panels that make recommendations to the directors of the respective foundations. Their opinions are reflected in the programs the foundations choose to fund.

Finally, private businesses and corporations that fund this type of research generally use a board or panel approach and approve of experiments within the guidelines set forth in both state and federal law, with an eye to accommodating the general will of the public.

In each of these three cases, an advisory committee is usually composed of senior researchers of a particular discipline—for example, biotechnologists to examine biotechnology questions—plus a philosopher to provide some historical depth and background, and members of interest groups or other public representatives. These panels make their recommendations based upon consideration of current circumstances as well as the potential future impact of the relative costs and benefits of the proposed research.

What sorts of issues does a panel consider when looking at a given experiment? With regards to animal testing for a new pharmaceutical, the dialog generally contains several crucial elements. The first step is to identify an experimental need. For example, a company may wish to test a new drug that would destroy fatty deposits in coronary (heart) arteries. The pharmaceutical company needs to conduct experiments to ensure drug safety and identify any possible side-effects for humans. Since federal law requires that any drug be thoroughly tested with an accurate experimental model to understand its effects before it is approved, one of the first questions to consider is how this may be best accomplished.

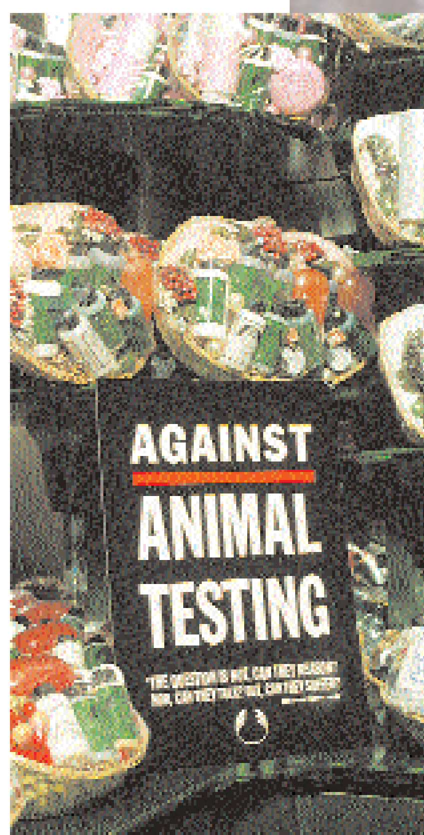
A variety of systems are available to model a drug's behavior. These include microbial models (not suitable in this case); tissue models (the heart tissue model might provide very good information with no apparent negative effects); computer modeling (not always appropriate for finding actual data); and finally, animal models—which have the potential to provide the most accurate information about the drug's likely effect on human beings.

The question of ethics arises during this process. In contemporary American culture, we tend to value human life above the lives of animals. Supporting this view are such culturally accepted practices as the consumption of certain animals as food, the production of drugs such as insulin from animals, and the pursuit of the longstanding hobbies of hunting and fishing for recreation and relaxation. Not everyone agrees that all of these practices are acceptable, however.

controversy a discussion marked by the expression of opposing views

Animal Rights vs. Human Lifestyle

The widespread use of animal life to maintain human life or lifestyle is a growing point of **controversy**. An increasing number of consumers are voicing the opinion that the use of animals in the development of products for human use should be restricted. This is especially true in regard to the cosmetics industry where products are used for appearance rather than health purposes. For example, many consumers, investors, and animal rights activists are offended by the ways in which a product like mascara may be tested on animals before it can be approved for human usage.



The Body Shop, an international manufacturer of hair and skin products, publicizes its refusal to use animals in the testing of their products.

There are those who believe that animal testing may be acceptable if used to develop new drugs that may save human lives. The necessary data regarding performance and safety cannot be gathered any other way. But the practice of killing an animal every time a shampoo changes its color is disturbing to many of these same people. While this may seem extreme, this happens under current law because every time something is added to an existing formula the new combination must be retested for safety and effectiveness, and animals do not always survive such testing.

At first, one might question why it is necessary to go to such lengths to test a nonmedical product. But what if a shampoo's new color proved to harmful to human skin? Or caused hair to fall out? Most consumers agree that it is not acceptable to have less stringent safety standards for such products, and yet there is disagreement about what this means in regard to the ethics of animal testing. It is impossible to set absolute moral guidelines, since each case is unique, but for a variety of reasons, current law is set to err on the side of physical human safety.

Questions in Bioethics

Bioethics requires the asking of questions that go beyond current legal requirements. Are there ways to guarantee safe cosmetics and personal care products that do not involve the use of animals? If animal testing is the only sure way to guarantee product safety, are there ways to keep from harming animals in the process? One option gaining in popularity is to restrict animal testing to the most humane and painless tests possible. Restricting the use of animals to the final stages of testing is another way researchers are trying to balance human safety with animal comfort.

Another issue confronting bioethicists has to do with the removal of animals from the wild for research purposes. In particular, the use of wild chimpanzees and other primates is under scrutiny. The dilemma arises because the public does not appear to support continued harvesting of primates from wild habitats for research purposes, yet the chimpanzee, for example, is the animal most closely related to humans, and thus most desirable for testing potential medicines.

There is little disagreement that creative minds are needed to explore alternative methods of assessing the effects of chemicals on human beings. Increasing knowledge about the human genome, and the promise of genetic treatments for human disease, suggest that animals will continue to have a role in medical research. Those involved in the field of bioethics will constantly be challenged to assess how and when to use animals for this research.

The field of bioethics addresses more than just the question of how to manage conflicting priorities and approaches to animal testing. Now that geneticists have created clones of nonhuman species of vertebrates, there are increasing questions regarding the ethical use of human genetic material. Should researchers be allowed to try to clone human organs for life-saving transplants? Should human embryonic tissue be made available for stem-cell research? Should doctors be allowed to test **gene therapy** on human patients who have exhausted all other treatment options?

gene therapy a process where normal genes are inserted into DNA to correct a genetic disorder

Scientists search for ways to apply a growing body of knowledge to the betterment of human life. Philosophers and others pose ethical questions concerning scientific advancement. Sellers of goods and services depend on the advancements of science to create and fill market needs. Bioethics is the field where life science, philosophy, and commerce meet, where practitioners negotiate boundaries, wrestle with guidelines, and seek balance within the natural world in the quest to improve the quality and quantity of human life. SEE ALSO Animal Rights; Animal Testing.

Brook Ellen Hall

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Biogeography

Why do different species occur in the places they do? Biogeography is the study of why animal species (and also plants) live in different regions on Earth. This includes both organisms alive today as well as those that have become extinct. Any particular animal species is found where it is because that species either evolved and originated there or came there from some other place. The two divisions of biogeography reflect these two ways that animals come to occupy an area. Biogeography can be broken down into historical biogeography, which studies the past history and evolution of a species, and ecological biogeography, which studies the environment of a species.

Ecological Biogeography

Ecological biogeography studies how animal species are distributed in relation to the environment. The environment that influences what animals are present in a region includes both nonliving, **abiotic** factors (such as climate or soil composition) as well as living, **biotic factors** (such as other plants and animals). Earth is divided into major ecological areas called **biomes**. Biomes are regions of distinct **climate** and plant life. There are several kinds of biomes. Examples include the dry, hot desert in which cactuses and other plants are adapted to low water conditions, and the tropical evergreen forest with heavy year-round rainfall and lush plant life.

abiotic nonliving parts of the environment

biotic factors biological or living aspects of an environment

biomes major types of ecological communities

climate long-term weather patterns for a particular region

Dispersal occurs when an animal moves away from the area in which it was born and lives in another area. Dispersal increases the biogeographic range of a species, spreading the population. However, the extent to which an animal can disperse may be limited by ecological factors. Animals that disperse into areas for which they are not adapted will not survive. For example, alligators cannot disperse into central North America because it is too cold during the winter. These ecological limits to dispersal help determine the range of an animal species.

Historical Biogeography

Historical biogeography is the study of how animals that are present in a geographical region today relate to the animals that lived there in the past. A major factor explaining why a species is present in a region today is the presence of the same species in the past, or the presence of a closely related species that once lived there and from which the current species has descended. That is to say, a species is located somewhere because it was there in the past, or because an ancestor of the species lived there.

Continental drift is a major factor in determining current species distributions. All the continents on Earth were once part of one single land mass called Pangaea. About 200 million years ago, this landmass began to drift apart to form the continents of today. There are correspondingly six major biogeographic regions. They are the Neararctic, covering North America; the Neotropical, covering South America; the Ethiopian, covering Africa; the Oriental, covering India and southeastern Asia; the Palearctic, covering Europe and northern Asia; and the Australian, covering Australia.

continental drift the movement of the continents over geologic time

Each of these regions has a group of animals that are more closely related to each other than to animals in other biogeographic regions. This is because of local diversification by speciation (the forming of new species) and the radiation (spread) of species within a biogeographical region; animals in a region are descendants from the ancestors that were previously there. The same is true for plants. Many animal species that are closely related stay in the same biogeographical region because it is hard to disperse or move between these regions. These regions are isolated from one another by an ocean or a very large mountain range, or are connected by only a narrow landmass (an **isthmus**). This isolation serves as a barrier to dispersal; most animals simply can not swim across the ocean to colonize another continent. Likewise, most animals that live in the Pacific Ocean cannot cross the land bridge that joins North and South America to reach the Atlantic Ocean, and vice versa.

isthmus a narrow strip of land

Sometimes a population of animals is split into two populations by the sudden appearance of a physical barrier across which no individual can disperse; this is called a vicariant event. These two populations can become separate species over time because of isolation. An example of a natural vicariant event is an earthquake making a new canyon that is too wide for mice on either side to disperse across. Humans create obstacles that can also cause vicariance, such as highways that would stop mice from dispersing.

An example of a species that created an ecological impact through its migration is the brown tree snake. This species began invading Pacific islands late in the twentieth century by stowing away on shipping boats. As no snakes were native to the islands, the local animals, especially birds, became easy prey for them, and the native bird populations on the islands were negatively affected.

Humans can help promote dispersal. As technology has increased worldwide travel and transportation in the nineteenth and twentieth centuries, some animals have been able to disperse into new biogeographic regions on boats, trucks, or planes. How all the organisms in one place interact with each other and their environment is called the community ecology of an area. Biogeographic regions strongly determine the community ecology of an area. As a consequence, species that successfully disperse to new biogeographic areas can cause huge ecological impacts. For example, the brown tree snake began invading Pacific islands late in the twentieth century. The local animals, especially birds, are easy prey for brown tree snakes because they have not adapted to snake predators. The snakes can quickly wipe out the bird populations that can not adapt fast enough. SEE ALSO Living Fossils.

Laura A. Higgins

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Biological Evolution

Biological evolution is the change in the allele frequency of a gene in a population over time. That is to say some genetic change has happened in the population between generations. Only populations can evolve, not individuals. Individuals can not change their genetic makeup. Only between generations, is there the possibility for genetic changes due to the forces of evolution. These forces are natural selection, mutation, gene flow, nonrandom mating, and genetic drift. Evolution is a measure of a population, not of an individual. Genetic variation, genetic differences between individuals, must exist for evolution to occur.

Charles Darwin defined evolution as descent with modification. However, Darwin did not understand the genetic basis to evolution. Not until Gregor Mendel's work was rediscovered in 1900 could modification with descent be understood in terms of maintaining genetic variation. The mathematical proofs of Godfrey Harold Hardy and Wilhelm Weinberg, known as the Hardy-Weinberg theorem, started the field of population genetics, the integration of Darwinian selection and Mendelian genetics. Their proof showed how variation can be maintained because each individual had two **alleles** for each gene. This is in contrast to Darwin, who specified a kind of blending inheritance in which offspring were intermediate to the parents. Just as importantly, their work specified the forces (causes) of evolution. Population genetics is the foundation for modern evolutionary biology. Other population geneticists, such as Ronald A. Fisher, John B. S. Haldane, and Sewall Wright, contributed to the foundations of the theory of population genetics from the 1920s to the 1940s.

This 50 million year old fossilized spadefish is a part of the fossil record scientists use to study evolution. The detail is particularly good here; the impression of the fish's eggs is visible.

All animals are the descendants of a single common ancestor. Biological evolution has created the diversity of organisms we see today, as well as extinct animals such as dinosaurs for which we have the **fossil record**. The diversifying action of evolution to create new species is called speciation. Speciation is the splitting of one former species into two species that are reproductively isolated from each other such that they no longer successfully reproduce and exchange genes. Speciation is the result of a combination of **biogeography**, natural selection, adaptations, and the other evolutionary forces.

There are two main modes of speciation: allopatric and sympatric. Allopatric speciation is the division of one population into two populations because of some geographical barrier. While separated, each population evolves differently from the other population. When contact is restored between the two populations, they cannot reproduce, and so are unable to exchange genes because of the differences they acquired while separated. Sympatric speciation is when one population splits into two without any geographical barrier. While this mode of speciation was doubted for years, in the 1960s Guy Bush conducted experiments on fruit flies that supported this mode of speciation. In the early 1980s, Bill Rice conducted laboratory experiments in which he was able to cause sympatric speciation. Even though sympatric speciation is possible, it is not as common as allopatric speciation.

alleles one of two or more alternate forms of a gene

fossil record a collection of all known fossils

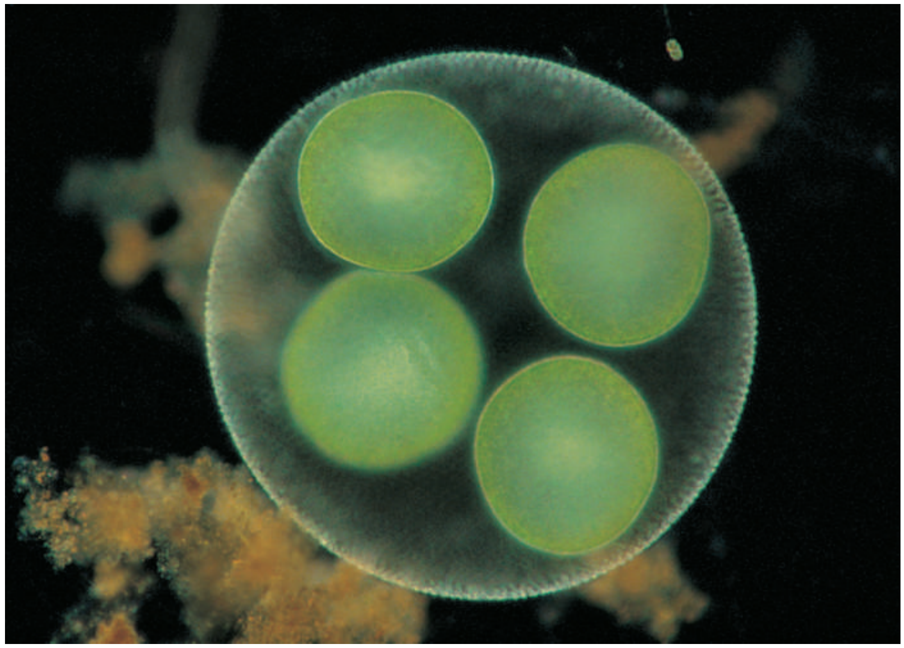
biogeography the study of the distribution of animals over an area

Causes of Biological Evolution

There are five forces that cause evolution: natural selection, mutation, gene flow, nonrandom mating, and genetic drift. All five depend on the existence of genetic variation, which is necessary for any evolutionary change. Natural selection is the differences in the survival and reproduction rates of individuals with different **phenotypes**. When phenotypes can be genetically inherited, natural selection produces adaptations as the population evolves. Natural selection can remove variation from a population if it is stabilizing selection. Diversifying selection can increase the amount of variation in a population. Directional selection changes the average trait in the population.

phenotypes the physical and physiological traits of an animal

Genetic mutations occur when errors are made in replicating (copying) and dividing DNA. Mutation is the ultimate source of genetic variation. Most of the time, mutations either have no effect on the phenotype, and



Reproduction—shown within this Chlorophyta Volvox protozoa that contains four daughter colonies—is a driving force behind biological evolution.

therefore are neutral, or have a harmful effect. Rarely, a mutation will create a phenotype that is better, and so natural selection will favor this beneficial mutation. Mutations happen naturally at low levels of frequency. These levels can be much higher under some conditions. For example, exposure to radiation and to some toxic chemicals produces higher mutation rates.

Gene flow is the exchange of genes among populations or species. The exchange of genes between species is called hybridization. Introducing new genes into a population changes the gene frequency and causes evolution. Gene flow can be positive or negative for a population. Lots of gene flow can prevent local adaptation because any evolution produced by natural selection is swamped by the invading genes. On the other hand, gene flow can introduce a new beneficial gene into a population. Natural selection can favor this new adaptation, and it can spread through the population.

genotype the genetic makeup of an organism

Nonrandom mating changes what combinations of genes are mixed together in sexual reproduction. Sexual reproduction creates new individuals, half of whose genetic information comes from the mother and half from the father. If individuals within a population who have a particular **genotype** pair off and mate at a rate different from the occurrence of that gentotype in the population, then nonrandom mating is occurring. Nonrandom mating can be caused by mating among close relatives, or inbreeding, which can result from population subdivision. Nonrandom mating also happens when individuals choose mates based on particular phenotypes. In some animal species, a few males get most of the matings because they have some highly desirable phenotype. Assortative mating also produces nonrandom mating, which is the mating of males and females of the same phenotype. For example, large male frogs mate with large female frogs and small males mate with small females.

Genetic drift causes evolution by random changes in the allele frequencies. One way for genetic drift to happen is for some of the alleles to be left after some kind of fluctuations in population size. For example, if disease wipes out most of a population, only some alleles will be left in the population. Also, only some combinations of alleles for different genes will be left. If natural selection is not acting on a gene, then random genetic drift can be a stronger force than if selection is present. The impact of drift depends on the population size. Drift is stronger in smaller populations; they are more susceptible to random changes in allele frequencies since there are not as many alleles present.

Limits to Biological Evolution

What can limit evolution? Three main factors restrict the amount of change evolution can make in a population: the degree of genetic variation is limited; natural selection produces adaptations that are a compromise in form and function; and most forces of evolution are not adaptive.

First, genetic variation is the ultimate barrier to evolution. If there is no genetic variation, no evolution can happen. Genetic variation is limited to the history of the organism. A bear will not suddenly gain wings in a few generations of evolution. No bear has ever had wings, and it is unlikely that any bear will evolve them. An organism contains only so much DNA and the amount of existing genetic variation, the raw material for evolution, is restricted by the past history of the species. A bear does not have the underlying genetic variation necessary for a mutation to produce wings from the existing variation.

Second, adaptations are usually compromises and therefore limit evolution. Natural selection works on a whole organism rather than just single traits, so it is the combination of traits that natural selection favors. A cheetah is a fast runner but a poor swimmer. Any cheetah with webbed feet would be a better swimmer but could certainly not run as fast. Adaptations are trade-offs.

Third, many forces of evolution are not adaptive. Natural selection is the force of evolution that produces adaptations but the other forces of evolution are not necessarily adaptive. Gene flow can introduce genes into a population that are better suited to another environment. Nonrandom mating can break up existing combinations of genes that work well together. Mutation is typically harmful. Random genetic drift is frequently not beneficial. Most forces of evolution are random and can be working counter to natural selection.

Rates of Evolution

Does evolution proceed at a fast pace or a slow pace? How much of evolution can we actually observe? In 1972 Niles Eldredge and Stephen J. Gould wrote an article that presented the idea of punctuated **equilibrium**. Some organisms for which there are good fossil records show long periods of no morphological evolution (evolution in the form and structure of organisms); the animals remain unchanged over thousands of years. But then there suddenly appears what looks like a morphologically similar new species. The theory of punctuated equilibrium is that long periods of no change are followed by short periods of rapid transition. This is in direct contrast to gradualism. Gradualism suggests slow but continuous change over geological time. How is one to know if the fossil record is incomplete, and that the seemingly rapid change is accounted for by missing intermediate stages?

equilibrium a state of balance

This question has inspired research on the rate of evolutionary change. It is possible to calculate rates of morphological evolution from the fossil record. Evolutionary rates can be measured over several generations in natural and laboratory populations. It is also possible to measure the relative rate of change in molecules for which the gene sequence is known. The sequence of a gene is the order of nucleotides within it. Sexual reproduction can also increase the rate of evolution compared to asexual reproduction. This is due to increased genetic variation by recombination and independent assortment. Gene sequencing has made it possible to investigate how the rate of evolution changes with the degree of underlying genetic variation, also called genetic **polymorphism**. In 1991 the first important test of rates of molecular evolution and molecular polymorphism was conducted by J. H. McDonald and Martin Kreitman. As the entire genetic material (genomes) of more and more organisms are sequenced, we will understand more about the rate and mechanisms of evolution. SEE ALSO ADAPTATION; GENES; GENETICS; NATURAL SELECTION.

polymorphism having two or more distinct forms in the same population

Laura A. Higgins

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Biological Pest Control

Scientists use different pest control methods that range from choosing a pesticide that will be least harmful to beneficial insects to raising and releasing one insect to attack another. Biological control of horticultural pests is a subject of increasing interest, especially to people who prefer to use chemicals as little as possible. The traditional and familiar use of chemical pesticides sometimes has detrimental effects on the environment (such as with DDT) and harmful effects on humans (such as the increased risk of cancer in individuals exposed to certain pesticides). There are, however, alternative pest control methods, such as biological pest control, that are less harmful to the environment and humans. Unfortunately, biological pest control methods alone are rarely sufficient. Research suggests that an integrated approach, using pesticides, biological pest control, and other techniques may be the most effective.

In general terms, biological pest control is the use of a specifically chosen living organism to control a particular pest. This chosen organism might be a naturally occurring parasite, predator, or disease that will attack a harmful insect. Biological pest control is a way to manipulate nature to increase a desired effect. There are three main ways to use natural enemies against unwanted insect pest populations: classical biological control, augmentation, and conservation.

Classical Biological Control

Classical biological control involves releasing an imported organism that establishes itself and spreads to permanently control a pest. In 1889, for example, the release of 129 imported Australian vedalia beetles resulted in a dramatic reduction of cottony cushion scale disease, which had threatened California's citrus industry. Successful biological control means no further costs are required to keep the pest under control.

Classic biological control may also mean traveling to the country or area from which a newly introduced pest originated and returning some of the natural enemies that attacked it and kept it from being a pest there. New types of insects are constantly arriving, accidentally or intentionally. Sometimes they survive. When they come, their enemies are left behind. If the insects become a pest, introducing some of their natural enemies can be an important way to reduce the amount of harm they can do. Although simple in concept, the process of locating the place of origin of the nonnative pest and then finding and introducing natural enemies from its place of origin presents many ecological and logistical challenges. For example, any introduced pest predator or parasite must undergo exhaustive testing before being released to be sure it will not harm nontarget organisms. Even when challenges are successfully met, projects can fail because of problems relating to such factors as climate differences, prior or current pesticide use, disturbances of the habitat by other agricultural operations, and the removal of noncrop vegetation that might otherwise offer food and shelter to the natural enemies.

Augmentation

Augmentation is a method of increasing the population of a natural enemy that attacks pests. This can be done by mass producing a pest in a laboratory and releasing it into the field at the proper time or breeding a better natural enemy that can attack its prey more effectively. Mass rearings can be released at special times when the pest is most susceptible and natural enemies are not yet present, or they can be released in such large numbers that few pests go untouched by their enemies. In one study, for example, male insects were sterilized by gamma radiation, and large numbers were released into the environment to mate with wild insects. The pest population was dramatically reduced because they were unable to produce viable offspring.

Scientists also grow microbes, such as bacteria and fungal spores, in the laboratory and spray crops and lawns with large numbers of these natural organisms to bring certain pests under control. About 1,100 species of viruses, bacteria, fungi, protozoa, rickettsiae, and nematodes are known to parasitize insects. Japanese beetle populations, for example, once created major crop infestations here in the United States but have been decimated by treating crops and lawns at intervals with spores of a bacillus bacterium that causes milky disease, a lethal pathogen for these beetles. These spores

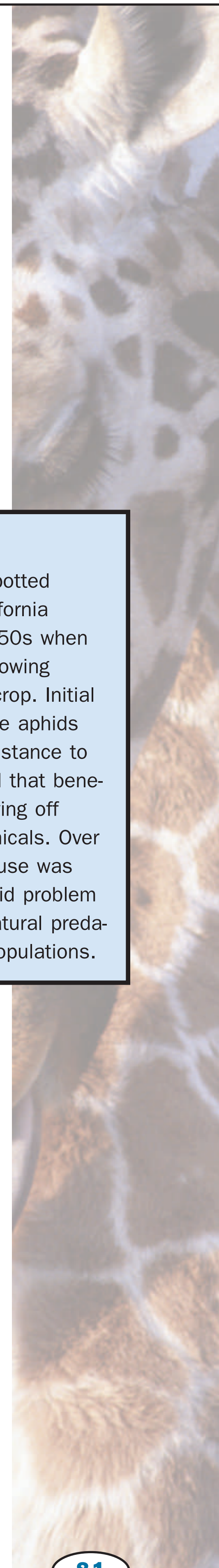
Farmers use the natural appetite of ladybug beetle larvae for aphids to help keep the population of aphids on their farms under control.

infect the Japanese beetle larvae but do not harm other animals in the environment.

Another bacterium, *Bacillus thuringiensis*, has been extensively exploited in the bacterial control of pest insect populations. Commercial preparations of *Bacillus thuringiensis* are registered by at least twelve manufacturers in five countries for use on numerous agricultural crops and forest trees for control of pests including the alfalfa caterpillar, bollworm, cabbage looper, fruit tree leaf roller, California oakworm, and fall webworms. Many other commercial bacterial products exist. For many years, a mixture of *Bacillus popilliae* and *Bacillus lentimorbus* has been marketed under the trade name Doom.

Viral diseases have also been studied as a means of controlling certain caterpillars and sawfly larvae. Crops are sprayed with a substance prepared from diseased insects in order to start an epidemic of a fatal disease in the pest population.

Augmentation is effective but it relies upon continual human management and does not provide a permanent solution, unlike importation or conservation methods.



Conservation

Conservation of enemies is an important part of any biological control effort. This strategy involves identifying any factors that limit the effectiveness of a particular natural enemy and changing them to help the beneficial species. Conservation of natural enemies involves either reducing factors that interfere with the natural enemies or providing needed resources that help natural enemies. Use of reflective aluminum strips mixed in with mulch in vegetable fields, for example, has reduced or prevented aphid attack and thus protected cucumbers, squash, and watermelons from infestation. The planting of cover crops, such as providing nectar-producing plants and sources of alternate hosts in and around fields, and the interplanting of different crops to provide habitat diversity are management techniques that lead to the buildup of natural enemy populations and result in enhanced biological control.

Other Alternative Nonchemical Control Methods

Physical energy is also known to kill insects. In a recent discovery, adult Indian-meal moths exposed to certain wavelengths of sound during their egg-laying period reduced their reproduction by 75 percent. These sound waves also had a similar effect on flour beetles. Light waves, high-frequency electric fields, and high-intensity radio frequencies also may offer helpful options. Sophisticated methods of pest control are continually being developed. Cutting-edge research with highly specific insect hormones was also underway at the beginning of the twenty-first century.

CASE STUDY

The battle against spotted alfalfa aphids in California began in the late 1950s when researchers noted growing damage among the crop. Initial tests showed that the aphids had developed a resistance to chemical sprays, and that beneficial insects were dying off because of the chemicals. Over the years, pesticide use was reduced and the aphid problem diminished as the natural predators regained their populations.

Integrated Pest Control Methods

Integrated pest control methods, which involve more than one method, may be the best answer. Combining disease-resistant plant varieties with an insecticide that leaves parasites and predators unharmed is one ideal strategy that seems to offer promise. It has been successful, for example, in combating the spotted alfalfa aphid in California. In other cases, first-line defenses such as chemical sprays combined with bait, followed by the sterile-insect technique were highly effective. The most important value of this control method is that far fewer chemical pesticides are used, and so the environment remains unaffected.

Biological pest control methods, in concert with proven agricultural practices such as destruction of crop residues, deep plowing, crop rotation, use of fertilizers, strip-cropping, irrigation, and scheduled planting operations, can further prevent or reduce crop damage. SEE ALSO DDT; PESTICIDE.

Stephanie A. Lanoue

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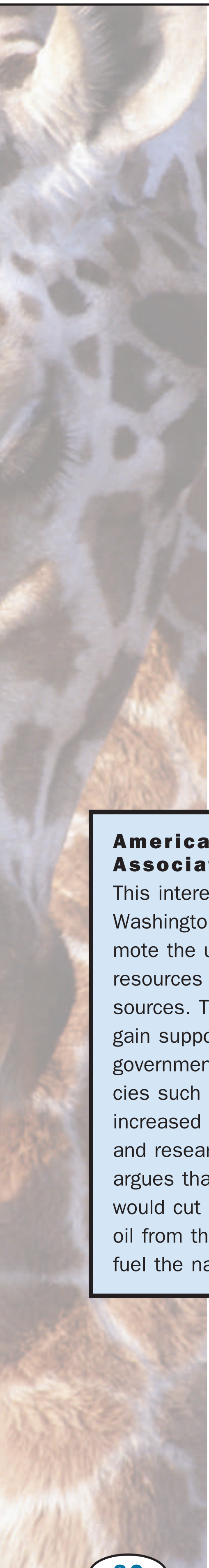

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Biomass

Suppose you take a walk in the forest one day and you look around you at all the trees and think, "That's a lot of wood, I wonder how much all these trees weigh?" Biologists ask the same question. Biomass is the total mass of all the trees (after the water has been taken out).

The term "biomass" is actually applied to three related but slightly different concepts. The total dry weight of all living organisms that can be supported at each **trophic level** in a food chain is known as the biomass. The term is also applied to the dry weight of all living organic matter in an entire ecosystem. Finally, people interested in alternative sources of energy use the term to apply to the total mass of all plant materials and animal wastes that can be used as fuel.

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

Plants use a complex chemical process known as **photosynthesis** to combine carbon dioxide, water, and sunlight to produce carbohydrates (sugar and cellulose), fats, and proteins. The solar energy that drives photosynthesis is stored in the chemical bonds of these molecules. These carbohydrates, fats, and proteins make up biomass. Biomass, then, can be considered to be stored solar energy.

photosynthesis the combination of chemical compounds in the presence of sunlight

The energy stored in carbohydrates and other compounds by photosynthesis can be released by burning or by metabolism. When animals eat plants, their bodies slowly release the energy stored in the chemical bonds and this energy becomes available to the animals for muscular activity or maintaining body temperature. When biomass is burned, the water and carbon dioxide are released back into the atmosphere. Therefore, biomass is a renewable energy resource.

American Bioenergy Association

This interest group located in Washington D.C., works to promote the use of bioenergy resources as alternative energy sources. The ABA strives to gain support through the federal government by proposing policies such as tax incentives, increased budget allocations, and research funding. The ABA argues that using biomass would cut U.S. dependence on oil from the Persian Gulf, and fuel the nation's economy.

The total amount of biomass produced each year is about eight times the world's energy consumption. However, the energy density of each unit of biomass is much smaller than the energy content of fossil fuels ("old" biomass), so much more mass must be burned to produce the same amount of energy. Also, the world's biomass is widely distributed, so concentrating and transporting the biomass remains a problem. There are experimental projects that convert biomass into alcohol or natural gas. But worldwide, only about 7 percent of the biomass produced each year is used as fuel, so this energy resource remains underutilized.

The amount of biomass generally decreases at each higher trophic level. In a temperate grassland, for example, the amount of biomass at each trophic level is only about 10 percent of the biomass of the level below it. If there are 10,000 kilograms (22,000 pounds) of producers (grasses and other plants), there will be only 1,000 kilograms of primary consumers (grasshoppers, voles, bison), 100 kilograms of secondary consumers (shrews, hawks, small cats), and only 10 kilograms of tertiary consumers (large cats, wolves, humans).

The remaining 90 percent of the available energy from biomass at each level is converted to waste heat. This energy loss at each trophic level generally limits food chains to no more than four or five levels.

Marine environments usually reverse the amounts of biomass in the first two trophic levels. The mass of primary consumers (small fish and shrimp) is generally much larger than the mass of producers. This happens because the primary producers are tiny phytoplankton that grow and reproduce rapidly instead of large plants that grow and reproduce slowly. SEE ALSO Biomes; Food Web.

Elliot Richmond

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Biomechanics

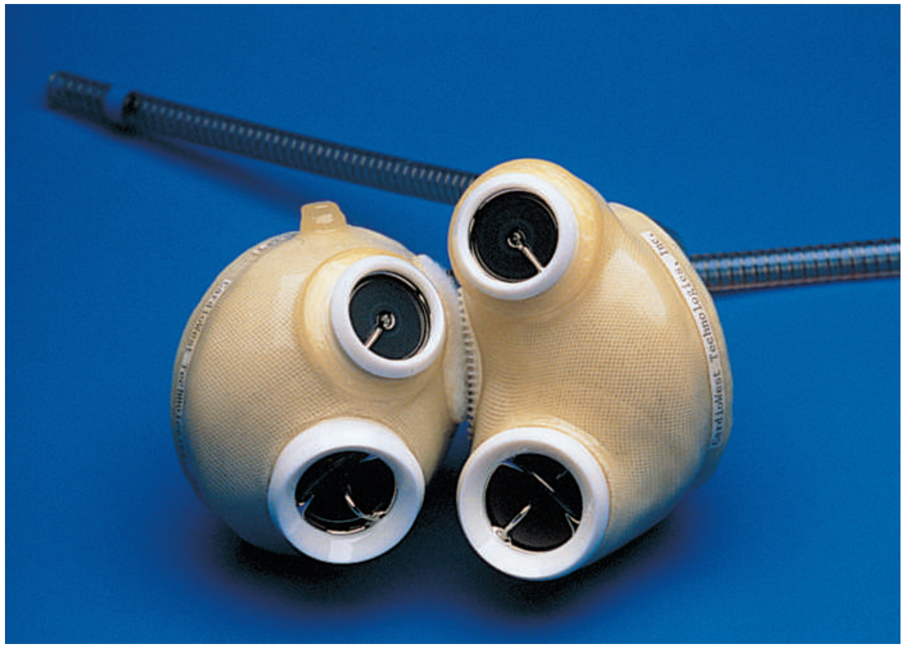
The science of biomechanics applies mechanical principles to the study of organisms. Biomechanics uses mathematical models and computer simulations to study living organisms, in addition to direct biological measurements.

Biomechanics helps us understand limitations on the size of organisms, problems with scaling, energy efficiency, the advantages of internal versus external skeletons, and other concepts. Biomechanics can even help biologists understand animal behavior, such as how a whale can remain submerged for extended periods of time.

For example, the largest single-celled organisms are protists about the size of the period at the end of this sentence. There are larger cells that are part of multicellular organisms, but no single-celled organisms. So why are there no large, single-celled animals? The primary restriction is surface-to-volume ratio. A cubical cell 100 µm on a side has a volume and mass 1,000 times as great as the volume and mass of a cell 10 µm on a side. This larger mass requires roughly 1,000 times as much oxygen, food, and water. It also produces 1,000 times as much waste that must be excreted.

Where does the cell exchange all this material? Exchange takes place through the cell membrane. But the cell membrane of the larger cell is only 100 times as large as the smaller cell, so 1,000 times as much material must pass through a membrane only 100 times as large. If the cell membrane is wrinkled and folded its area is increased, but the cell will ultimately reach a point where it will be unable to feed or breathe through the membrane. This places a practical limit on the maximum size a single-celled organism can attain. Large organisms must be multicellular and have a complex system of specialized cells that can transport food, oxygen, and waste.

If you compare a house cat (*Felis sylvestris*) and a Bengal tiger (*Felis tigris*), it is obvious that multicellularity is not a sufficient solution to the problems of scaling up an organism to larger size. Weight is proportional to volume, so weight increases with the cube of height. Muscle and bone strength is



Production of this artificial heart by Cardiowest Tech was made possible by the close study of the mechanics of the human heart.

proportional to cross-sectional area and increases with the square of height. This means the tiger requires much thicker legs than the house cat, relative to its overall size, to support its larger mass and move quickly.

A detailed biomechanical study of the effects of scale that considers factors such as weight, air resistance, muscle strength, heat loss, and bone stress can explain some surprising observations. For example, an impala, a domestic cat, a domestic dog, and a domestic horse can all jump to roughly the same height above the ground. Biomechanics helps us understand why. Biomechanics can also explain why large whales (air-breathing organisms) can remain submerged for a long time compared to small dolphins and seals. Underwater, body size is advantageous. In contrast, large hawks can only hover for a short time, whereas hummingbirds, kestrels, and kingfishers can hover for extended periods. In the air, large size is a disadvantage.

One of the most productive applications of biomechanics has been in the field of athletic competition. Coaches study the principles of biomechanics to learn how to improve the performance of the athletes they train. Ideas of conservation of angular momentum from physics can help coaches teach athletes how to improve their ability to throw a discus or put the shot. Energy conservation helps marathon runners learn how to train more effectively and run more efficiently.

The biomechanics of running, especially amateur running, has been an area of intense research and interest. Some sports doctors videotape their patients to study abnormalities in their gait that have the potential to cause injury. Doctors can then prescribe shoe inserts or other shoe modifications to help prevent injury. They may also recommend a change in running style or training regimen based on a runner's idiosyncrasies. For example, a doctor might notice that the runner is swinging his or her arms across the body. This causes an excessive rotation of the pelvis, which can lead to hip pain. If this is the case, the doctor may train the runner to move his or her arms parallel to the direction of motion.

Another important area of research in biomechanics is automobile safety design. Most people have seen films of crash-test dummies. Crash-test dummies are designed to simulate humans. Their joints move the same way that human joints move. By analyzing how car accidents affect the dummies, engineers can design safer automobiles.

More recently, biomechanics is moving toward computer models that can be used. The advent of fast, powerful computers and improved mathematical models make it possible to analyze the effects of a crash on humans with greater accuracy and less expense than is possible through mechanical simulations such as dummies.

Elliot Richmond

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Biomes

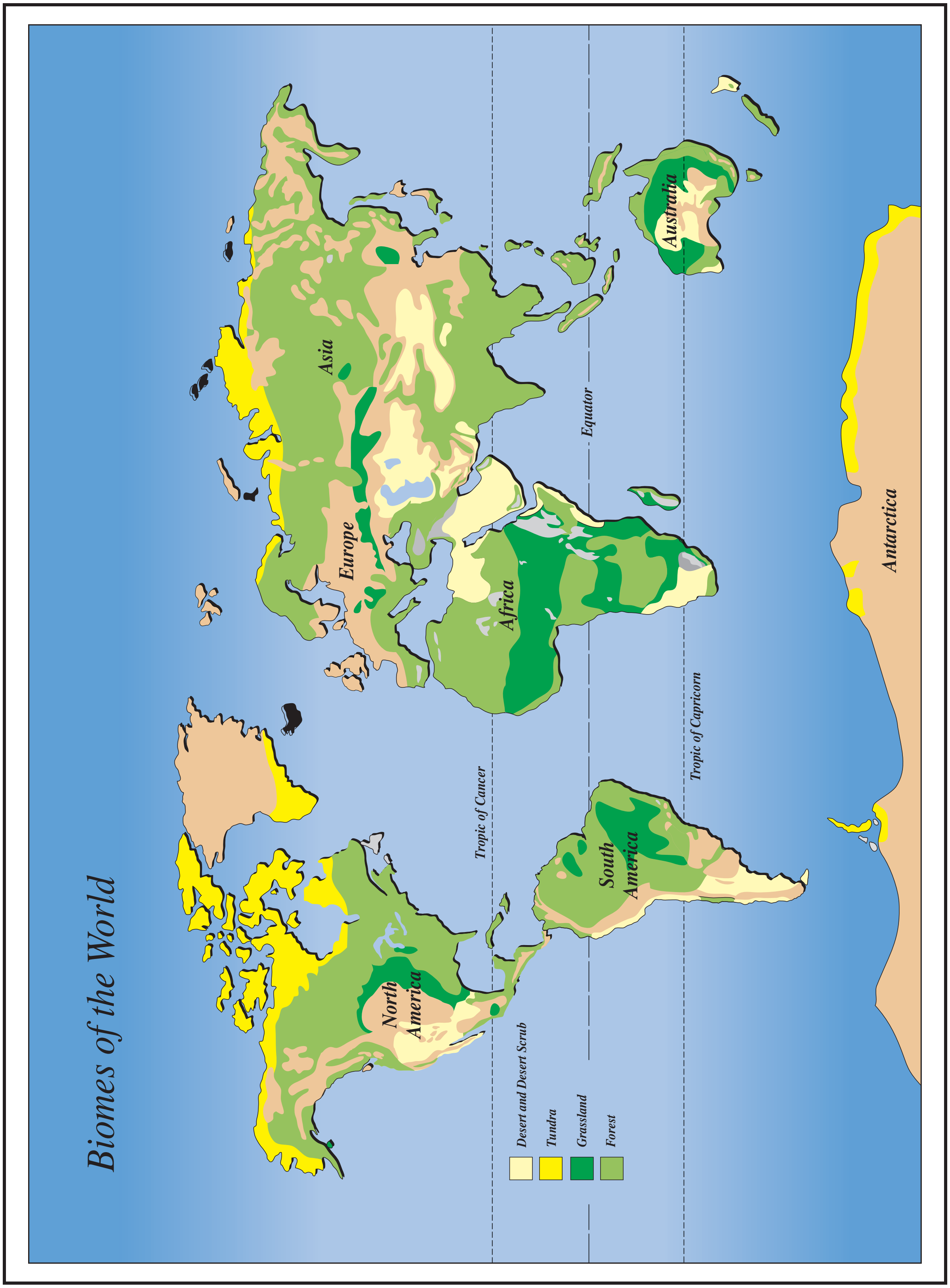
An ecosystem is a community of organisms that interact with each other and with the **abiotic** (chemical and physical) factors in their particular environment. A biome is the largest well-defined ecosystem. Biomes include vast grasslands, continent-wide deserts, and sweeps of arctic tundra. Biomes also include such well-defined ecosystems as coral reefs, lakes, and river systems.

abiotic nonliving parts of the environment

Biomes are characterized by climate, by typical vegetation, and by the way organisms have adapted to that environment. Biomes are not permanent. Grasslands can be transformed into deserts; forests can be converted into grasslands. Climate change at the end of the last Ice Age dramatically altered the biomes of North America because of natural changes in climate and the movements of land masses. Since the Industrial Revolution, human activity has become an increasingly important factor in alteration of biomes.

Biomes are usually classified on the basis of average temperature and precipitation. This classification scheme results in many different biomes. Five typical biomes are:

- Aquatic
- Deserts
- Forests
- Grasslands
- Tundra


Biomes of the World
Desert and Desert Scrub
Tundra
Grassland
Forest
Tropic of Cancer
Equator
Tropic of Capricorn
North America
South America
Europe
Africa
Asia
Australia
Antarctica

Aquatic Ecosystems

Water covers about 75 percent of Earth's surface (including both freshwater and marine environments). While some ecologists reserve the term "biome" to refer to terrestrial ecosystems, aquatic ecosystems play a very important part in the ecology of Earth. Aquatic ecosystems can be freshwater (such as ponds and lakes, streams and rivers, and wetlands) or marine (such as oceans, coral reefs, mangrove swamps, salt marshes, and **estuaries**).

estuaries areas of brackish water where rivers meet the oceans

Freshwater Regions. Water is classified as fresh if it contains less than 1 percent salt (sodium and potassium chloride and other salts) in solution. Most freshwater plants and animals are unable to tolerate higher concentrations of salt in the water.

Ponds may be only a few square meters, whereas the largest lakes cover thousands of square kilometers. Ponds and lakes are scattered all over Earth. Many important ponds are seasonal and last for only one or two months at a time. These seasonal ponds may still be important resting places for migrating birds and other animals. Some large lakes have lasted for tens of thousands of years.

Lakes and larger ponds can be divided into three different "zones," determined by depth and distance from the shore. The littoral zone is the top layer of water near the shore. It may be warmer than the average temperature of the lake, but it also may have wider seasonal temperature variation. This is generally the most biologically diverse community in the lake, including algae (like diatoms), rooted and floating aquatic plants, grazing snails, clams, insects, crustaceans, fishes, and amphibians. Insect larvae may also inhabit this zone. The vegetation and animals living in the littoral zone provide food for other creatures such as turtles, snakes, and ducks.

The open water surface of the lake is known as the limnetic zone. Since this zone receives the most sunlight, it is a rich source of plankton. These plankton are the base of the food chain for the whole lake. Small fish also inhabit the limnetic zone, where they eat plankton or food that falls on the surface of the lake.

The bottom of the open water portion of the lake is known as the profundal zone. Since little light penetrates this region, its inhabitants are **heterotrophs**, which eat the small fish and other animals from the littoral and limnetic zones. Other inhabitants are detrivores, subsisting on material falling into the deep water from the surface.

heterotrophs organisms that do not make their own food

The temperature of a pond or lake will vary seasonally. In colder climates, the surface of the lake may freeze solid. In large lakes the deep water will never freeze, remaining about 4°C (39° F) all winter. During spring and fall, substantial mixing of the lake water can occur (sometimes called "turning over").

A river is a long, narrow body of water flowing downhill. A river may start in the mountains and flow all the way to the ocean. Or it may start in a lake or spring and flow a short distance before joining another river or entering a lake. The start of the river will have a lower temperature, clearer water, and more oxygen. The middle part of the river will be wider and slower moving. The water will be warmer. There will be more species diversity,

The mountains and alpine meadow of Denali National Park, Alaska, are part of a larger ecosystem which is otherwise known as a biome.

including plants and algae. Close to the mouth of the river, the water may be filled with sediment. Fish that can tolerate less oxygen and warmer temperatures, such as carp and catfish, will be found near the mouth.

Wetlands are areas of standing water that support aquatic plants. Marshes, swamps, and bogs are all wetlands. The water in wetlands flows slowly or is still. Wetlands can be seasonal or permanent. Since the water in wetlands is often low in oxygen, plant species often require special adaptations. Wetlands have the highest species diversity of all ecosystems, with many species of amphibians, reptiles, birds, and fur-bearing mammals living in them.

Marine Regions. Marine ecosystems, which cover about three-fourths of Earth's surface, include oceans, seas, saltwater marshes, estuaries, and coral reefs. Because of their size, marine ecosystems are important parts of the atmospheric carbon dioxide cycle. Marine algae take in huge amounts of carbon dioxide from the atmosphere and release much of the world's oxygen supply. Marine ecosystems also supply most of the atmospheric water vapor that falls as precipitation on land.

Oceans are the largest of Earth's ecosystems. Like lakes, oceans are subdivided into separate zones: intertidal, pelagic, abyssal, and **benthic**. All four zones have a great diversity of species. The intertidal zone is the region along the shoreline between average low tide and average high tide. In other words, this region goes through cycles of submergence and being exposed to air. Animals in this zone must be able to survive the extended periods of exposure. The pelagic zone includes all the open ocean water. The abyssal zone is the deep ocean water, between 2,000 and 6,000 meters deep. The benthic ocean includes the deep ocean bottom inhabited by organisms.

benthic living at the bottom of a water environment

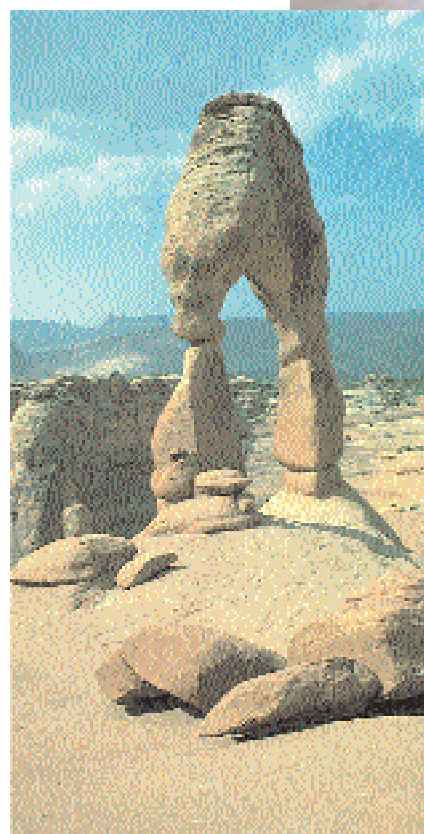
Deserts

Deserts cover about one-fifth of Earth's surface. The identifying characteristic of the desert biome is low annual rainfall. Some deserts receive large amounts of rain in the form of heavy thunderstorms, but these occur for a short time and run off rapidly. On average, any region that receives less than 50 centimeters of rainfall per year is considered a desert. The driest deserts receive less than 2 centimeters of rainfall per year. The Atacama in Chile may get no rainfall at all for years at a time.

Most of the world's deserts occur in a band between 10° and 40° of the Equator. Cold deserts, such as the basin and range area of Utah and Nevada and parts of western Asia, occur at higher latitudes. Most deserts have a wide variety of specialized vegetation, as well as many specialized animals. Because there is little rainfall, most desert soils have high nutrient levels. However, the humus (organic matter) in soils is very low.

Desert plants are typically low-growing shrubs and short woody trees. Leaves are of many different types, but all show various degrees of specialization because of the lack of rainfall. Many plants have small leaves that are covered with a waxy film to retain water. The thorns of cacti are highly modified leaves that shade and protect the plant. The thickened and often flattened stems of cacti have taken over the job of photosynthesis.

While mule deer, pronghorns (which resemble antelopes), desert bighorns (a type of wild sheep), and mountain lions are all found in the relatively humid deserts of North America, the dominant vertebrates of warmer and drier deserts are small reptiles and amphibians. Mammals are usually small, like the kangaroo mice of North American deserts. There are also insects, arachnids, scorpions, and birds. The animals stay inactive in protected hideaways during the hot day and come out to forage during twilight hours or at night.



The "Delicate Arch" of the Arches National Park in Utah sits on top of a large sandstone formation. The climate of the park is desertlike, with temperatures reaching highs of 38°C (100°F) in the summer months, and lows of 0°C (32°F) in the winter.

Forests

Forest biomes are ecological communities dominated by trees. There are three major types of forests distinguished by latitude: tropical, temperate, and boreal forests (taiga).

Tropical forests include the greatest diversity of species of any of the world's biomes. By definition, tropical forests occur in the tropics, within 23.5° of the equator. Instead of the four seasons typical of temperate regions, most tropical forests have two seasons, a dry season and a wet season. The temperature and amount of daylight are fairly constant. However, because of the heavy forest canopy, little sunlight reaches the forest floor.

The annual rainfall in tropical forests is generally 200 centimeters or more. This high amount of rainfall results in soils that have lost most of the nutrients. A square kilometer of tropical forest may contain 100 species of trees and thousands of species of insects. Orchids, bromeliads, ferns, mosses, and palms grow in the trees and on the forest floor. Birds, bats, small mammals, and insects live in and around the trees.

flora plants

deciduous having leaves that fall off at the end of the growing season

Temperate forests are characterized by four distinct seasons, including a winter season with extended periods below freezing. The tree canopy allows light to penetrate to the forest floor, so there is an understory of shade-tolerant trees and shrubs. This results in a stratification of the **flora** and fauna of the temperate forest, with distinct sets of plants and animals present in the treetops, the mid-levels, and on the forest floor. Most trees are broad-leaved **deciduous** trees that drop their leaves each fall; mixed in are some evergreen conifers. Typical tree species include oak, hickory, maple, elm, willow, and dogwood. Animals include rabbits, squirrels, skunks, many species of birds, deer, mountain lion, bobcat, timber wolf, fox, and black bear. Reptiles and amphibians inhabit the forest floor.

acidic having the properties of an acid

Boreal forests are cold forests of northern latitudes that experience many months of snow cover and below-freezing temperatures. Extensive boreal forests occur north of 50° north latitude to beyond the Arctic Circle. Boreal forests are found in a broad belt extending from Siberia across Alaska, into Canada and parts of the northern United States, and also in Scandinavia. These forests may also be found farther south at higher altitudes. Seasons are divided into short, moist, moderately warm summers and long cold, dry winters. The length of the growing season in boreal forests is very short, around 100 days. Precipitation is primarily in the form of snow, the equivalent of 40 to 100 centimeters of rainfall annually. Soil is generally thin, nutrient-poor, and **acidic**. The dense canopy permits little light to reach the forest floor, so the forest understory is limited. The trees are mostly evergreen conifers such as spruce, pine, and fir. Animals include woodpeckers, hawks, owls, many other bird species, moose, bear, weasel, fox, lynx, and deer.

Grasslands

Grasslands are lands dominated by grasses. Large shrubs or trees are restricted to stream banks and to isolated stands. There are two main divisions of grasslands: tropical grasslands, called savannas, and temperate grasslands.

Savanna. A savanna is grassland with widely scattered individual trees or small groups of trees. Savannas of one sort or another cover most of central Africa and large areas of Australia, South America, and India. A savanna is not as arid as a desert but receives roughly the same amount of rainfall as a temperate forest. The annual rainfall ranges from 50 to 130 centimeters per year. However, the rainfall occurs in a "wet" season of four to six months. The wet season is followed by a dry season. During the dry season, drought and fires can occur. The drought and fires suppress the growth of trees and shrubs. This cycle of wet and dry seasons, fires, and drought maintains the savanna conditions.

Human activity can inadvertently convert a forest into a savanna. If the trees are removed and grass grows rapidly enough to cover the bare ground before the trees can recolonize, then fires may become the dominant force, and the savanna will become more or less permanent. The relatively infertile soil of savannas has discouraged the conversion of savannas to farming of wheat and other grasslike crops. When farming is instituted, the organic material is quickly exhausted and the soil then requires the addition of chemical fertilizer to remain productive.

Fire is essential to the life of a savanna. Most animals killed by the fires are insects and small animals. Large animals are able to escape the fire. Birds and other opportunistic feeders move in quickly to eat the killed animals or to prey on the animals fleeing the fire. The grass quickly sprouts from the extensive root structure out of reach of the fire. Many shrubs and woody plants are killed by the fire.

The shrubs and trees that survive have special adaptations that allow them to survive the fire or to sprout quickly when the rains come. The life cycle of animals that live on the savanna is tied to this same cycle. Calves are born soon after the start of the rainy season, when plenty of new grass is available. Other animals that live completely or partly on the savannas around the world (not all in the same place) include giraffes, zebras, buffaloes, kangaroos, mice, moles, gophers, ground squirrels, snakes, worms, termites, beetles, lions, leopards, hyenas, and elephants.

Temperate Grassland. Temperate grasslands also have grasses as the dominant vegetation. Trees and large shrubs are restricted to the banks of streams. Temperatures vary widely from summer to winter. The amount of rainfall is less in temperate grasslands than in savannas. The plains and prairies of central North America were typical temperate savannas before the land was converted to farming. As in savannas, the cycle of seasonal drought and fire is essential to maintaining the **biodiversity** of temperate grasslands.

biodiversity the variety of organisms found in an ecosystem

The soil of the temperate grasslands contains a thick layer rich in organic matter from the growth and decay of grass roots. The organic material holds the soil together and provides nutrients for new growth. Seasonal drought, fire, and grazing by large mammals all prevent woody shrubs and trees from invading and becoming established. Some trees, such as cottonwoods, oaks, and willows, grow along streams and in river valleys. Many annual plants, such as wildflowers, grow among the grasses.

Temperate grasslands also experience a wet season and a dry season. Most precipitation occurs in the late spring and early summer. The rest of the year is relatively dry, with rainfall averaging 50 to 90 centimeters per year. The temperature range of temperate grassland is very wide. Summer temperatures can be well over 40°C (104°F), while winter temperatures can drop as low as -40°C (-40°F).

Animals found in temperate grasslands in different parts of the world include gazelles, zebras, rhinoceroses, wild horses, lions, wolves, prairie dogs, jackrabbits, deer, mice, coyotes, foxes, skunks, badgers, blackbirds, grouse, meadowlarks, quail, sparrows, hawks, owls, snakes, grasshoppers, leafhoppers, and spiders.

Tundra

Tundra is the coldest of all the biomes. "Tundra" is derived from the Finnish word *tunturia*, which means "treeless plain." Extremely low temperatures, little precipitation, poor nutrients, and short growing seasons characterize tundra. Dead organic material functions as a nutrient pool for nitrogen and phosphorus. Because of the constant freezing and thawing of the ground, the tundra is strangely humped into low mounds, often with a pentagonal or hexagonal shape.

In addition to the cold climate, tundra typically has low biological diversity, with only a few plants and animals present in any region. The vegetation is small and low to the ground. Drainage is very poor because there is frequently a layer of permafrost (permanently frozen soil) just below the surface. In the short summer after the surface ice melts, the tundra is covered with pools of water that provide breeding opportunities for millions of mosquitoes, blackflies, and other biting insects. Animals that live on the tundra often show large oscillations of population.

Arctic Tundra. Arctic tundra is found in the Northern Hemisphere between the taiga and the Arctic Ocean. The growing season is around fifty to sixty days. The average winter temperature is -34°C (-29°F), and the average summer temperature is around 10°C (50°F). Total precipitation varies widely but is typically quite low. The rainfall equivalent may be around 15 to 25 centimeters a year, about the same as a desert. The soil layer is thin. Soil forms very slowly and is somewhat acidic. Below the soil is a layer of frozen gravel and silt. During the short growing season, water saturates the upper surface, forming bogs and ponds. A wide variety of plants are nevertheless able to survive these odd conditions, including small willows only a few centimeters tall, sedges, reindeer mosses, liverworts, and grasses. More than 400 varieties of flowers take advantage of the short growing season.

herbivores describes animals that eat only plants

All the plants have adapted to fierce winds and cold temperatures by growing close together and close to the ground. The tallest plants in the tundra are only a few centimeters tall. In the winter a protective blanket of snow covers the plants, which have evolved the ability to conduct photosynthesis with very little light and at low temperatures. Because of the short growing season, most plants reproduce by budding and division rather than by flowering. Arctic **herbivores** include caribou, arctic hares, squirrels, lemmings, and voles. These are preyed on by bears, wolves, and foxes. The birds are migratory, and include ravens, snow buntings, falcons, loons, sandpipers, terns, and various species of gulls. Insects include lots of mosquitoes, blackflies, moths, and grasshoppers.

The animals all migrate south in the winter or hibernate. The mammals have developed the ability to breed and raise young quickly in the short summer. Almost no reptiles or amphibians live in the arctic tundra.

Alpine Tundra. Alpine tundra is generally similar to arctic tundra. However, alpine tundra has a longer growing season. Alpine tundra is found at high altitudes above the tree line throughout the world. The closer to the equator, the higher the altitude required. Even on the equator, there are still mountains high enough to have some areas of alpine tundra. Alpine tundra soils are generally well drained, but rocky subsoils serve the same func-

tion as arctic permafrost. Alpine tundra has a unique community of organisms different from arctic tundra. Animals include mountain goats, pikas, and marmots. Typical plants include heather, short bunchgrasses, and small trees. SEE ALSO Ecosystem; Habitat.

Elliot Richmond

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Biometry

Biometry is the application of mathematical models to living systems. The use of statistics and mathematics as a tool for interpreting experimental data has proven invaluable to biologists, public health practitioners, researchers, and environmental scientists in areas such as genetics, toxicology, neurology, and clinical trials. Once considered a fledgling application of mathematics, biometry has proven to be a vital field playing a central role in substantive scientific and social issues of the day.

History of the Discipline

English scientist Francis Galton (1822–1911) is considered the founder of the biometric school. He strongly believed that virtually everything could be proven mathematically—that everything was quantifiable. Following this belief, Galton's first experiments (performed around 1850) included using statistical models to measure beauty and the effectiveness of prayer. Later, he came up with his own theory to explain inheritance: the theory of ancestral **heredity**. This theory held that each parent contributes one-half of the offspring's traits, each grandparent one-fourth, and so on.

heredity the passing on of characteristics from parents to offspring

It was not until the 1940s, though, that the application of statistics to biological questions began to have a profound impact on the scientific community. Scientific articles appeared in various journals, spurring the

biometrics section of the American Statistical Association to publish the *Biometrics Bulletin*, in 1945. Two years later the International Biometric Society (IBS) was established. According to its constitution, the IBS is "an international society for the advancement of biological science through the development of quantitative theories, and the application, development, and dissemination of effective mathematical and statistical techniques." Shortly thereafter, the IBS began publishing *Biometrics*, a journal directed toward biologists who saw statistics as a powerful tool in their work. Since its inception, *Biometrics* has been the premiere source for biometry-related scientific articles.

The first biometry studies were primarily concerned with agriculture in its broadest definition, specifically the design of experimental techniques. The first issue of *Biometrics* illustrates the type of analyses being performed in 1947. Articles included: "Some Uses of Statistical Methods in Plant Breeding," "Statistical Methods in Forestry," "Some Uses of Statistics in Plant Pathology," and "Some Applications of Statistical Methods to Fishery Problems." Biologists soon began writing articles relating more to the actual tools of their trade, such as the manipulation of slide rules, early calculators, and other devices. Indicative of the difficulty of applying complex statistical equations to biological queries in the days of clunky desk calculators, these reports attempted to ease the burden caused by less than stellar technological advances. Stressing the importance of collaboration between statisticians and researchers also became widespread, as the use of biometry in biological experimentation grew more commonplace. By sharing statistical methodologies, experimental designs, and the basic "how's" and "why's" of using appropriate mathematical models, both statisticians and researchers began to carve out a truly unique field of study.

The Expanding Field of Biometry

Medical uses, in the form of clinical trials, were part of the second wave of compelling applications of biometrical principles. The 1954 trial of the poliomyelitis vaccine, in the United States, was considered one of the largest experiments ever conducted. This was also a key precursor to the array of clinical studies conducted in later decades for diseases such as AIDS, cancer, influenza, measles, and malaria. Clinical trials paved the way for biological scientists to explore biometrical doctrines in such areas as social sciences, physical sciences, and engineering.

The widening scope of possibility for biometry has always been reliant on technology. New techniques in exploratory data analysis and computer graphics allow for statistical development in the areas of organismal, cellular, and molecular biology, neuroscience, and neural networks. Attracting enormous attention in the year 2000 was the **Human Genome Project**. Mapping and sequencing human genes would have been severely limited without the application of mathematical and statistical principles and computational advances. Additionally, the advent of the World Wide Web and expanded communication technologies have had an incredible impact on the sharing of information as well as locating research materials.

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

When issues involving the environment—ecology, global change, biological diversity, oceanography, and meteorological data—became widely apparent in the 1970s, biometrical principles arising mainly out of the geo-

sciences opened up new opportunities for biometricians. Similarly, changes in social and economic conditions, especially in developing nations, also provide a wealth of statistical problems that demand biometrical attention and expertise, much of which depends on new methodologies.

A new field of particular interest is that of "seafloor biology," the birth of which began with the launching of *Deep Flight I*, a kind of underwater aircraft that was sent to explore the ocean floor. This endeavor will certainly necessitate further innovative developments in statistical methodologies to process and learn from the resulting data.

Ann Guidry

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Biotic Factors

An ecosystem is a community of organisms that interact with each other and with the **abiotic** and **biotic** factors in their environment. Abiotic factors are chemical and physical factors such as temperature, soil composition, and climate, along with the amount of sunlight, salinity, and pH. Biotic means living, and biotic factors are the other, living parts of the ecosystem with which an organism must interact. The biotic factors with which an organism interacts depend on whether it is a producer, a consumer, or a decomposer.

abiotic nonliving parts of the environment

biotic pertaining to living organisms in an environment

Producers are also known as **autotrophs**, or self-feeders. Producers manufacture the organic compounds that they use as sources of energy and nutrients. Most producers are green plants or algae that make organic compounds through **photosynthesis**. This process begins when sunlight is absorbed by chlorophyll and other pigments in the plant. The plants use energy from sunlight to combine carbon dioxide from the atmosphere with water from the soil to make carbohydrates, starches, and cellulose. This process converts the energy of sunlight into energy stored in chemical bonds with oxygen as a by-product. This stored energy is the direct or indirect source of energy for all organisms in the ecosystem.

autotrophs organisms that make their own food

photosynthesis the combination of chemical compounds in the presence of sunlight

A few producers, including specialized bacteria, can extract inorganic compounds from the environment and convert them to organic nutrients in the absence of sunlight. This process is called **chemosynthesis**. In some places on the floor of the deep ocean where sunlight can never reach, hydrothermal vents pour out boiling hot water suffused with hydrogen sulfide gas. Specialized bacteria use the heat to convert this mixture into the nutrients they need.

chemosynthesis obtaining energy and making food from inorganic molecules

Only producers can make their own food. They also provide food for the **consumers** and decomposers. The producers are the source of the energy that drives the entire ecosystem. Organisms that get their energy by feeding on other organisms are called **heterotrophs**, or other-feeders.

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

heterotrophs organisms that do not make their own food

Some consumers feed on living plants and animals. Others, called detrivores, get their energy from dead plant and animal matter, called **detritus**. The detrivores are further divided into detritus feeders and decomposers. The detritus feeders consume dead organisms and organic wastes directly. Decomposers break the complex organic compounds into simpler molecules, harvesting the energy in the process.

detritus dead organic matter

The survival of any individual organism in an ecosystem depends on how matter and energy flow through the system and through the body of the organism. Organisms survive through a combination of matter recycling and the one-way flow of energy through the system.

Food Chain

The food chain begins with producers, living things that take minerals and gasses from the environment for support. Consumers feed off of producers. Herbivores are plant-eating animals, while carnivores eat other animals. Onmivores are people and animals who eat both plants and other animals. The last link on the chain contains decomposers, who feed off dead plants and animals, reducing their remains to gasses and minerals.

The biotic factors in an ecosystem are the other organisms that exist in that ecosystem. How they affect an individual organism depends on what type of organism it is. The other organisms (biotic factors) can include predators, parasites, prey, symbionts, or competitors.

A predator regards the organism as a source of energy and matter to be recycled. A parasite is a type of consumer organism. As a consumer, it does not make its own food. It gets its food (energy and matter to be recycled) from its host. The organism's prey is a source of energy and matter. A symbiont is a factor that does not provide energy to the organism, but somehow aids the organism in obtaining energy or matter from the ecosystem. Finally, a competitor reduces the organism's ability to harvest energy or matter to be recycled. The distribution and abundance of an organism will be affected by its interrelationships with the biotic environment.

Humans are one of the few organisms that can control how the other biotic factors affect them. Humans are omnivores, consuming both producers and other consumers. Humans can also adjust the length of the food chain as needed. For example, humans who must deal with shortages of food resources usually alter their eating habits to be closer to the energy source. This is sometimes called eating lower on the food chain. Since approximately 90 percent of the energy available at each level of the food chain is lost to the next higher level, shortening the food chain saves energy and uses food more efficiently.

Humans are also biotic factors in ecosystems. Other organisms are affected by human actions, often in adverse ways. We compete with some organisms for resources, prey on other organisms, and alter the environment of still others. SEE ALSO Ecosystem; Habitat.

Elliot Richmond

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Birds *See Aves.*

Blood

The life fluid of the body is blood. All animals, including humans, require that nutrients and oxygen be available for metabolism and that wastes be removed. In animals that measure 1 millimeter or less in diameter, these substances are transported within the body by diffusion between the cells and nearby body parts. In larger, more complex animals, circulatory systems have evolved with arteries, veins, and capillaries to transport respiratory gases, nutrients, waste products, hormones, antibodies, and salts to parts of the body.

Blood, the medium for transporting nutrients and waste products, is both a tissue and a fluid containing many specialized types of cells. It is a tissue because it is a collection of similar cells that serve a particular function. These cells are suspended in a liquid matrix called plasma, which allows the blood to act as a fluid.

Blood plays an important role in nearly all body functions. Oxygen is one of the crucial substances that enters the blood. Oxygen passes through the walls of the lungs, gills, or skin of the animal. The blood picks up and carries oxygen to all parts of the body. As the oxygen-laden blood moves through the circulatory system, it passes through cell walls and provides fuel for the working parts of the body.

Blood also carries digested food from the intestines to the muscle cells. When the muscles work, they produce waste products that must be disposed of. These waste products pass through the walls of the circulatory system into the blood. The blood then carries wastes to the kidneys, where they are eliminated from the body. The work of the muscles creates heat, which is transferred by blood throughout the body. In warm-blooded birds and mammals, blood maintains the temperature of the body.

Blood plays a critical part in the fight against diseases in animals. Blood contains many kinds of disease-fighting substances such as antibodies and white blood cells. Blood tests can reveal a great deal about how well the body is working.

Plasma
Plasma is unquestionably essential for the survival of human beings. Along with carrying important minerals and dissolved salts like calcium, sodium, and potassium among others, disease-fighting antibodies are contained in plasma.

Blood Composition

The blood of mammals—including humans—is complex. About half of the volume of blood is made up of blood cells, which originate in the bone marrow. Blood cells begin as stem cells, then develop into many other kinds of cells—red cells, white cells, and **platelets**. Blood is composed of 55 percent plasma and 45 percent other elements.

platelets cell fragments in plasma that aid in clotting

Plasma is the watery part of the blood. Plasma is 90 percent water and carries most of the chemicals in the blood. These chemicals include minerals such as sodium, potassium, vitamins, hormones, enzymes, and glucose. Some of these substances are manufactured in the body; others enter through the lungs or with food. Plasma also carries dissolved gasses, especially oxygen, carbon dioxide, and nitrogen.

Blood's red color, seen in the mosquito's "sac," arises from its oxyhemoglobin.

erythrocytes red blood cells, cells containing hemoglobin that carry oxygen throughout the body

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

Most stem cells become red blood cells, or **erythrocytes**. Human blood contains 4.8 to 5.4 billion red blood cells per milliliter of blood. Red blood cells' primary function is to carry oxygen from the lungs to every cell throughout the body. The outer layer, or membrane, of the red blood cell is flexible and can bend in many different directions without breaking.

Red cells have an iron-containing substance or pigment known as **hemoglobin**. As hemoglobin passes through the lungs, it picks up oxygen, forming a red-colored compound known as oxyhemoglobin, which gives the blood a distinctive red color. As the blood passes through body tissues, hemoglobin releases oxygen to cells throughout the body. During this passage, the hemoglobin gives up some of its oxygen. In response, the tissues send a waste gas, carbon dioxide, into the blood.

leukocytes a type of white blood cells that are part of the immune system

granulocytes a type of white blood cell where its cytoplasm contains granules

monocytes the largest type of white blood cell

lymphocytes a type of white blood cells that completes its development in bone marrow

thromboplastin a protein found in blood and tissues that promotes the conversion of prothrombin to thrombin

White blood cells, or **leukocytes**, form a wandering system of protection for the body. Composed of **granulocytes**, **monocytes**, and **lymphocytes**, these cells originate in the bone marrow, where there is a ratio of one white cell to 700 red cells. Two-thirds of white cells are granulocytes, which travel to places in the body where bacteria or other foreign substances are located and swallow up these invaders. Monocytes, another type of white cell, also swallow up foreign substances and assist the body in overcoming and resisting infections. Lymphocytes produce antibodies, which are released into the blood to target and attach to foreign substances.

The smallest of the blood cells are called platelets. These cells assist in blood clotting by sticking together and plugging small holes in the walls of the blood vessels. As these tiny platelets flow out of a cut on the wall of the blood vessel, they release a chemical known as **thromboplastin**. This self-sealing characteristic of blood is critical to an animal's survival.

Differences among Animals

One-celled organisms have no need for blood. They are able to absorb nutrients, expel wastes, and exchange gases with their environment through a

process called diffusion. In some invertebrates, such as flatworms and **cnidarians**, oxygen is dissolved in the plasma. Simple multicelled marine animals such as sponges, jellyfish, and anemones use seawater to bathe cells and perform the function of blood. The immune system of invertebrates is less developed than that of vertebrates, lacking the white blood cells and antibody system found in mammals.

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

Differing oxygen requirements play a significant role in the composition of blood and the design of animals' circulatory systems. Crustaceans and other arthropods have an open type of circulatory system, while more complex vertebrates—including humans—have a closed circulatory system. Larger and more complex animals have greater oxygen needs and have developed respiratory pigments to help transport oxygen in the blood. These specialized compounds, hemoglobin or **hemocyanin**, are able to carry greater amounts of oxygen because of the metal atoms in the pigments reacting with and transporting additional atoms of oxygen.

hemocyanin respiratory pigment found in some crustaceans, mollusks, and arachnids

The red pigment hemoglobin contains iron, transports oxygen, and is found in all vertebrates as well as some invertebrates with a closed circulatory system, such as earthworms. The blue pigment hemocyanin, which contains copper, is found in some animals with an open circulatory system, including some crustaceans such as crabs, and in some mollusks. This pigment transports oxygen to body tissues and gives the blood a bluish color. The blood of insects is clear or yellow. The red fluid from some squashed insects actually comes from blood they have eaten, not from their own blood, as they have no pigments.

Although the blood of complex animals tends to be similar to human blood, there are differences at the cellular level. For example, reptiles, fish, and amphibians have red blood cells with a nucleus, unlike humans and other mammals. Some arctic fish are able to produce a specialized protein that acts as a type of antifreeze, allowing them to survive where the blood of other animals would freeze. SEE ALSO Circulatory System.

Leslie Hutchinson

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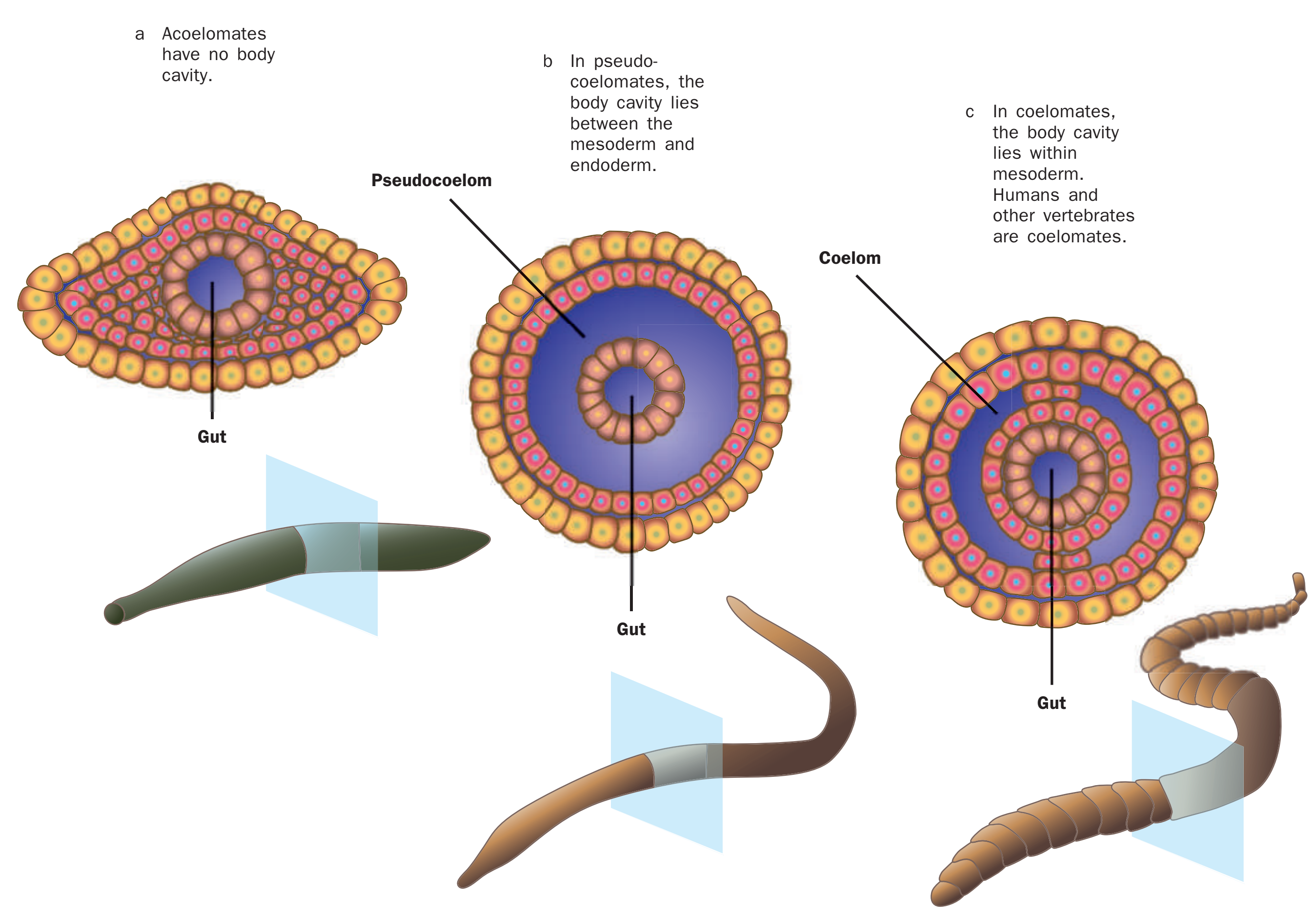
Body Cavities

The evolution of body cavities within the kingdom Animalia has a very interesting history. In fact, the increasing complexity of animal form and function during the evolution of the group can be directly linked to the evolution of ever-more-sophisticated body cavities.

The most primitive animal phyla possess only a single body cavity, which typically has either digestive or circulatory functions, or both. There is no



The cross sections visually represent the structural differences between the acoelomate, pseudocoelomate, and the coelomate. Redrawn from Holt et al., 1998.

acoelomates animals without a body cavity

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

coelom a body cavity

eucoelomates animals that have a true body cavity that is completely surrounded by mesoderm

spongocoel the central cavity in a sponge

secondary body cavity, or coelom, and consequently these phyla are referred to as the **acoelomates**.

Most animal phyla, however, have evolved a second body cavity of one form or another. The pseudocoelomates, which include a number of worm-like phyla, are characterized by a secondary body cavity known as the **pseudocoelom**. The pseudocoelom has some but not all of the characteristics of true coeloms. Finally, several animal phyla, including those that possess the most complex body plans in the kingdom, are characterized by a body cavity known as a true **coelom**. These phyla are known as the **eucoelomates**.

The Acoelomate Phyla

The most primitive animal phylum is that of the sponges (phylum Porifera). Sponges have a single body cavity known as the **spongocoel**. The spongocoel is critical to the food gathering strategy of sponges. Water enters the organism through numerous small pores known as ostia. Small food particles are filtered from the water by cells in the sponge walls. The water then flows through the spongocoel and leaves through a large opening known as the osculum. The one-directional flow of water through the sponge is controlled by special flagellated cells which line the spongocoel.

The second most primitive animal phylum is generally considered to be the cnidarians (phylum Cnidaria), which includes the jellyfish, sea anemones, and hydras. Cnidarians are diploblastic, meaning that they have two distinct tissue layers, an ectoderm and endoderm, separated by a third layer called the mesoglea. Cnidarians are characterized by a single **gastrovascular cavity**, an internal body cavity that functions in digestion. The gastrovascular cavity has a single opening that serves as both mouth and anus, and is typically surrounded by tentacles that are responsible for food gathering.

gastrovascular cavity a single cavity where digestion occurs

The other acoelomate phyla are more advanced than the sponges and cnidarians since their species are characterized by bilateral (left-right) symmetry, as well as the presence of three distinct tissue layers, the ectoderm, mesoderm, and endoderm. In these acoelomate bilatarian phyla, there is no body cavity other than the gastrovascular cavity. The mesoderm is solid. Bilaterally symmetric acoelomates include such taxa as the flatworms (phylum Platyhelminthes) and the ribbon worms (phylum Nemertina).

The "Tube-within-a-Tube" Body Plan

Animal species with a secondary body cavity, either a pseudocoelom or a true coelom, have what is called a "tube-within-a-tube" body plan. The secondary body cavity lies between the two tubes. The outer tube (also called the body wall or the **somatic** tube) typically contains the sense organs and muscles. Structures of the body wall are generally under voluntary control and are most often involved in mediating between an organism and its external environment. The inner tube (also called the gut tube or visceral tube) typically includes structures that control an organism's internal environment. These tubes perform functions such as digestion, blood circulation, the maintenance of internal homeostasis, and reproduction. The functioning of elements of the visceral tube is generally under involuntary control.

somatic having to do with the body

monophyletic a taxon that derived from a single ancestral species that gave rise to no other species in any other taxa

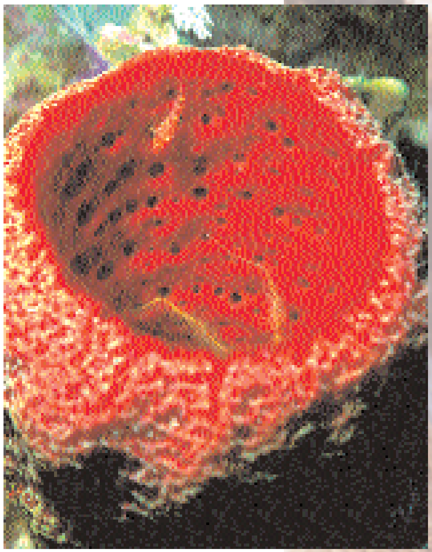
Both the pseudocoelom and the coelom are fluid-filled body cavities that lie between the outer body wall and the inner tube of the digestive tract. The distinction between the two lies in the tissue layer origin of the walls of the cavity.

The Pseudocoelomates

The pseudocoelom is an internal body cavity that develops between the mesoderm and the endoderm. Developmentally, the pseudocoelom is the persistent blastocoel, or fluid-filled cavity, of the developmental stage known as the blastula stage.

Several phyla of invertebrate animals are characterized by pseudocoeloms. These include the roundworms (phylum Nematoda) and the rotifers (phylum Rotifera), as well as a number of lesser-known phyla of wormlike animals.

At one point, all the pseudocoelomate taxa were grouped together in the phylum Aschelminthes. However, recent phylogenetic studies have shown that in all likelihood they do not form a **monophyletic** taxon (one that shares a common ancestor), and the group has since been split into numerous separate phyla. It is even possible that the pseudocoelom has evolved more than once.



A member of the phylum Porifera, this vase sponge uses its spongocoel to gather food.

The pseudocoelom serves many of the same functions as the true coelom, which is discussed below. However, certain complex physiological systems are found only in the eucoelomates. Unlike the eucoelomates, for example, the pseudocoelomates lack circulatory systems. Nevertheless, certain innovations made possible by a true coelom can also be found among the pseudocoelomates. In roundworms, for example, the pseudocoelom is fluid-filled and pressurized and functions as a hydrostatic (fluid dependent) skeleton.

The True Coelom and the Eucoelomates

The true coelom differs from the pseudocoelom in that it is lined on either side with cells originating from the mesoderm. It is filled with a fluid known as the coelomic fluid. The surfaces of the coelom are covered with a slick epithelial layer known as the **peritoneum**.

peritoneum the thin membrane that lines the abdomen and covers the organs in it

The cells of the peritoneum are responsible for regulating the transport of substances into and out of the coelom. The visceral peritoneum covers the viscera (internal organs). The parietal peritoneum lines the outer body wall. The lubricated surfaces of the peritoneum allow for the smooth, sliding motion of the organs within the coelom. The internal organs are suspended from the walls of the coelom by membranous sheets called **mesenteries**.

mesenteries the membranes that suspend many internal organs in the fluid filled body cavity of vertebrates

pericardial cavity the space within the membrane that surrounds the heart

pleural cavity the space where the lungs are found

peritoneal cavity the space within the peritoneum membrane that surrounds the abdomen and covers the organs within it

The coelom may be a single body cavity or may be divided into separate compartments during the course of development. In humans, the coelom is divided into three separate coelomic cavities. The **pericardial cavity** contains the heart, the **pleural cavity** contains the lungs, and the **peritoneal cavity** contains the rest of the viscera, including the digestive organs, liver, kidneys and excretory organs, and reproductive organs. The pleural and peritoneal cavities are separated by the pleuroperitoneal membrane and the diaphragm (which has a critical role in respiration), while the heart and lungs are separated by the pleuropericardial fold.

Species with a true coelom are called eucoelomates. Within the eucoelomates, two different groups may be distinguished based on the way in which the coelom forms during development. The protostomes are characterized by one method, called schizocoely, while the deuterostomes are characterized by another, called enterocoely. The method of coelom formation is in fact one of the key characteristics that separate these two important phylogenetic groups.

Two rival theories attempt to explain the evolutionary origin of the coelom. The acoelomate theory argues that the coelom evolved in an acoelomate ancestor. The enterocoel theory suggests that the coelom evolved from the gastric pouches of cnidarians. Current evidence appears to favor the enterocoel theory. It is unclear whether the pseudocoelomates represent an intermediate evolutionary stage between acoelomates and taxa with a true coelom, or whether pseudocoelomates evolved from an eucoelomate ancestor.

Development of the True Coelom

Among the eucoelomates, the coelom develops differently in the protostomes, which include the Annelida, the molluska, and the Arthropoda, and the deuterostomes, consisting of the Echinodermata, Hemichordata, and

Chordata. This is one of a few key characteristics distinguishing these two subkingdoms.

In both protostomes and deuterostomes, coelom formation occurs directly after gastrulation, the developmental stage in which the three tissue layers—the ectoderm, mesoderm, and endoderm—become distinguished. In both groups, coelom development is closely linked to the origin of the mesoderm.

The protostomes are **schizocoelous**. In protostomes, the mesoderm develops during gastrulation as cells migrate from the already existing ectodermal and endodermal layers to form a solid mesodermal layer that lies between the ectoderm and endoderm. This solid mesodermal mass subsequently splits ("schizo-" = "split") to form a hollow cavity that becomes the coelom.

schizocoelous the mesoderm originates from existing cell layers when the cells migrate

The deuterostomes are **enterocoelous**. In deuterostomes, the mesoderm originates as outpocketings of the endodermal archenteron, or embryonic gut. The mesodermal pouches extend toward one another as they grow, ultimately joining to form a single cavity that becomes the coelom.

enterocoelous a cavity formed by the in-folding of the wall of the intestinal cavity in a gastrula

The Importance of the Coelom

The evolution of the coelom was a crucial step in the history of the Animalia. The presence of a secondary body cavity, and the acquisition of the tube-within-a-tube body plan, was critical for the evolution of increasing size and complexity within the animal kingdom.

One major disadvantage of having only a single body cavity is that muscle contractions, such as those necessary for locomotion, cause the gastrovascular cavity to become squeezed and distorted. This not only restricts the flow of nutrients and other materials but also makes the evolution of an effective circulatory system impossible. As a result, acoelomate taxa must rely either on diffusion or on muscle contractions for the transport of nutrients, respiratory gases, and waste products around the body. Both these transport strategies are considerably less efficient than those permitted by the evolution of a coelom.

Consequently, the body sizes, shapes, and complexities that can be supported are severely constrained. Many acoelomate groups are small in size and characterized by a flattened, elongated morphology, or shape, one that is suited to diffusion as a transport mechanism, and that makes a complex circulatory system unnecessary. Not surprisingly, the result is that acoelomate phyla all have comparatively simple body plans. Even the pseudocoelomates are generally fairly small in size and lack circulatory systems. They have only simple locomotory behaviors, which in addition to motion, help to circulate nutrients in the pseudocoelom.

With the evolution of the coelom, the digestive and circulatory functions are separated, which allows for the possibility of separate specialization and improvement in efficiency. The evolution of the coelom permits the internal organs to grow, change shape, and shift in position. The coelom provides not only space but also protection for complex organ systems, because the fluid-filled environment helps to shield the internal organs from injury. The gastrovascular cavity becomes specialized for digestion alone, and the different portions of the digestive system can expand and contract

during the processes of feeding and digestion. This increase in efficiency in both digestion and circulation allows for the support of larger body sizes and increased metabolic rates, both of which are prominent features in the evolution of the Animalia.

In some taxa, the coelom can serve other functions as well. In many species, the fluid-filled, pressurized coelom is important in providing hydrostatic support. This is important in the Annelida, for example, which have evolved a compartmentalized coelom, with one coelomic compartment present in each segment of the organism. Slugs are another example of a group that uses the coelom as a hydrostatic skeleton involved in support and locomotion. Echinoderms such as starfish are characterized by a well-developed water vascular system derived from the coelom, which functions in the locomotion of the tube feet.

Modification and Reduction of the Coelom

The coelom has been modified in different ways in different phyla. The compartmentalization of the coelom in some vertebrates, including humans, has already been discussed. The creation of the pleural cavities, which contain the lungs, through the development of the muscular diaphragm is essential to the respiratory strategy of mammals, providing yet another example of a physiological function for which the evolution of the coelom has been necessary.

The unusual segmented coelomic compartments of annelids have also been mentioned. In this case, segmentation affects numerous components of annelid anatomy, and the coelom is only one more instance of this.

hemocoel a cavity between organs in arthropods and mollusks through which blood circulates

In addition, the coelom has been reduced in several other phyla that have evolved other structures to perform its usual functions. Arthropods, for example, have a hard chitinous exoskeleton (external skeleton) that provides support. The coelom is significantly reduced in the group, persisting only as a cavity around the gonads and excretory organs. (The **hemocoel**, a component of the arthropod's open circulatory system that bathes the internal organs in blood, is unrelated.)

Mollusks also have a body plan in which the coelom is reduced, in this case to a small body cavity that encloses only the heart. It is likely that the sedentary lifestyle of mollusks such as bivalves made a fully developed coelom unnecessary. Like arthropods, mollusks also possess a large hemocoel that bathes the organs in nutrients. SEE ALSO Body Plan.

Jennifer Yeh

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Body Size and Scaling *See Functional Morphology.*

Body Plan

The term "body plan" refers to the general similarities in development and form and function among members of a particular phylum. Another name for these similarities is *baüplan*, which is the German word for "body plan."

A body plan is a group of structural and developmental characteristics that can be used to identify a group of animals, such as a phylum. All members of a particular group share the same body plan at some point during their development—in the embryonic, larval, or adult stage. Biologists have long observed that anatomy and embryology reflect shared underlying structural plans. These plans can be used to define taxonomic groups (usually phyla) and to construct hierarchical classifications within groups (organisms with similar body plans tend to be more closely related).

Similarities and differences in adult shape and form, as well as the developmental pattern of embryos, provide the framework for modern taxonomic classification. These comparisons are the basis of phylogenetic systematics. Embryonic development is relatively consistent among animals with similar body plans, although similar larval forms may give rise to very different adults in some groups. The timing, pattern, and scale of developmental events determine the shape of an organism, and closely related groups are more likely to share structural and developmental similarities than those that are more distantly related. Homologous structures and developmental stages—those that are similar among related groups because they are inherited from a common ancestor—are the basis of modern biological classification.

The fossil record suggests that **metazoans** (organisms with multiple cell and tissue types) first appeared about 500,000 years ago early in the Cambrian period. It is likely, however, that soft-bodied forms were present well before this but left no fossilized remains. Metazoans rapidly diversified into myriad forms that eventually gave rise to the diversity of metazoans we have today. Biologists refer to this historic event in the history of animal life as the Cambrian Radiation, sometimes referred to as the Cambrian Explosion. All living animals are descendents of a common ancestor that existed at the beginning of the Cambrian period, and their various evolutionary paths were established by the end of this biological supernova. A few body plans did not survive into the present, but the majority of readily fossilized metazoan body plans can still be found today. The distribution of diverse body plans among living metazoans provides a record of the evolutionary history of this group that dates back to its origin.

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

Multicellularity in organisms permits specialization of cell structure and function. During the Cambrian Radiation, an increased overall complexity and the subsequent **differentiation** of embryonic and adult cells and tissues, a widespread phenomenon among metazoans called compartmentalization, provided the opportunity for evolutionary experimentation and innovation.

differentiation differences in structure and function of cells in multicellular organisms as the cells become specialized

Animal Characteristics

Parazoa	Phylum Porifera (sponges)	No true tissue or loose tissue organization. Body is asymmetrical or radially symmetrical.
Eumetazoa – Radiata	Phylum Cnidaria (anemones and jellyfish)	Diploblastic—two layers: gastrodermis (derived from endoderm) and epidermis (derived from ectoderm). Radial symmetry, planula larva, dimorphic life cycle: polyps and medusa. Oral and aboral, no cephalization. Gastrovascular cavity: mouth opening, no anus. Specialized stinging cells (cnidocytes and nematocysts), muscles and nerves.
	Phylum Ctenophora (comb jellies)	Diploblastic, "mesoglea," eight rows of fused cilia, balance sense organ, two tentacles, bioluminescence.
Eumetazoa – Bilateria – Acoelomates	Phylum Platyhelminthes (roundworms)	Triploblastic (endoderm, mesoderm, ectoderm), bilateral symmetry, acoelomates, cephalization. Larval stages, no respiratory or circulatory system, incomplete digestive system (no anus).
Pseudocoelomates Characteristics: eumetzoa, bilateral symmetry, body cavity other than digestive cavity (pseudocoele).	Phylum Rotifera (wheel-bearing animals)	Triploblastic, complete digestive tract, pseudocoele, hydrostatic skeleton, organs located in pseudocoele, parthenogenesis, crown of cilia.
	Phylum Nematoda (roundworms)	Triploblastic, complete digestive tract, tough cuticle, only longitudinal muscles, pseudocoele, hydrostatic skeleton.
	Phylum Nemertea	No pseudocoele, body is acoelomate, has coelom-like structure for storing proboscis, complete digestive tract, circulatory system with hemoglobin.
Eucoelomates-Protostomes Characteristics: eumetazoa, triploblastic, bilateral symmetry, cephalization, blastopore becomes mouth, eucoelomates, schizocoelous, spiral cleavage, determinate cleavage.	Phylum Molluska (chitons, snails, slugs, clams, oysters, octopuses, and squids)	Most have external shells of calcium carbonate, although some have internal shells and some have none. Three body parts – foot, visceral mass, and mantle. Mantle cavity – houses gills and other organs, no body segmentation.
Coelomates have internal body cavities (coeloms) which contain digestive organs, some of the excretory and reproductive organs, and a thoracic cavity that contains the heart and lungs. Coelomates also form a variety of internal and external skeletons.	Phylum Annelida (earthworms, polychetes, and leeches)	Triploblastic, segmentation and body segment specialization, coelom.
	Phylum Arthropoda (crustaceans, insects, and spiders)	Triploblastic, segmentation, hard exoskeleton, jointed appendages, specialized appendages, antennae, mouthparts, legs, molting, variety of gas exchanges or respiratory structures.
Deuterostomes Characteristics: bilateral symmetry, some have secondary radial symmetry, enterocoelous, blastopore becomes anus, radial cleavage, indeterminate cleavage.	Phylum Bryozoa (moss animals)	Exoskeleton, sessile, and a lophophore, a ring of ciliated tentacles centered on the mouth. The mouth opens into a U-shaped gut; the anus is located just outside the lophophore. The body also contains a coelom and gonads; there is a small central ganglion, or "brain," but no specialized excretory or respiratory systems.
	Phylum Brachiopoda	Resemble bivalve clams with two shells surrounding a lophophore.
	Phylum Phoronida (tube-dwelling marine worms)	Lophophore present; three body parts in larval and adult forms, each containing its own coelom; prosome, mesosome, metasome. U-shaped digestive track, nervous system, specialized excretory organs, closed circulatory system.
	Phylum Echinodermata (sand dollars, urchins, and sea stars)	Calcareous endoskeleton composed of separate plates or ossicles, bilateral symmetry in larval stage, radial symmetry as adults (pentagonal), endoskeleton, water vascular system; regeneration, decentralized nervous system.
	Phylum Chordata (amphioxus, sea squirts, and vertebrates)	Bilateral symmetry; segmented body; three germ layers; well-developed coelom. Notochord present at some stage in life cycle. Single, dorsal, tubular nerve cord; anterior end of cord usually enlarged to form brain. Pharyngeal gill slits present at some stage in life cycle. Postnanal tail, usually projecting beyond the anus at some stage but may or may not persist. Segmented muscles in unsegmented trunk. Ventral heart with dorsal and ventral blood vessels; closed circulatory system. Complete digestive system. Cartilaginous or bony endoskeleton present in the majority of members (vertebrates).

New combinations of cells and tissues led to greater complexity and the exploitation of new ecological resources.

Important differences among body plans are present in the embryo although they may be apparent at any stage during the development of a given group. Conditions presented early in development set in motion a cascade of changes in cell growth, proliferation, and differentiation that operate throughout development to produce the body plans specific to a particular group of organisms.

Body plans vary among phyla in terms of egg-cleavage patterns (how the egg divides in early development), **gastrulation**, axis specification, and embryonic cell structure. The egg may be completely divided by the cleavage furrow (holoblastic cleavage), or only a portion of the **cytoplasm** may be cleaved (meriblastic cleavage) as in bird eggs. **Deuterostomes**, such as **echinoderms** and chordates, develop by radial cleavage. In this form of cleavage, the daughter cells sit on top of previous cells. **Protostomes**, such as mollusks, annelids, and arthropods, develop by spiral cleavage (the daughter blastomeres are not direclty over or beside each other but are tilted to the left or right 45 degrees).

Gastrulation is the coordinated movement of cells and tissue in the embryo that determines later cell and tissue interactions. Gastrulation involves the combination of cell and tissue. These combination types differ among phyla.

Axis formation in the embryo is responsible for determining patterns of symmetry and polarity. Organisms may be **asymmetrical** (no symmetry) or **symmetrical** (a single line, or plane, of symmetry). Symmetry may be spherical, radial, or bilateral. Animals with spherical symmetry, like sea urchins, have a hollow globe of cell layers organized around a central point. Animals with radial symmetry, like jellyfishes, have body parts that radiate from a central point, like the spokes of a wheel. Animals with **bilateral symmetry**, like earthworms, have bodies that if cut lengthwise, form right and left halves that are mirror images.

Bilateral symmetry is a critical prerequisite for the concentration of sensory organs and the development of the head. **Dorsal**-ventral (back-belly), **anterior**-**posterior** (mouth-anus), and right-left axes are specified in different ways among phyla. The primary body axes of annelids and vertebrates, for example, are determined by different mechanisms during early development. In most cases, the presence of multiple embryonic developmental axes is associated with cell diversity and tissue complexity. Cells and tissues in the embryo give rise to all classes of cells, tissues, and structures present in the adult stage. The specific fate of embryonic cells and tissues is determined early in development and varies among body plans.

Most metazoan body plans can be described as a "tube-within-a-tube," with a body wall made up of layers of different tissue types surrounding a central cavity. In almost all metazoans, the body wall has three cell layers (ectoderm, mesoderm, and endoderm), although some, such as sponges (Porifera), have no organized cell layers, and others, such as jellyfishes (**Cnidaria**) have only two layers in the adult. Multicellular metazoan ancestors had an inside-outside, two-layered organization with an endoderm and ectoderm. In **triploblasts**, such as flatworms, a middle layer of mesoderm also evolved.

The body wall surrounds a coelum (central cavity) between the digestive tract and body wall that is completely lined by mesoderm. The coelom allows the digestive system and body wall to move independently. Because of this, internal organs can be more complex. The coelom may also serve as a storage area for eggs and sperm, facilitating development of these gametes

gastrulation the formation of a gastrula from a blastula

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

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

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

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

asymmetrical lacking symmetry, having an irregular shape

symmetrical balanced body proportions

bilateral symmetry characteristic of an animal that can be separated into two identical mirror image halves

dorsal the back surface of an animal with bilateral symmetry

anterior referring to the head end of an organism

posterior behind or the back

Cnidaria a phylum of aquatic invertebrates such as jellyfishes, corals, sea anemones, and hydras

triploblasts having three germ layers, ectoderm, mesoderm, and endoderm within the animal body. Coelomic fluid helps in respiration and circulation by diffusing nutrients and in excretion by accumulating wastes. This fluid has the same function as several organ systems in the higher animals. In addition, coelomic fluid protects internal organs and serves as a hydrostatic skeleton. Metazoans have a mouth at one end of the coelom and an anus at the other. Protostomes develop so that the first opening in the embryo is the mouth (the word "protostome" means "first mouth"). Deuterostomes develop an anus first, then a mouth.

Of the thirty-five living phyla of metazoans, the ten largest contain nearly 2.5 million species in total, the other twenty-five account for only 5,000. Although some phyla have obviously been more successful than others in terms of the sheer number of species that they contain, all existing metazoan body plans are survivors of the Cambrian Radiation. The following is a description of the body plans of the ten most diverse metazoan phyla, presented in order of increasing complexity.

Porifera: Sponges

sessile immobile, attached

Sponges have a diploblastic embryo, which means they have a two-layered body wall (ectoderm and endoderm but no mesoderm). Adults are **sessile** (nonmobile and usually fixed to a single point) and have no coelom. Sponges have flagellated cells that move water around the body, and an internal skeleton with spicules, needle-shaped skeletal elements that occur in the matrix between the epidermal and collar cells. Adult sponges have no definite nervous system.

Cnidaria: Corals, Jellyfishes, and Anemones

diploblastic having two germ layers; ectoderm and endoderm

Cnidarians have a body that is a simple, soft-walled sac. Cnidarians have two distinctive body forms, a mobile, bell-shaped medusa (jellyfish, for example) or a sessile polyp (sea anemones, for example). Either or both forms may be present during development, depending on the species. Cnidarians may live on their own, as do anemones, or live in colonies, as do corals and jellyfishes.

All cnidarians have radial symmetry. They are **diploblastic**, which means they have two embryonic tissue layers, the ectoderm and endoderm, which give rise to the ectodermis and gastrodermis of the adult. The latter layers enclose a single opening, the enteron, or "inner cavity."

The shell on this snail—a member of the phylum Molluska—has been formed by the secretions of its mantle. The mantle is a characteristic feature of mollusks.

They have a mouth but no anus; and have a central body cavity called a coelenteron (hollow gut), and a nerve net, which serves as a primitive nervous system. Cnidarians are the only metazoans that have tentacles with nematocysts (stinging cells) and statocysts (organs that sense orientation).

Platyhelminthes: Flatworms

Flatworms are bilaterally symmetrical and have flattened, wormlike bodies. All platyhelminthes are triploblastic. They have unique flagellated cells called flame cells, which regulate the contents of extracellular fluid and are used for excretion, and a nervous system with a simple brain.

Rotifera: Wheeled Animals

Rotifers have several complex traits that are further developed in other phyla. The rotifer body is unsegmented, bilaterally symmetrical, and spherical with a bifurcate (split) foot and anterior wheel organ and a cuticle (extracellular protective layer). Rotifers feed using a pharynx with jaws. They have protonephridia, a primitive excretory organ, and a simple nervous system with vision receptors.

Nematoda: Roundworms

Nematodes have triploblastic embryos and cylindrical, unsegmented bodies in the adult stage. They have a **pseudocoelom**, a closed, fluid-containing cavity that acts as a hydrostatic skeleton to maintain body shape, circulate nutrients, and hold the major body organs. Nematodes also have a cuticle without cilia, longitudinal muscle fibers, a triradiate (three-chambered) pharynx, and an excretory system that consists of gland cells and canals.

pseudocoelom a body cavity that is not entirely surrounded by mesoderm

Molluska: Slugs, Snails, and Clams

The mollusk body has a head and a foot, and a **mantle**, a membranous or muscular structure that surrounds the visceral mass (internal organs) and secretes a shell if one is present (as in clams and branchiopods). Mollusks have an alimentary canal, a relatively complex nervous system, respiratory gills, and an active circulatory system with blood and a hemocoele, an enlarged, blood-filled space. Some groups of mollusks have a reduced coelom.

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

Annelida: Segmented Worms

The annelid body is bilaterally symmetrical, segmented, and fluid filled. Annelids have a hydrostatic skeleton, which supports the body through the pressure of fluid contained within body cavities. The external surface of the body is protected by a cuticle. Annelids also have chaetae, or bristles, and a triploblastic body wall. The annelid nervous system consists of paired nerves and ganglia (clusters of **neuron** bodies or soma) arranged along the length of the body. They have simple excretory organs called nephridia, or coelomoducts, and a closed, tubular circulatory system.

neuron a nerve cell

Arthropoda: Crustaceans, Spiders, and Insects

Arthropods have triploblastic embryos. Their bodies are bilaterally symmetrical, with metameric segmentation, in which each repeating segment is similar to the next. Arthropods have an exoskeleton, a hard, jointed, external covering that encloses the muscles and organs, made of chitin (a tough, flexible carbohydrate); paired, jointed appendages; and one or more pairs of jaws. The digestive system consists of a tubular gut. Arthropods have **striated muscles**, a ventral nerve cord of segmental ganglia, ciliated sense organs, a reduced coelom, a haemocoel, and a heart that pumps a circulatory fluid called haemolymph.

striated muscles a type of muscle with fibers of cross bands usually contracted by voluntary action

Echinodermata: Sea Urchins, Starfishes, and Sea Cucumbers

Echinoderms have a swimming larval stage called a pluteus and a nonswimming, headless adult stage with pentamerous (five-sided) symmetry.

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

Echinoderms have a coelom that is divided into three sections, and an internal mesodermal skeleton (a supportive framework of **connective tissue**) with calcium carbonate spicules (conical masses of hard, shell-like matrial). Echinoderms have digestive systems but lack excretory organs. They have a water vascular system (also called the ambulacral system), which is a set of hydraulic canals derived from the coelom and equipped with tube feet, and which is used for gas exchange, movement, food handling, and sensory reception.

Chordata: Chordates, Including Vertebrates

notochord a rod of cartilage that runs down the back of chordates

Chordate embryos (and adults) are triploblastic. Chordate larvae and adults are bilaterally symmetrical and have a well-defined anterior-posterior axis (the "head" is easily identified from the "tail"). Adults have a complex nervous system with a dorsal nerve chord and **notochord** (some groups, including vertebrates, have a brain), various sense organs, gill slits, and a well-developed digestive tract. Chordates reproduce sexually. SEE ALSO ALLOMETRY.

Andrew G. Gluesenkamp

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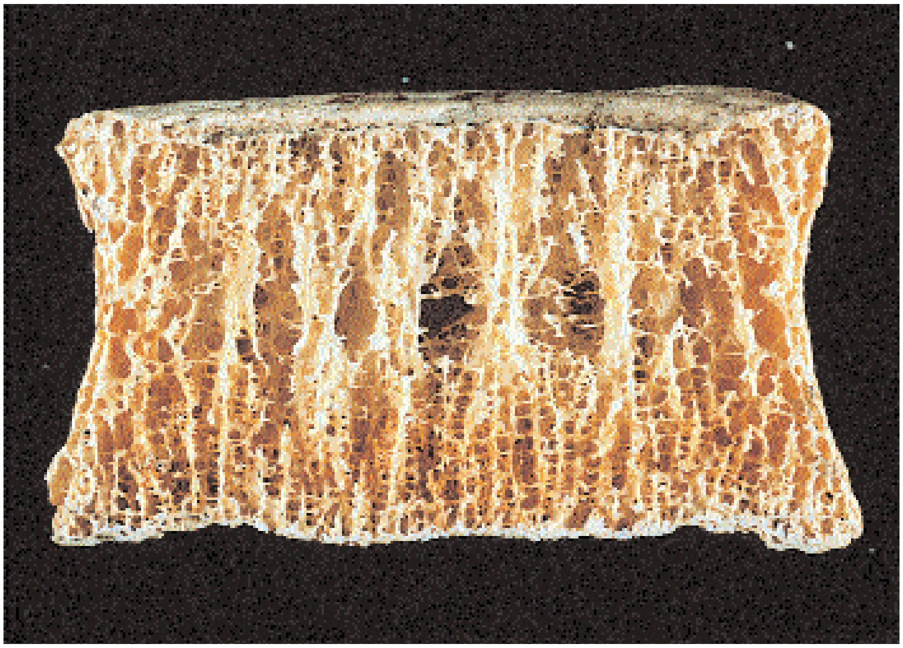
Bone

Bone is the major component of the adult vertebrate skeleton. It is a hard connective tissue comprised of living material, including bone cells, fat cells, and blood vessels, and an inorganic matrix, which is made up largely of water and minerals.

All connective tissues support and connect various parts of the body, and the specific functions of bones are diverse. As the main element of the skeleton, they provide structure and support to vertebrate bodies. They also act as levers for body movement, their position controlled by the muscles attached to them. Bones also protect the delicate internal organs from external impact. For example, the skull encases and protects the brain, and the rib cage houses the lungs and heart.

platelets cell fragments in plasma that aid in clotting

As well as serving these structural and protective functions, bones play two important physiological roles. They serve as deposits for calcium, a mineral that makes the bones stronger and is essential for the operation of nerves and muscles. Red blood cells, white blood cells, and **platelets** are all manufactured in the core of the bone, or bone marrow.



Cross section of a lumbar vertebra showing spongy bone tissue. The spongy bone consists of a honeycomb of small bone pieces called trabeculae that are filled with red or yellow bone marrow.

Bones change and develop along with the rest of the body. During the early stages of embryonic development, the vertebrate skeleton consists entirely of cartilage. As the fetus grows, calcium and phosporous deposits form around the cartilage as the mineralization process begins. At birth, the skeleton still consists mostly of cartilage and experiences further changes as the child matures. For instance, the bones of an infant's skull do not fuse until several months after birth. A newborn human has over 300 bones, which over time fuse into the 206 bones of an adult. Cartilage gradually replaces bone through the process of **ossification**, which is achieved through the activity of **osteoblasts**, the bone precursor cells.

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

osteoblast potential bone forming cells found in cartilage

Bone is made up of osteocytes, living bone cells that are surrounded by the matrix. Osteoblasts secrete the matrix and collagen, a protein that gives bone a slightly elastic quality and prevents it from shattering when bearing weight. The osteoblasts also secrete mineral salts, which harden the bone. As the bone matures, the osteoblasts are transformed into osteocytes, and new osteoblasts are released into the system to build more bone.

Bone tissue can be categorized as compact or spongy. Compact bone, also called cancellous bone, has a honeycomb structure that is designed to withstand stress from multiple directions. Compact bone is denser and harder than spongy bone, and is present in the main bones of the arms and legs. It is made up of long, cylindrical units called osteons, which help the bone bear weight. Blood vessels and nerves run through the center of each osteon.

Many bones are composed of an outer layer of compact bone and an inner core of spongy bone. The skull, pelvis, ribs, breastbone, and vertebrae all contain spongy bone, as do the ends of the arm and leg bones. Trabeculae are the bony struts that create the criss-cross formation of spongy bone. Bone marrow fills the spaces between the trabeculae. A thin, two-layered membrane called the periosteum surrounds and protects both bone types. Nerves and blood vessels run throughout the outer layer of the periosteum into the bone. Osteoblasts are the main constituent of the inner layer.

Bones are connected to each other at junctions called joints. There are several types of joints, each with a different range and pattern of movement. The fused joints of the skull do not permit movement, the hinge joints of the elbow and knee allow movement in one direction, and the pivot joints found between certain neck vertebrae permit side-to-side twisting motions. The ball-and-socket joint in the shoulder allows a wide range of movement.

Bone is a dynamic tissue with a structure and composition that adapt to environmental stresses. It undergoes constant breakdown and rebuilding. As a calcium deposit, bone is responsible for maintaining required levels of this mineral in the blood. When calcium levels drop, cells called osteoclasts break down bone to release calcium into the blood. Through the activity of osteoblasts, bones also thicken in response to exercise and impact.

When a bone breaks, several processes contribute to its repair. First, cells from the periosteum transfer to the site of the break and create a fibrous network. Then other cells produce cartilage around this network. In the final step, osteoblasts arrive and convert the cartilage into bone. This healing process may take weeks or months, depending on the severity and location of the injury and the individual's age and general health.

As an individual ages, the rate at which bone breaks down slowly begins to exceed the rate at which it is formed. The bone is weakened, and its size reduced. Developing and maintaining proper exercise and nutrition habits at an early age ensures that bones remain healthy in old age. SEE ALSO Skeletons.

Judy P. Sheen

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Burgess Shale and Ediacaran Faunas

The Burgess Shale was one of the most famous and important fossil localities known at the end of the twentieth century. Charles Walcott, who at the time was secretary of the Smithsonian Institution, discovered this fossil-rich rock bed in 1909 while exploring the Canadian Rockies of British Columbia. The Burgess Shale, which is now a part of Yolo National Park, is famous for the wide diversity of fossils of soft-bodied marine animals that are embedded in it. These fossils are approximately 530 million years old, and represent an array of life-forms present during the early–middle years of the Cambrian period (545–495 million years ago). The area originally quarried by Walcott is surprisingly small given the array of unique animal forms found in it. His initial survey covered an area that is only 10 feet tall and 200 feet long, the length of one city block.

The fossils of the Burgess Shale are significant for a number of reasons. The quality of their preservation provided the first opportunity to examine, in astonishing detail, the morphology (form and structure) of early soft-bod-

Many fossils from the early–middle Cambrian period have been uncovered at Burgess Shale sites such as this one in Yoho Valley, British Columbia, Canada.

ied life forms. In addition, these fossils are an early record of the novel body plans that were created during the Cambrian Explosion (approximately 570–540 million years ago), a geologically abrupt time period during which multicellular forms organized in a variety of new ways. The Burgess Shale does not depict the Cambrian Explosion itself, but the aftermath. The fossils are impressive not only for the novelty of the body plans represented, but also for the diversity of body plans.

Fossils of soft-bodied forms are rare because the process that creates fossils works better at preserving bones and hard structures. Before the discovery of the Chingjiang fossils in Yunnan Province, China, in the late 1980s, the Burgess Shale fossils provided the only evidence of the early soft-bodied animals that appeared during the Cambrian Explosion. The quality of these fossils indicates that they were created under **anoxic** (low oxygen) conditions. Many millions of years ago, the site of the Burgess Shale was underwater and located near the equator. Soft-bodied marine animals were carried by strong currents from surrounding highly oxygenated areas to the site of the Burgess Shale and were buried in an underwater mudslide. The

anoxic an environment that lacks oxygen low oxygen content of these waters killed the animals and protected their remains from decay.

Classifying the Burgess Animals

Approximately 120 species are found in the Burgess Shale, including familiar forms as well as several species belonging to previously unknown phyla. Some of the fossilized species are members of groups (phylum) that still exist. These species can be categorized as members of the phyla Porifora (sponges), Annelida (segmented marine flatworms), Arthropoda (insects, crabs, and trilobites), and Echinodermata (sea urchins, sea fans, and sea lilies), and one species is the earliest representative of the phylum Chordata (which includes vertebrates). Most of these animals were scavengers, and a few were predators. Of these Burgess Shale animals, the aptly named *Hallucigenia* (phyla Annelida) is probably one of the most famous for its bizarre morphology. Seven pairs of stiltlike legs support its long, cylindrical body. It is hard to tell for certain which end is "head" and which end is "tail," but most scientists designate the head end by the bulbous projection that is prominent on one end of its body.

The previously unseen animal forms found within the Burgess Shale include a number of wormlike and segmented organisms, some of which were assigned to novel phyla (phyla Priapulida and Onychophora) while others remain "unclassified to this day." *Opabinia* was a five-eyed, 3-inch-long creature with a frontal "nozzle" that was presumably used in its search for worms and other fossorial (living in burrows) prey. *Anomalocaris* ("unusual shrimp") was a fierce, 2-foot-long predator with robust forelimbs for grasping its prey and a square-shaped mouth rimmed with multiple rows of sharp teeth. Because *Anomalocaris* existed in the Burgess Shale only as separate pieces, Walcott first reconstructed it as two animals: a bivalved (having two symmetrical, shelled parts joined by a hinge) arthropod and a jellyfish. Fossils of related species later found in China reached a length of up to 6 feet! *Wiwaxia*, a spike-covered, sluglike animal, was a bottom feeder that was protected from hungry predators by its scaly back.

In attempting to fit these new forms into the preexisting classification scheme, which included only phyla Porifora, Annelida, Arthropoda, Echinodermata, and Chordata, Walcott erroneously classified these animals as worms and arthropods. His categorization of the Burgess animals as ancestors of modern-day animals conformed to the idea that the diversity of life-forms arose in a manner resembling the shape of an inverted cone, with the large number of species that exist today arising from a small number of ancient organisms.

It was not until H. B. Wittington of Cambridge University examined the fossils forty years later that these forms were placed into unique phyla. Whittington's reclassification caused a major upheaval in the way people thought about the origin of animals. Instead of the popular view that a small number of general body plans originated during the Cambrian period and gave rise to all the animals seen today, Whittington contended that the body plans evident today represent only some of the novel forms that were created during the Cambrian period. He argued that many different body plans were created then, a number of which went out of existence while the remainder continued and gave rise to the forms we see today. This premise formed the basis for his reclassification of the Burgess animals.

Ediacaran Fauna

Before the Cambrian Explosion and the associated appearance of new animal forms, there existed the Ediacaran Fauna (also known as Vendian Biota), a group of multicellular organisms with relatively simple body plans. Geologist Reginald Sprigg first discovered the fossil traces of these organisms in 1946 while exploring the Ediacara Hills of Australia. Since the initial discovery of the Australian fossils, additional Ediacaran fossils have been found on every continent except Antarctica. The age of the rocks containing these fossils range from 600 million to 544 million years old. Before the discovery of the Ediacarans, it was believed that animals did not exist before the Cambrian Period (before 545 million years ago).

In contrast to the Burgess Shale fossils, most of the Ediacaran fossils are burrows and trace fossils—casts and molds of the organisms they depict. The fossil traces of these simple animals can be broadly divided into those that are **radially symmetric** and those that are segmented. The radially symmetric traces are believed to have been formed by polyplike and disk-shaped organisms. The more complex, segmented forms are traces of tubelike units. The shape of these soft-bodied forms was preserved during rapid burial under sand on the ancient marine floor bed.

radially symmetric wheel-like symmetry in which body parts radiate out from a central point

The classification of the Ediacarans as animals remains controversial. The superficial similarity that some of the Ediacaran forms bear towards sea anenomes and jellyfish led some scientists to conclude that they are true animals, precursors to the animals that exist today. Various Ediacarans have also been mistakenly classified in the past as algae, lichens, or giant protozoans.

However, some scientists believe that the Ediacarans were not animals as we know them, and they did not evolve into such animals. These scientists focus upon characteristics of the Ediacarans that are not found in the body plans that evolved during the Cambrian. Based on information gleaned under close examination of the fossil traces, they concluded that the Ediacarans underwent a set of embryonic/morphological development processes that differs radically from the normal pattern of development experienced by true animals. SEE ALSO CAMBRIAN EXPOLSION; CAMBRIAN PERIOD; GEOLOGICAL TIME SCALE.

Judy P. Sheen

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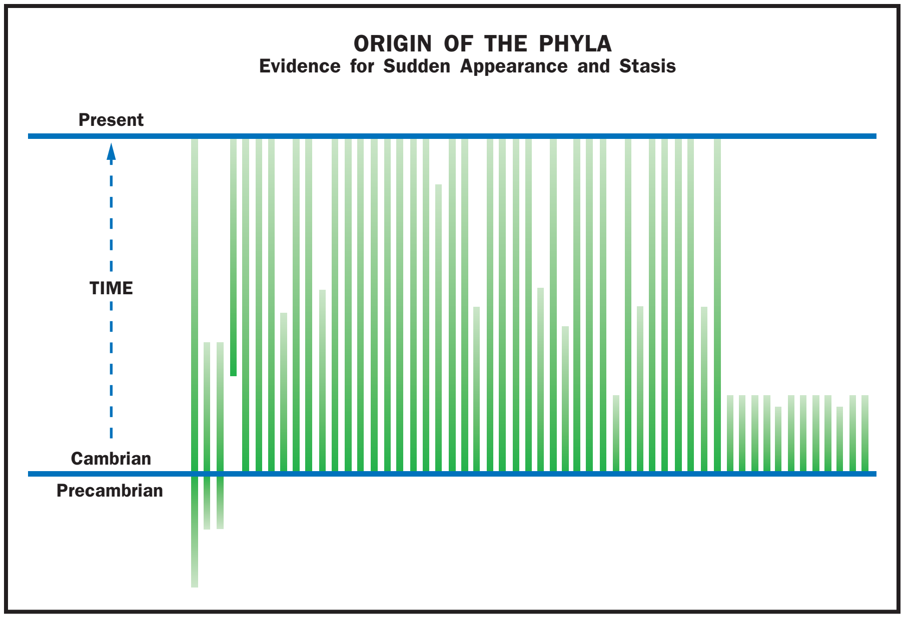
Cambrian Explosion

The Cambrian Explosion, known informally as Biology's Big Bang, refers to the event that greatly increased the variety of animal species and created the major types of animals that exist today. Scientists refer to this event as an "explosion" not because it was a period of violent activity, but because



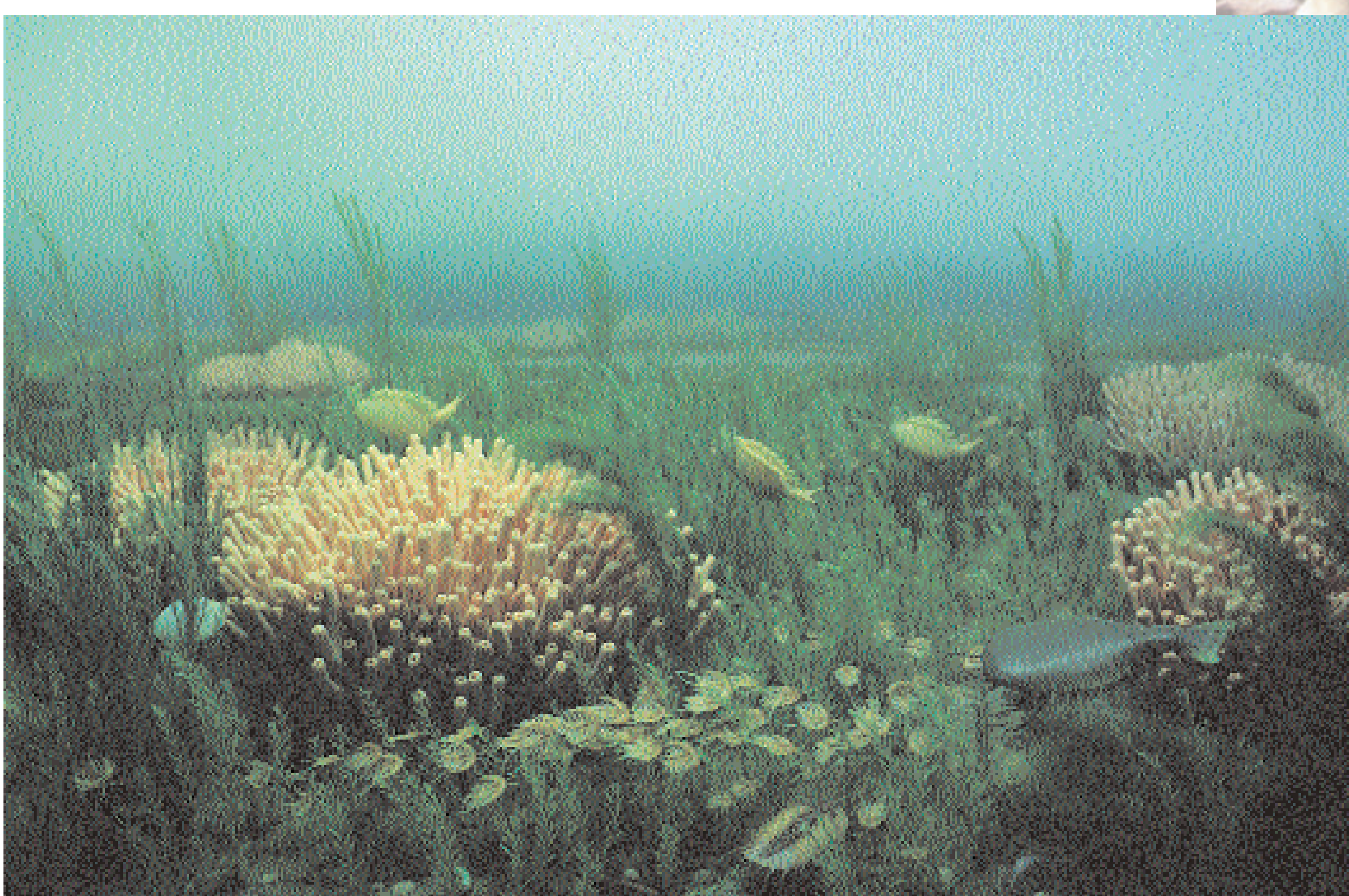
Study of fossils provided the information to create this chart.

an incredible amount of evolutionary activity occurred in a relatively short length of time. This burst of evolution occurred during the early years of the Cambrian period (approximately 570 million to 495 million years ago). The Cambrian Explosion ran its course over several tens of millions of years, but this time period is quite brief considering the length of time that multicellular life has existed on Earth (about 600 million years).

In addition to the phyla that are still present today (phyla Porifera [sponges], Cnidaria [jellyfish], Platyhelminthes [flatworms], Nematoda [nematode worms], Molluska [clams], Annelida [roundworms], Arthropoda [insects, spiders], Echinodermata [sea urchins], and Chordata [vertebrates]), a number of other phyla were created and have since become extinct (including phyla Priapulida, Onychophora, and some unclassifiables).

The Burgess Shale (in British Columbia, Canada) and the Chingjiang (in Yunnan Province, China) provide fossil evidence for the outcome of the Cambrian Explosion. The fossils of both localities are impressive for the details they provide of early, soft-bodied marine organisms, and for the diversity of animal forms they display. Prior to Charles Walcott's 1909 discovery of the Burgess Shale in the western Canadian Rockies, life was thought to have evolved at a gradual, constant rate. The Burgess Shale fossils, formed 530 million years ago, shortly after the Cambrian Explosion, showed that the diversity of animal forms arose abruptly relative to the age of animal life as a whole.

No one knows exactly how the Cambrian Explosion started, but a number of theories have been offered. Many scientists believe that violent and abrupt changes in climate forced animal life to diversify and adapt to new and harsh conditions. Prior to the Cambrian Explosion, the present-day continents of Africa, South America, India, Antarctica, and Australia formed a giant landmass called Gondwana. Shortly before the Explosion, the abrupt shifting of Gondwana and Laurasia (ancestral North America) across Earth's surface caused volcanic eruptions and earthquakes, creating a hostile environment in which marine animals had to compete for survival.



Many of the marine-based life-forms recognized today originated in the Cambrian period.

These dramatic geological events mixed more oxygen dissolved into the water, which helped make possible processes such as respiration, cell division, and the synthesis of proteins that are important in body structure and support. In this respect, the movement of tectonic plates that resulted in an upheaval of Earth's geology contributed to the creation of complex body plans. The evolution of organs such as brains, digestive guts, and shells opened the door for the new creatures to increase in complexity. These animals were then able to forage more effectively, move more efficiently, and protect themselves.

The tectonic shift created a new ecological battleground for these animals to compete. The breakup of Gondwana and its subsequent reorganization created a larger area of marine habitat in which the new creatures would compete. This competition catalyzed the adaptive radiation (evolution of a large variety of specialized forms) of the lineages into their respective niches.

Another mystery surrounding the Cambrian Explosion is why new phyla, or major lineages, have not evolved since then. Some scientists assert that after successful body plans arose during the Cambrian, genetic limitations dictated that change occur only within the set lineages. Rather than create dramatically new body forms, these existing forms were modified into more complex animals. Because modern animals have been evolving and adapting for millions of years since their ancestors first appeared, they would have an advantage over any new "hopeful monsters" that may come about through mutation. Hopeful monsters are forms that are so different from the "tried and true," existing with low chances of survival.

Late twentieth-century efforts to solve the mysteries of the Cambrian Explosion focused on molecular genetic techniques. New technology allowed scientists to extract DNA from fossils of the first Cambrian animals and to study certain aspects of these animals' biology. In this manner, scientists can learn about the development and evolutionary relationships of these animals. SEE ALSO Burgess Shale and Ediacaran Faunas; Cambrian Period; Geological Time Scale.

Judy P. Sheen

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Cambrian Period

The Cambrian period (570 million years ago) marks an extraordinary shift in the evolution of life. It ushers in the beginning of the Paleozoic Era (the age of ancient life).

Cambrian period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

prokaryotes single-celled organisms that lack a true cell nucleus

In the Precambrian, a three-billion-year period of evolutionary stasis, the dominant life-forms were **prokaryotes** (tiny one-celled bacteria) and blue-green algae, both of which thrived in the steaming waters and nitrogen- and sulfur-rich air of a geologically turbulent Earth. Prokaryotes are the simplest forms of life, undifferentiated cells with no nucleus that reproduce by fission, the splitting of the parent cell into two. Prokaryotes live off hydrogen, sulfur, and nitrogen and they release free oxygen as a waste product. The prokaryotes' leisurely existence continued for five-sixths of recorded time, during which their massive colonies of cyanobacteria, fossilized as stromatilites, bubbled out enough oxygen to form eventually an atmosphere and a corresponding ozone shield against sterilizing ultraviolet radiation. This development appears to have set the stage for what has been described as the Big Bang of Biology, the Cambrian Explosion.

This trilobite fossil is one of 120 different fossilized species found in the Burgess Shale in Yoho National Park, British Columbia, Canada.

Cambrian rock is named after the Latin "Cambria," meaning Wales. It was there that Cambrian rock was first studied for fossils in the late 1800s. Since then it has been found on every continent, with a particularly fertile deposit having been discovered in British Columbia, Canada. The latter is known as the **Burgess Shale**, a fine-grained, mudstone siltstone rock unit only about 200 feet long and 8 feet thick. Stephen Jay Gould has described it as the most important fossil deposit ever found. Dating to the mid-Cambrian of about 520 million years ago, the Burgess Shale has more than 120 animal species represented in it. The Burgess fossils demonstrate that the Cambrian period was a riot of experimentation in size, shape, and abilities. Animals that swam, that burrowed, and that foraged appeared at this time. A huge diversity of forms emerged. Some would succeed and continue to exist, while many others would disappear forever. The beginnings of every existing major **phyla** of animals can be found in the Burgess Shale and in other layers of Cambrian rock in Greenland and China. Over 900 species of marine life have been discovered at these locations, including sponges, jellyfish, annelids, mollusks, arthropods, and chordates with rudimentary backbones. One of the most interesting innovations found in Cambrian period animals was their ability to secrete a mineralized skeleton.

Burgess Shale a 570 million year old geological formation found in Canada that is known for well-preserved fossils

phyla broad, principle divisions of a kingdom

What could have caused this remarkable outburst of evolutionary life? The single most galvanizing event of the late Precambrian was the appearance of **eukaryota**, life-forms that stored DNA in a nucleus and were capable of organizing bodies consisting of more than one cell. Eukaryotes allowed for the possibility of specialization, since the individual cells did not each have to perform every task as long as they could communicate chemically with one another. This cooperation between cells set life-forms free to explore every design and variable in size and shape imaginable. Eukaryotes also developed the capability for sexual reproduction, which increases genetic diversity. Rather than duplicating the genetic material exactly as simple **fission** does, sexual reproduction ensures that a constant shuffling of genetic material will maximize the number of mutations and variations possible. This again allows for radical divergences in the exploration of the environment. These

eukaryota a group of organisms containing a membrane-bound nucleus and membrane-bound organelles

fission dividing into two parts

advances in eukaryote organisms, combined with the new, oxygenated atmosphere of the planet, would appear to have allowed for the outburst of metazoans—multicelled animals—in the Cambrian rocks. SEE ALSO Geological Time Scale.

Nancy Weaver

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Camouflage

Predation is an instinctive animal behavior that involves the pursuit, capture, and immediate killing of animals for food. Birds that capture insects in flight, starfish that attack marine invertebrates, and tigers that pursue gazelle are all examples of predators. Predatory animals may be solitary hunters, like the lion, or they may be group hunters, like wolves. Natural selection favors the development of a variety of quick defenses against predators including camouflage and predator avoidance behaviors.

Camouflage is a form of deceptive coloration that is essential to the survival of most animals. Camouflage can make it extremely difficult to spot an animal in its natural habitat because the animal appears to blend into its surroundings. This adaptation is beneficial because it can provide protection from predators. At the same time, it can also conceal an animal and allow it to be a stealthy predator able to inconspicuously hunt down or snatch its unsuspecting prey.

This walking stick insect hides from its predators by blending into its environment. The insect's slow walk mimics the movement of branches swaying in the wind.

Types of Camouflage

Animals camouflage themselves in many ways, including background matching, color changing, disruptive coloration, and countershading.

Background matching. Background matching is probably the most common type of concealment. The animal and its surroundings are so close in color that they appear as one. Fish eggs, for example, often have very little pigmentation and appear transparent against the blue of the open sea. Polar bears appear to merge into the ice and snow of the Arctic, and grasshoppers blend perfectly with green grasses and shrubs.

Color changing. Color changing is another way to achieve camouflage. Emotion seems to play a role in color change in some animals, such as cephalopods and certain fish, which are capable of rapid color changes completed in a half-second or less. These animals, when excited, can exhibit spectacular displays of color, with waves of color rippling across their bodies. As the animal's eyes register the colors in its immediate environment, hormonal reactions send chemical messages to chromatophores, pigment-bearing cells in the animal's skin. The chromatophores undergo rapid changes in pigment concentration, distribution, and position, allowing the animal to seemingly change color almost instantly. Most vertebrates, however, undergo color changes less rapidly, requiring several minutes to several hours.

Disruptive coloration. Disruptive coloration may appear as patterns in which an animal's markings do not coincide visually with its body shape or outline. Flatfish, for example, are marked in such a way that their skin patterns do not reveal their contour when they rest on the ocean bottom. Many reef fish also have disruptive patterns in their coloration, which enable them to school safely over reefs during daylight hours. When a predator approaches, the fish form dense schools in which all of the individual fish orient themselves in the same direction. The movement of many fish, coupled with their similar disruptive coloration of vertical banding or horizontal stripes, presents an extremely confusing spectacle. This makes it difficult for a predator to attack any individual fish.

Some forms of disruptive coloration also function to hide movement. Forward movement of concentrically banded snakes, for example, is difficult to perceive when the animal moves between reeds or tall grasses.

Countershading. Countershading, a type of camouflage coloration in which the upper surfaces of an animal's body are more darkly pigmented than the lower areas, gives the animal's body a more uniform darkness and lack of depth relief because the underside of the body is shadowed. Light-producing organs found in some deepwater fish provide a unique form of countershading. The light-producing organs often occur in bands along the fish's undersides and are directed downward. This unique arrangement, coupled with the utter darkness of the ocean at deep depths, may provide camouflage by obliterating the fish's silhouette when a predator views it from below.

Some animals camouflage themselves through mimicry by showing an imitative resemblance to inanimate objects in their environment, such as the leaves or twigs of a tree. Stick insects, for example, may resemble twigs when resting on trees.

Predator Avoidance Behaviors

In addition to camouflage, animals use predator avoidance behaviors or protective adaptations to avoid being killed. Warning calls and visual and chemical signals that are unique to different animal species may evoke avoidance behaviors such as freezing, crouching, fleeing, escaping, and stinging. For example, many perching birds will gather in a mob when stimulated by the sight of an owl.

Freezing or immobility usually makes detection less likely. Many animals, such as rabbits and squirrels, exhibit this reflex-like behavior when startled. Some groups of animals commonly keep in touch by calls or by movements such as tail flicks, which are exhibited during freezing.

Many animals posses protective reflexes, armor, and spines that enable them to avoid predation. Stick insects resembling twigs and leaves, for example, exhibit unusual reflex behaviors, such as swaying to imitate moving foliage. Mollusks, like oysters and clams, may retract their soft bodies into

their shells when disturbed. Turtles and other slow moving animals may retreat into their armor for protection. Still other animals, such as porcupines, protect themselves from predators with a thick coat of sharp quills.

Chemical means of defense may help an animal escape predators. An animal may eject a poisonous substance from a body reservoir or spine. Jellyfish, for example, may sting to avoid being captured. Snakes may inject venom through their fangs to kill or deter menacing predators. Some animals, like skunks, may even squirt substances at their enemies. The skin of some toads contains substances that make them distasteful to predators. Ants produce strong substances that attract other ants at low concentrations and in high concentrations produce fast movement, defense postures, and even fleeing.

Fleeing and escaping are two of the most common predator avoidance reflex behaviors. When an animal is startled or subjected to pain, it may run or jet away. Squids, for example, use jets of water to propel themselves quickly out of danger. Bony fish have structures that initiate escape-swimming when agitated. SEE ALSO HABITAT; MIMICRY.

Stephanie A. Lanoue

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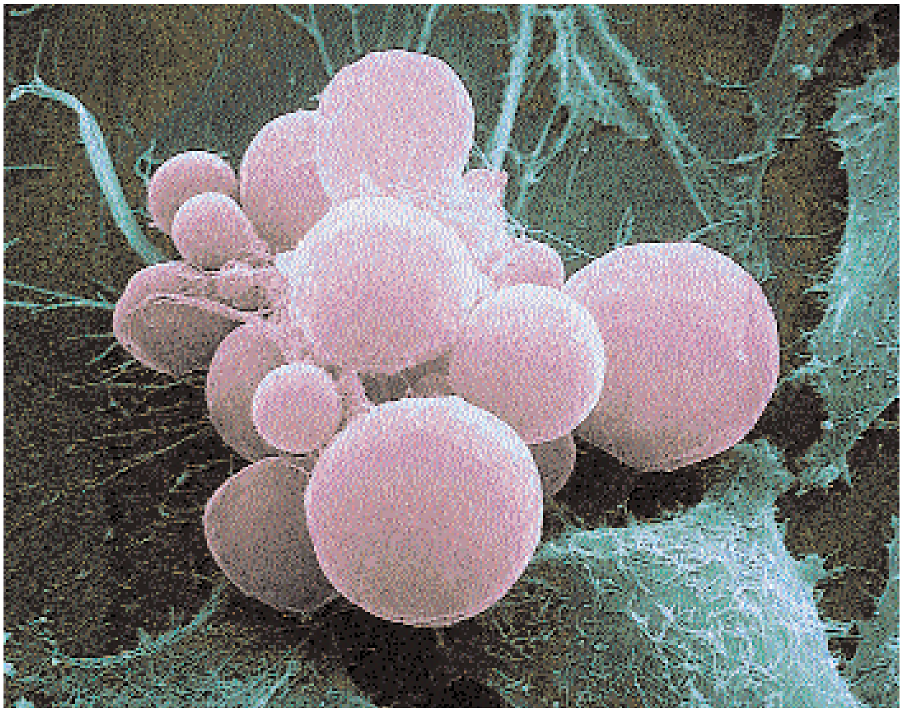
Cancer

Cancer is the uncontrolled growth of cells. This abnormal growth is the result of mutations in the genetic material of the cells, either spontaneous or brought on by environmental factors such as ultraviolet radiation or asbestos. This growth leads to a collection of mutated cells called a tumor. The tumor can be benign, meaning that it is comparatively harmless and restricted to one type of tissue. Alternately, it can be malignant, which means it can grow into surrounding tissue or migrate to different parts of the body. When a malignant tumor spreads to other tissues, this is known as metastasis.

Cell replication

Normally, animal cells grow with a variety of checkpoints. For example, when a person cuts her finger, skin cells will divide and grow to fill the opening, but they will stop growing once the cut is closed. The body has a number of mechanisms to prevent unchecked cell growth, and in order to become cancerous, abnormal cells must defeat several of them. Some of these mechanisms determine division rates; others manage DNA repair. Like any other controls in the body, these can go awry when a mistake arises in the DNA encoding them.

Excessive cell division. Suppose, again, that a person gets cut. First, skin cells must decide when it is time to divide and when it is time to rest. Of-



A scanning electron microscope magnifies mammalian cancer cells 7,500 times. These cancer cells could quickly reproduce, creating enough cells to form a tumor.

ten cells will receive signals from outside their membranes instructing them what to do, and the signals must pass down a cascade of messengers inside the cell for them to be conveyed. Each step along the cascade, then, can be a control point: a surface molecule on a skin cell is told that it must divide to heal a cut, and the surface molecule sends a signal to a protein inside the cell, which sends the signal to a different protein, and so on, all the way to the nucleus, which then initiates **DNA replication** and cell growth. At each step, it is possible that a mistake might start or halt the cell replication process. For example, overexpression of ras, an intracellular messenger that resides in the pathway between the surface and the nucleus, can lead to excessive cell division.

DNA replication the process by which two strands of a double helix separate and form two identical DNA molecules

Viruses and cancer. There are a number of ways that a protein such as ras can be overexpressed, including the involvement of a virus or a genetic mutation. Certain viruses are associated with cancers: for example, sexually transmitted human papilloma virus has been known to increase rates of cervical cancer. Out of all cancers, 10 to 15 percent are thought to be virus-related. Alternately, the genetic mistake might be spontaneous in one of three ways. A gene encoding the protein could be accidentally copied more than once, and, as a result, each copy would churn out the protein when activated. The gene could be misplaced and put near a region of DNA that encourages protein expression. Lastly, a mutation inside the gene might make it unusually active or resistant to later degradation. When such errors initiate uncontrolled cell growth, the gene involved is called an oncogene (*onco* is Greek for "tumor"). Before the mutation occurs, the gene may be called a proto-oncogene. Proto-oncogenes usually have the important function of controlling cell-cycle function, as is the case with ras, or may be involved in keeping the cell alive during times of stress, as in the case of Bcl-2, a molecule that prevents stressed or damaged cells from committing apoptosis (cell suicide). Certain viruses can cause these mutations and make oncogenes out of the protoncogenes.

How Cells Curb Their Own Growth

Mutations in cell-cycle control genes can obviously be a problem for an individual, so there are mechanisms in place to prevent this from happening. As mutations can happen during DNA replication, DNA copying is a tightly controlled process. Additionally, there are genes that have the task of DNA repair and mutation surveillance. One such gene is p53. If there is genetic damage, p53 will halt the cell cycle, may initiate DNA repair mechanisms, and may activate cell suicide if repair is not feasible. P53 and other genes that conduct DNA repair and damage surveillance are called "tumor suppressor genes."

organelles membrane bound structures found within a cell

cytosolic the semifluid portions of the cytoplasm

macrophages a type of white blood cells that attacks anything foreign such as microbes

Apoptosis. Apoptosis is a way for damaged cells to prevent themselves from causing more problems. Once apoptosis is initiated, the cell cleaves its own DNA and falls apart in a tightly regulated fashion. The dying cell will pinch off into small pockets of membrane and **organelles**, known as apoptotic bodies, in order to prevent toxic **cytosolic** compounds from being released. Then the apoptotic bodies will be swept up and cleared from the area by **macrophages** or other cells.

"Slipperiness." Aside from cell-cycle control and tumor suppressor genes, there are other means by which cells curb their own growth. For example, if one grows ordinary skin cells on a plate with growth media, the cells will grow until a bed covers the entire plate. But the cells will not grow beyond that; nor will they grow on top of one another. This is why a cut on one's finger will not grow into a huge lump after it closes. Normal cells will also adhere tightly to one another by secreting proteins that stick to other cell surfaces, whereas many cancer cells do not. Medical doctors use this lack of adhesion, this slipperiness, as one way of distinguishing cancerous tumors from other kinds of lumps.

nucleotide chain a chain composed of five-carbon sugar groups that forms the basis for nucleic acid

nucleotides the building blocks of a nucleic acid that are composed of a five-carbon sugar bonded to a nitrogen and a phosphate group

Telomerases. Another common mutation seen in cancers is the activation of telomerases. When DNA divides, the replication machinery moves down the **nucleotide chain** until the very end. It is unable to copy the very end of the molecule (the telomere), however, so with each successive round of replication, the DNA chain gets shorter. In mammals, the telomeres contain repetitive DNA sequences that encode no protein; the idea is that these useless **nucleotides** can be discarded as cells divide. As the telomeres get shorter, though, the cell will eventually start deleting useful DNA. Some scientists think this is a reason animals grow old: The more cells divide, the greater the likelihood that certain genes will be eliminated and that the new cells will be dysfunctional.

Cancer Cells

Cancer cells, on the other hand, have no such problem. They usually express telomerases, which are enzymes designed to prevent the elimination of the telomeres during cell division. Cancer cells can therefore divide many times and not delete any genetic information crucial to their survival.

Cells require more than one mutation to become cancerous. Mutations in cell-cycle control and tumor suppressor genes are usually required for a tumor to be considered a full-fledged cancer. While many of the tumor suppressor genes are dominant traits (requiring only one allelic deletion to deactivate), many proto-oncogenes are **recessive**, meaning that both **alleles** must be destroyed in order for the cells to grow improperly. Such a combination of mutations in a single cell is unlikely, which is why some scientists think that cancers do not begin to show in humans until late in life, when repeated cell division has had a chance to accumulate a number of mistakes in the DNA.

recessive a hidden trait that is masked by a dominant trait

alleles one of two or more alternate forms of a gene

After p53 or other genes that screen DNA get deleted, the cells begin to spin out of control genetically and produce many different kinds of mutations. Like most mutations, the majority of these will simply kill off the cells possessing them. But as tumor cell division is unchecked, other cells will quickly replace them. As the tumor grows and accumulates more mutations, it may gain the ability to grow in different types of tissue.

Cancers may acquire a number of traits useful for their own growth. For example, certain tumors are angiogenic, meaning they draw blood vessels toward themselves to feed the growing tumor. The malignant cells do this by secreting certain hormones necessary for vessel formation. These new vessels also provide conduits for cancer cells to spread throughout the body. In the early twenty-first century, researchers also found that some tumor cells can create new lymphatic vessels, a process called lymphangiogenesis. These newly generated vessels may make it easier for the cancer to spread itself to other parts of the body.

Cancer Treatment

As one might predict, cancer treatment primarily seeks to stop the division of the cells. One method is radiation, which disrupts DNA replication entirely. Other pharmacological means seek to do the same. As cancers are usually the only collection of rapidly dividing cells in the body, halting replication can slow them down, although such treatments can impede healing or immune system function.

More recently, researchers have been using compounds designed to prevent angiogenesis to curb tumor growth. In the early twenty-first century, the National Cancer Institute was conducting clinical trials of anti-angiogenic compounds in a variety of cancers, including stomach, breast, prostate, lung, brain, and ovary, and in some leukemias and lymphomas.

Certain cancers produce tumor antigens, proteins recognizable by the body as hailing from a cancer. Prostate cancer, for example, generates tumor antigens specific enough to be used as a diagnostic tool in patients. Thus, it is theoretically possible to create a prostate cancer vaccine by teaching the body to recognize these antigens before cancer ever arrives and to fight off malignant cells, just as antivirus vaccines fight off virally infected cells. By the beginning of the twenty-first century, however, researchers had found vaccines to be of little use in specifically stimulating the body's immune system to reject tumors.

Cancers, ordinary cells gone wrong, defy normal biological conventions of regulation and **homeostasis**. As they can quickly reproduce and replace lost daughter cells, they are ripe for rapid mutation and evolution within the body. A variety of treatments exist, but cancers vary widely in origin and nature, as there are different regulatory mechanisms that control different cell

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

HELA CELLS

Although Henrietta Lacks died of cancer in 1951, little bits of her are alive everywhere. She is the originator of the first immortal cell line, HeLa cells. These are cancer cells scraped from her cervix, and they grew so well that they proved ideal for study in laboratories all over the world. Unfortunately, they grew so well in culture that they invaded other cell lines and ruined countless experiments. It became such a problem that in 1968, the premier standard-bearer of cell lines in the world, the American Type Culture Collection, tested all thirty-four of its "pure" cell lines and found that twenty-four of them were HeLa cells instead.

types. A more detailed understanding of cell-cycle regulation and mutation surveillance may yet unlock the secrets to curing the disease. SEE ALSO CELLS.

Ian Quigley

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Carboniferous

The Carboniferous period dates from 360 million to 280 million years ago. It gets its name from the vast deposits of coal produced when fluctuating seas drowned the tropical forests that covered much of North America and Europe.

Carboniferous period and surrounding time periods.

Era	Period	Epoch	Million Years Before Present
Paleozoic	Permian		286
	Pennsylvanian		320
	Missipian		360
	Devonian		408
	Silurian		438
	Ordovician		505
	Cambrian		570

amniote a vertebrate that has a fluid-filled sac that surrounds the embryo

CARBONIFEROUS OR MISSISSIPPIAN AND PENNSYLVANIAN?

In the United States, the Carboniferous Period is usually broken down into two periods—Mississippian and Pennsylvanian. Sedimentary rocks that formed in shallow oceans characterize the Mississippian or "Lower Carboniferous." These rocks are usually found along the Mississippi River. Coal bearing sedimentary rocks that formed in swamps and river deltas characterize the Pennsylvanian or "Upper Carboniferous. These rocks are usually found in the northeastern United States.

The later Paleozoic (286 million to 570 million years ago) was a world that would be recognizable to us. By this time the teeming marine and land plants had expelled enough oxygen to produce an atmosphere very similar to our own. Vast forests greened the supercontinent Pangaea and supported a thriving animal population. We would be struck by the sheer size and variety of the flora and fauna: horsetails and scale trees that stood from 50 to 100 feet tall and dragonflies with 2-foot wingspans. Drippingly humid and silent, the monotonously green rain forest abounded with scuttling creatures familiar and unfamiliar. Animals that swam, crawled, and flew populated the tropical swamps of the forest. Snails and cockroaches and myriapods made a living on the rich forest floor, along with 6-foot centipedes and crocodile-like amphibians.

By this time all the major characters of evolution had come into being. There would still be millennia of ingenious refinements of size and shape and function, variations on the main themes to exploit the new Devonian (408 million to 438 million years ago) environment of land and air. The Phylum Chordata, comprised of animals with backbones, had previously experimented with fishes and amphibians; now, in the Carboniferous period, the chordates would diverge into reptiles.

In a remarkable adaptation referred to as the **amniote** radiation, amphibians had evolved from needing large bodies of water in order to reproduce. The method was a semipermeable, shelled or leathery skinned egg filled with enough nutrients to sustain an embryo until it was fully developed. This dry-land form of reproduction necessitated yet another biological innovation, namely internal fertilization. These two features enabled the former amphibians to radiate out into every **niche** of the giant land mass, in turn encouraging further evolutionary branching. As the tetrapods (four-limbed animals) spread through the luxuriant vegetation, they made adjustments in their dentition and digestive tracts to take advantage of the untapped food source on land.

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

Three distinct groups of reptiles emerged, differentiated by the number of small holes in the skull located behind the eyes at either side. Anapsids had no holes and included the turtles and their now-extinct relatives. Synapsids, with a single pair of temporal openings, included all of the mammal-like reptiles, now extinct, and their distant relatives, the true mammals. Diapsids were reptiles with two pairs of openings. Petrocalosaurus was a rapid, 16-inch **insectivore** whose genes gave rise to lizards, snakes, crocodiles, dinosaurs, and birds.

insectivore an animal that eats insects

By the Carboniferous period, the constant ebb and flow of **continental drift** had once again pushed the land masses back together into one supercontinent, Pangaea, whose northern forests were periodically flooded by shallow tropical seas. The cycle of vegetation and flooding produced organic beds of peats that were compressed into coal layers over 3,000-feet thick. Exquisitely preserved fossils appear in this coal, especially near the Czech mining town of Nyrany. Here, hundreds of specimens have been collected, representing twenty amphibian and four reptile species as well as unusual fishes and small, shrimplike creatures.

continental drift the movement of the continents over geologic time

In the Carboniferous seas, huge limestone reefs were being laid down by limy coral, brachiopod, and crinoid skeletons. These reefs were home to starfish, **gastropods**, and sea urchins, while giant coiled nautiloids and bony fish swam overhead. SEE ALSO Geological Time Scale.

gastropods mollusks that are commonly known as snails

Nancy Weaver

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Carson, Rachel

Biologist and Author
1907–1964

Rachel Carson alerted the world to the dangers of environmental pollutants with works like the ground-breaking *Silent Spring.*

Rachel Louise Carson was born on May 27, 1907, the youngest child of farming and teaching parents in Springdale, Pennsylvania. The 24-hectare (60-acre) homestead was an oasis of orchards, streams, and woods in the grimy Allegheny River Valley, which had been heavily polluted by the coal and steel industries. Carson's parents were a particularly gentle couple who encouraged in their daughter a love of books and nature and a deep belief in sharing Earth with all other living beings. She became a published author for the first time at the age of eleven and later said that the thrill of seeing her story in print and the princely prize of ten dollars set her on her life's course.

Carson received a scholarship to Pennsylvania College for Women and made the shocking decision to major in biology at a time when there were virtually no jobs for women scientists. Upon graduation, she was offered a summer internship at Woods Hole, Massachusetts—a famous ocean research center—and a full scholarship to John Hopkins University, where she earned her master's degree in biology. During the massive unemployment of the Great Depression of the 1930s, Carson took the civil service exam and became the first woman to be hired as a biologist by the U.S. Bureau of Fisheries. During World War II (1939–1945) she was assistant to the chief of the office of information at the newly renamed U.S. Fish and Wildlife Service. During this period she began a series of books about the ocean and how the lives of its inhabitants—birds, fish, eels, and crustaceans—are intricately linked to one another and to the sea around them. All three of the books—*Under the Sea-Wind*, published in 1941, *The Sea Around Us*, published in 1951, and *The Edge of the Sea*, published in 1955—became best-sellers, and they catapulted Carson into national celebrity and allowed her to become a full-time writer.

pesticide any substance that controls the spread of harmful or destructive organisms

In 1962 the publication of her fourth book, *Silent Spring*, caused a nationwide uproar over the dangers and benefits of unregulated **pesticide** use. Government study panels were convened, grassroots conservation and environmental movements were organized, and laws were passed in the wake of this latest Carson best-seller, which was promptly translated into over a dozen languages. Despite vicious attacks by the chemical interests, other scientists validated the warnings in *Silent Spring*, and Carson became a national hero. She was awarded numerous honors by such groups as the American Academy of Arts and Letters, the National Wildlife Federation, and the Animal Welfare Institute. She was the first woman to be awarded the Audubon Medal, and she received a posthumous Medal of Freedom. Carson died of breast cancer on April 14, 1964, with the hope that she would be remembered in connection with all that is lovely and beautiful. SEE ALSO DDT; PESTICIDE; SILENT SPRING.

Nancy Weaver

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Cartilage

Cartilage is a fibrous and rubbery connective tissue found throughout the vertebrate skeletal system. As with other connective tissues, the general function of cartilage is to support and connect different parts of the body. Connective tissues originate from cells in the embryonic mesoderm, the middle layer of embryonic tissue.

Cartilage is made up of specialized cartilage cells called chondrocytes, which are suspended in an acellular matrix made up largely of a protein called collagen. All connective tissues have a **matrix**, and in the case of cartilage, the matrix is solid. A protective membrane named the perichondrium covers the surface of the cartilage and gives the subtance a shiny, cloudy-white appearance.

matrix the nonliving component of connective tissue

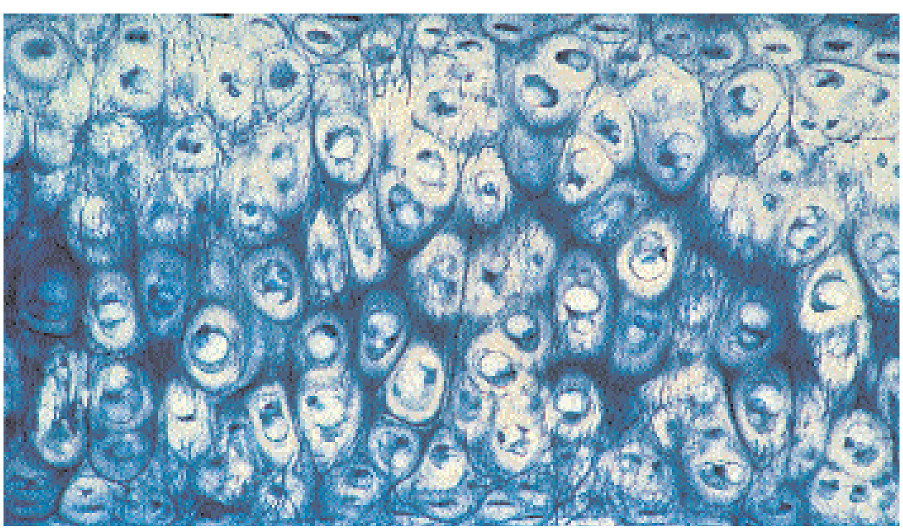
Early in development, cartilage makes up most of the vertebrate skeleton. As an individual grows older, calcium deposits form around the skeleton, and bone eventually replaces most of the cartilage. This process is called ossification. Ossification begins in humans when the fetus is still in the womb and is not complete until early adulthood. The skeleton of a young child tends to be less brittle than that of an adult because a certain amount of cartilage is still present.

This cartilage-to-bone conversion occurs in all vertebrates except for sharks, rays, and skates. These related “cartilaginous fishes” maintain a completely cartilaginous skeleton through adulthood. Cartilage is also found in branchiostomates such as tunicates, sea squirts, and **lancelets**, the closest relatives of the vertebrates. These animals have a cartilaginous rod called a notochord, which runs along the length of their back.

lancelet a type of primitive vertebrate

Cartilage is softer, more compressible, and more elastic than bone. In vertebrates whose skeletons do undergo ossification, cartilage is maintained in certain areas of the body that require this flexibility. Adults have cartilage in joints, in the nose, ears, breastbone, trachea, and larynx, and at the ends of bones.

Cartilage also helps to reduce friction between the bony elements of a joint. A lubricating liquid called synovial fluid helps the cartilage-covered



A photomicrograph of elastic cartilage. Cartilage is a fibrous and rubbery connective tissue that is found throughout the vertebrate skeletal system.

bones of the shoulder slide over each other more easily. Cartilage found in joints with a large range of motion is called smooth cartilage. In joints that experience more limited motion, cartilage plays a different role. In this kind of joint, the cartilage that holds the bones together is called elastic cartilage. Immovable joints are held together by fibrous cartilage. SEE ALSO Bone; Skeletons.

Judy P. Sheen

Cartilaginous Fishes *See Chondricthyes.*

Catadromous—Diadromous and Anadromous Fishes

Diadromous fishes describe species that spend part of their lives in freshwater and part in saltwater. There are two categories of diadromous fishes, **catadromous** and **anadromous**.

catadromous living in freshwater but moving to saltwater to spawn

anadromous moving from the ocean up a river to spawn

Catadromous fishes hatch or are born in marine habitats, but migrate to freshwater areas where they spend the majority of their lives growing and maturing. As adults they return to the sea to spawn. The word "catadromous" means "downward-running," and refers to the seaward migration of adults. The best-known group of catadromous fishes are the true eels. In these species, females spend their lives largely in freshwater, while males live primarily in the brackish water of estuarine areas. Individuals breed in the seas and die after spawning once.

Anadromous fishes are the opposite of catadromous fishes in that hatching and a juvenile period occur in freshwater. This is followed by migration to and maturation in the ocean. Adult fish then migrate back up rivers—"anadromous" means "upward-running"—in order to reproduce in freshwater habitats. The length of the initial freshwater period and of the oceanic period vary greatly by species. Similarly, the length of the migration can vary tremendously. Some species travel hundreds of kilometers between their marine habitat and their breeding grounds, while others migrate only a short distance upstream from brackish water to reach freshwater spawning grounds.

There are approximately 100 known species of anadromous fishes. Several of these are well-known and of great commercial value, including many species of salmon along with striped bass, steelhead trout, sturgeon, smelt, shad, and herring. Salmon in particular have long been admired for their lengthy, arduous migrations up rivers to their original spawning grounds, as well as for the unusual homing ability that allows them to accomplish this. Their ability to navigate back to appropriate breeding areas is particularly impressive since migration often follows a lengthy period at sea, often as long as four or five years. Chemical cues are believed to guide them in this journey.

In some anadromous species, the majority of individuals die immediately after spawning, with only a few returning downstream and surviving to spawn again. In other species, multiple migrations and spawning bouts are common.

The Rigors of Making Freshwater–Saltwater Transitions

Diadromous fishes are of particular interest to physiologists because of the great challenges posed by freshwater-saltwater transitions. In particular, freshwater and saltwater environments make strikingly different demands on water-balance systems, so these fishes must make the necessary **physiological** adjustments whenever they pass from one type of **aquatic** habitat to the other. Every diadromous species migrates at least twice, once from freshwater to saltwater, and once in the other direction. Because of their ability to tolerate a variety of salinity regimes, diadromous species are also described as **euryhaline**, meaning "broadly salty."

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

aquatic living in water

euryhaline animals that can live in a wide range of salt concentrations

Freshwater fish are in an environment in which they are hyperosmotic. That is, the concentration of salts and ions in their bodies is greater than that in the external aquatic environment. As a result, they have a tendency to lose important ions through **diffusion** across the skin and **gills**, and simultaneously to gain water from the environment. To maintain **homeostasis**, freshwater species have special adaptations for retaining ions and getting rid of excess water. First, they actively take in ions across their gills and skin, a process that requires energy. Second, to get rid of excess water they excrete nitrogenous waste products in great quantities, in the form of a highly diluted urine.

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

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

homeostasis a state of equilibrium in an animal's internal environment that maintains optimum conditions for life

In marine environments the challenges are the opposite. Saltwater species must deal with an environment in which their salt and ionic concentrations are significantly lower than that of the surrounding aquatic environment. Saltwater species tend to lose water to the ocean and to gain ions from it. To obtain and conserve water, saltwater species increase their drinking rate, and excrete smaller amounts of a highly concentrated urine. In addition, they eliminate excess ions through specialized salt-excretion cells in the gills and in the lining of the mouth.

Euryhaline species must adopt the tactics of freshwater species while in freshwater environments, and those of marine species in saltwater environments. Frequently, physiological adjustments are made while organisms are in the intermediate, brackish waters of estuaries. These include changing their drinking rate, the degree of concentration of their urine, and the direction of ion-pumping in the gills and **integument**.

integument a natural outer covering

In addition to these physiological changes, associated with osmoregulation, other changes are made by diadromous species during transitions between freshwater and saltwater habitats. In some diadromous species, external features such as coloration change. For example, in some salmon species, individuals lose their typical red coloration before migrating to sea, where they take on a more silver-colored form. They regain their freshwater coloration when they reenter the freshwater environment.

Considering both the rigors of the long migratory journey and the serious physiological challenges faced by diadromous species, it makes sense to ask why these species have evolved a complex life cycle that requires

multiple transitions between salt and freshwater environments. The likely answer is that species are able to take advantage of the benefits offered by each habitat, and that these benefits overshadow the burdens of the repeated migrations. For anadromous species such as salmon, for example, there appears to be a significantly greater safety for eggs in freshwater habitats yet the possibility for much faster growth in the ocean, where the food supply is more plentiful. The increase in growth rate that salmon exhibit once they have migrated to the ocean is dramatic.

The Benefits of Transitions

The rigors of the journey from saltwater to freshwater habitats, or vice versa, including the stresses related to physiological adjustment, is likely linked to the observation that many diadromous species are **semelparous**, that is, they reproduce in one large reproductive bout and then die. This is also known as "big-bang" reproduction. Semelparity is contrasted with the reproductive strategy of **iteroparous** species, which reproduce multiple times. Iteroparity characterizes numerous species, including humans.

semelparous animals that breed only once and then die

iteroparous animals with several or many reproductive events in their lives

Some formerly anadromous species have lost anadromy, having evolved to remain in freshwater habitats throughout the entire life cycle. For example, some species of salmon use lakes rather than oceans for the period of growth and maturation. However, they continue to migrate up rivers in order to find appropriate spawning grounds.

In other species, such as the steelhead trout, anadromy appears to be optional. Individuals that are spawned farther from the ocean have a tendency to remain in freshwater habitats during maturation, while those closer to river mouths have a tendency to retain the anadromous condition. This probably relates to differences in the costs of migration.

Perils to Diadromous Fishes

Diadromous fishes are particularly dependent on estuarine areas, the brackish areas linking freshwater rivers and saltwater environments. It is within the estuaries that diadromous species make the physiological adjustments necessary for transitioning between fresh and salt water. Unfortunately, many of these estuarine habitats are under threat. This is only one factor responsible for the dangerous declines in the **populations** of many anadromous species. Others include increasing river pollution that damages critical spawning habitats, the building of dams and other man-made barriers that make the upward migration difficult, and the overfishing of commercially important species. However, the release of young salmon into reclaimed rivers has met with some success, and in some areas special passages for migrating salmon allow individuals to get upstream to the spawning grounds. SEE ALSO Excretory and Reproductive Systems.

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

Jennifer Yeh

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Cell Division

Cell division is the basis of life itself; it is how animals grow and reproduce. When cells divide, two daughter cells are produced from one mother cell. Each new cell has exactly the same genetic material (DNA) as the cell that produced it.

Cellular division has three main functions: (1) the reproduction of an entire unicellular organism, (2) the growth and repair of tissues in multicellular animals, and (3) the formation of **gametes** (eggs and sperm) for sexual reproduction in multicellular animals. The process of **mitosis** produces identical cells for the first two functions listed above; the process of meiosis forms gametes.

gametes reproductive cells that only have one set of chromosomes

mitosis a type of cell division that results in two identical daughter cells from a single parent cell

Cellular division has two steps. First, the genome is divided up inside the nucleus by either mitosis or meiosis. Second, the **cytoplasm** (the rest of the content of the cell) is divided. The cell is actually split in two in a process called cytokinesis, in which the cellular membrane is pinched in the middle like a balloon squeezed in the center.

cytoplasm fluid in eukaryotes that surround the nucleus and organelles

Most of the life of a cell is spent growing and replicating DNA. This phase in the cell cycle is called interphase. Cells grow with materials produced from within the cell, using specialized structures called **organelles**. Before cell division takes place, the entire genome (the genetic material) has been copied, and there are now two complete copies in the cell nucleus.

organelles membrane-bound structures found within a cell

Diploid eukaryotes have two copies of DNA on two sets of chromosomes. The DNA of eukaryotic animals is packaged into chromosomes. Chromosomes come in pairs. Like pairs of shoes, they are almost the same but with slight variations. Humans have forty-six chromosomes, or twenty-three pairs. When DNA is replicated before the cell divides, each chromosome has two identical copies of DNA called sister chromatids. Sister chromatids can be compared to two left and two right shoes.

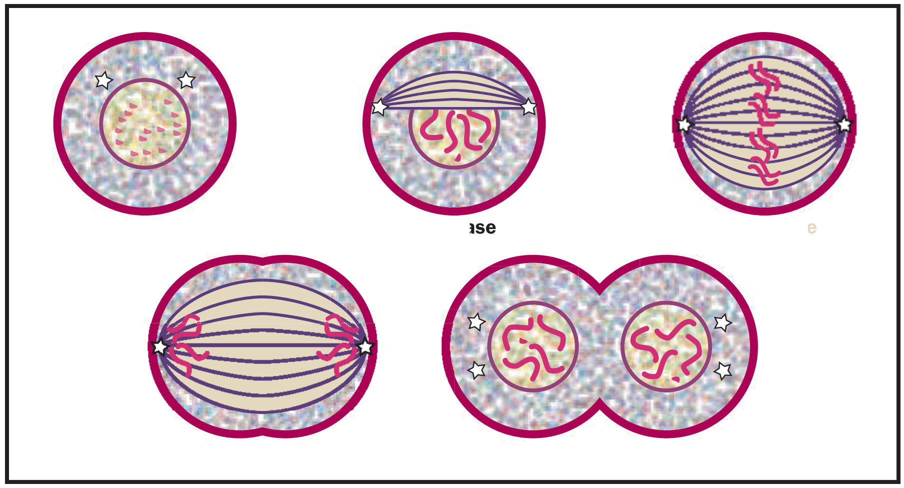
Mitosis

Mitosis is the process of cellular division that produces identical daughter cells from one mother cell. In single-cell organisms like protists, mitosis produces two whole organisms. In multicellular organisms, mitosis is the process by which the animal grows and repairs its tissues.

There are five steps in mitosis.

1. Prophase. The shape of the DNA changes. Other changes take place in the cytoplasm.
2. Prometaphase. Chromosomes start to move because microtubules are attaching to them.
3. Metaphase. Chromosomes line up in the middle of the cell, pulled there by microtubules. Sister chromatids line up on each side of the metaphase plate. This can be compared to putting one left shoe on one side of the plate and one right shoe on the other side of the plate.

The phases of mitosis.



4. Anaphase. Pairs of sister chromatids split and are pulled to opposite sides of the cell by the microtubules. This is like putting the left shoes into different sides of the cell; the same thing happens with the right shoes. At the end of anaphase, there is one complete set of chromosomes on each side of the cell and the sets are identical.
5. Telophase. DNA returns to the state it was in during interphase.

Cytokinesis then divides the rest of the cell, and two identical cells result.

Meiosis

Meiosis is the process of cellular division that produces the gametes which take part in sexual reproduction. Where mitosis produces two daughter cells from one mother cell, meiosis produces four daughter cells from one mother cell. The end products of meiosis, the gametes, contain only half the genome of a organism. This is like each cell ending up with only a single shoe; there are not pairs in these cells anymore. The two gametes fuse to produce a **zygote**. Because each gamete has half the genetic material of the mother cell, this **fusion** results in a zygote with the correct amount of genetic material.

zygote a fertilized egg

fusion coming together

There are two stages in meiosis, meiosis I and meiosis II. There are five steps in meiosis I.

- Interphase I. Chromosomes replicate, resulting in two identical sister chromatids for each chromosome.
- Prophase I. Chromosomes change shape. Homologous pairs of chromosomes, each with two sister chromatids, come together in a process called synapsis. This tetrad of chromatids is joined in several places, called chiasmata, and crossing-over occurs.
- Metaphase I. Tetrads line up on the metaphase plate, still joined.
- Anaphase I. Homologous chromosomes split apart. Sister chromatids remain together. Microtubules pull each homologue to opposite sides of the cell. This is like putting the left shoes on one side and the right shoes on the other.
- Telophase I and Cytokinesis. The cell divides. Each cell contains a pair of sister chromatids.

Meiosis II is similar to mitosis—sister chromatids split apart into new cells—and the same steps occur in the same order. Pairs of chromosomes were split in meiosis I, and sister chromatids are split in meiosis II. Meiosis II results in four separate chromosomes (two pairs of sister chromatids), each packaged separately. Crossing-over produces slight variations among all four cells. These four cells are gametes, either eggs or sperm.

Laura A. Higgins

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Cells

All living organisms are comprised of one or more cells. Most animal cells range in size between 10 and 100 micrometers and have several key elements.

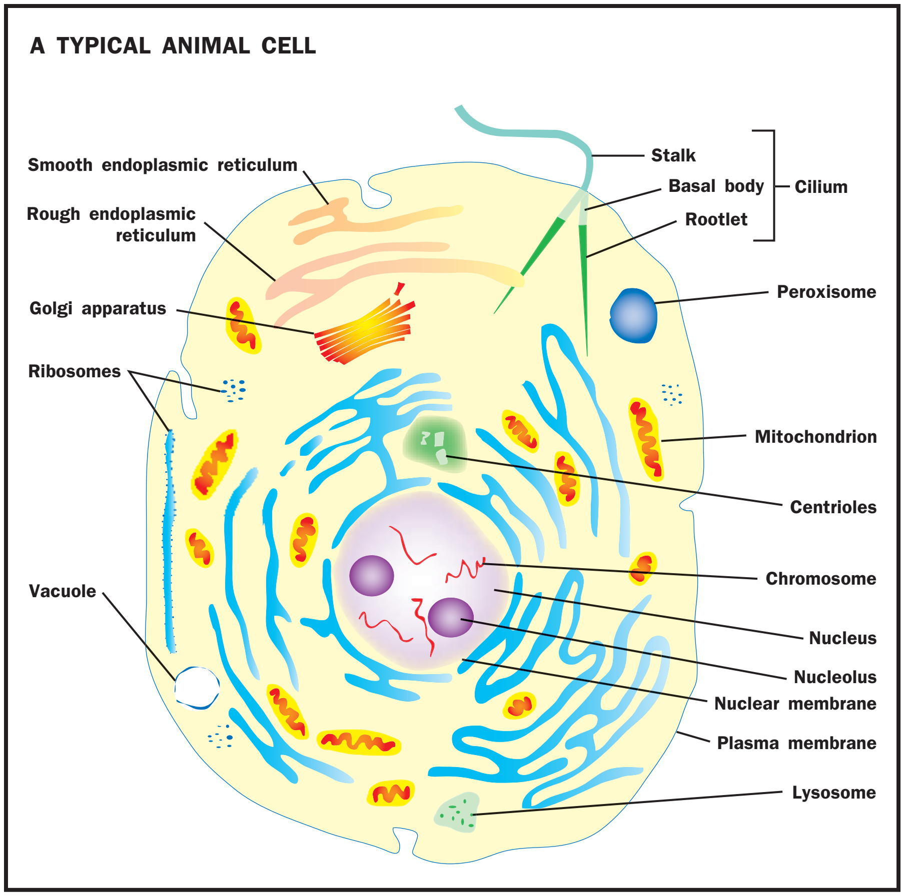
The outer layer of a cell, the cell membrane, consists of a **phospholipid** bilayer, which serves primarily as a barrier from the external environment, and integral proteins which function mainly to regulate transport. The cell membrane creates an enclosed space in which the chemical processes, or metabolism, of the cell can occur. It also serves as a gatekeeper for the cell, carefully regulating what passes in and out. For example, nutrients pass in, and metabolic waste passes out.

phospholipid molecules that make up double layer membranes; one end of the molecule attracts water while the other end repels water

The inside of an animal cell contains several **organelles**, specialized structures that perform specific functions for the cell. These organelles are suspended in a thick aqueous solution, the cytoplasm. The coordinated activity of the organelles is required for the survival of the cell. Many organelles are enclosed by membranes that generate separate compartments within the cytoplasm. One of the most important compartments is the nucleus. The nucleus contains genetic material, which acts as a blue print for the production of the proteins that perform most cellular functions. Protein synthesis is performed by ribosomes and takes place in the cytoplasm. Ribosomes attach to the endoplasmic reticulum (ER) during synthesis of those proteins that are to be exported, incorporated into the membrane, or placed into organelles. These proteins are then shipped from the ER to another compartment, the Golgi apparatus, where they are modified and then shipped to their final destinations. In recycling compartments, known as the lysosomes, old proteins and other molecules are broken down so that their components can be reused. Diverse chemical processes (e.g. the synthesis of the gas Nitric Oxide that functions as an important signal between cells) that produce toxic molecules (peroxides) as side products, take place in specialized chemical compartments of the cell which are called peroxisomes. As

organelles membrane-bound structures found within a cell

Redrawn from *New York Public Library Desk Reference*, 1998.



a result, the peroxides can be broken down safely within the peroxisomes without harming the cell.

The transport of cargo between individual compartments through the cytoplasm is the job of transport vesicles, tiny membrane-enclosed compartments that contain the cargo and transport it through the cytoplasm. Every cell produces many transport vesicles, and each type is specialized for a distinct shipping route within the cell, for a kind of cargo, or even for the storage of substances (e.g., **neurotransmitters** for communication between cells).

neurotransmitters chemical messengers that are released from one nerve cell that cross the synapse and stimulate the next nerve cell

The energy for all the chemical processes in the cell is generated in compartments called **mitochondria**, which can be considered the cell's powerhouses. Mitochondria produce ATP, the energy source of the cell, using sugars and oxygen in a process called oxidative phosphorylation.

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

The shape of cells is maintained by a cytoskeleton, or cell skeleton, made of three membrane-free organelles—microtubules, actin filaments, and intermediate filaments. Together these organelles form a network of molecular cables and struts that stabilizes the cell shape.

In contrast to plant cells, which are further stabilized by a cell wall that surrounds the outer cell membrane, animal cells are stabilized by a cytoskeleton and an extracellular matrix made mostly of **glycoproteins**. However, because they are less rigid, animal cells can change their shape more easily and even use these shape changes to move. Animal cells such as the

glycoproteins organic molecules that contain a carbohydrate and a protein infection-fighting white blood cells can be sophisticated "crawlers." In the absence of a rigid cell wall, they assemble and disassemble parts of their cytoskeleton in such a way that specific shape changes leading to cell movement will occur. Microfilaments are also responsible for the movement of specific organelles within the cell, and microfilaments and microtubules together are essential for cell division. While microtubules ensure the distribution of duplicated chromosomes to the two daughter cells, the microfilaments will finish the separation of the original cell by pinching in the outer cell membrane.

Whereas in single-celled organisms all life functions are performed by a single cell, in multicellular organisms, such as animals, division of labor and specialization among cells occurs. For example, humans have about 200 different cell types that differ in structure and in function. In all but the simplest animals, the sponges, specialized cells that have a similar structure and function are arranged together into tissues. Although there are many different types of animal cells, scientists group them all into only four general tissue types—epithelial tissue, muscle tissue, nervous tissue, and **connective tissue**. The cells in a tissue may be held together by the extracellular matrix that makes the cells sticky or ties them together.

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

In all animals except sponges and jellyfishes, different tissue types may form a functioning unit called an organ. Organs may also be part of an organ system, such as the digestive system and reproductive system, where several organs function together. Each organ system has a different function, but just like the organelles within an individual cell, the function of each organ system must be regulated and coordinated to ensure the survival of the whole animal. SEE ALSO Cell Division; Homeostasis.

Kathrin F. Stanger-Hall

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anterior referring to the head end of an organism

posterior behind or the back

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

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

Cephalization

Cephalization is the process in animals by which nervous and sensory tissues become concentrated in the "head." The evolution of a head allows scientists to distinguish between the head end, or **anterior** end of an animal's body, and the opposite end, the **posterior**. Although cephalization is associated primarily with **bilaterally symmetrical** species, even some of the more primitive, **radially symmetrical** animals show some degree of cephalization.

Cephalization evolved several times within the animal kingdom, suggesting that it offers certain inherent advantages. In particular, with the evolution of cephalization, the anterior end of the animal became most likely to first encounter food, predators, and other important features of the external environment. Because brain and sense organs are also concentrated in the anterior end, the organism is well prepared to deal with these features.

Cephalization in the Animal Kingdom

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

Even hydras, which are primitive, radially symmetrical **cnidarians**, show some degree of cephalization. They have a "head" where their mouth, photoreceptive cells, and a concentration of neural cells are located.

Flatworms (phylum *Platyhelminthes*) are the most primitive animals with bilateral symmetry. They also have a fairly advanced degree of cephalization, with sense organs (photosensory and chemosensory cells) and a brain concentrated at the anterior end. Consequently, scientists believe that cephalization characterized all bilaterally symmetrical animals from their origins. However, flatworms differ from more advanced animals in that their mouths are in the center of their bodies, not at the anterior end.

In arthropods, cephalization progressed with the incorporation of more and more trunk segments into the head region. Scientists believe this was advantageous because it allowed for the evolution of more effective mouthparts for capturing and processing food.

Cephalization in vertebrates, the group that includes mammals, birds, and fishes, has been studied extensively. The heads of vertebrates are complex structures with many features not found in close relatives such as the cephalochordates. The cephalochordate *Branchiostoma* (formerly called *Amphioxus*), which is the closest relative of vertebrates, is a burrowing marine creature which lacks most of the head structures that are so distinct in vertebrates, such as distinct sense organs; a large, multilobed brain; teeth; and a tongue.

There was a persistent debate during the twentieth century as to whether the vertebrate head is "old" or "new." Scientists who champion the idea of an "old" head suggest that the vertebrate head resulted from the evolution of important modifications to a previously existing head. The idea of a "new" vertebrate head was proposed originally by American vertebrate morphologists Carl Gans and Glenn Northcutt in 1983. They suggested that the vertebrate head is a new structure, which has no corresponding structure in close relatives such as *Branchiostoma*.

Evidence to support a "new" vertebrate head comes from the observation that most important features of the head are derived from neural crest cells, embryonic cells found only in vertebrates. The neural crest cells are of **ectodermal** origin—rather than mesodermal or endodermal—and arise during the process of neurulation, the time at which the dorsal hollow nerve cord forms.

ectodermal relating to the outermost of the three germ layers in animal embryos

Neural crest cells are exceptional in that they are highly mobile, migrating in streams throughout the head region and the rest of the body, and because they give rise to an unusual diversity of features. The neural crest cells are responsible for forming the bones of the face and jaws, the structures of the tongue and larynx, the teeth, and portions of the eye. Experi-

Cephalopods—such as this Sepioidea Squid, native to waters near Bermuda—exhibit an advanced degree of cepahalized development with regard to sense organs and brain location.

ments in which the neural crest was removed from developing animals confirmed that these critical head structures failed to develop without it.

Scientists hypothesize that increased cephalization in vertebrates, including the evolution of many of their novel head features, is related to adaptations for predation. Sensory structures—the jaw and large brain—are all requirements for a successful existence as a predator.

Losses of Cephalization

Cephalization has been lost in some groups. One example comes from the echinoderms, the phylum that includes the starfishes and sea urchins. These species have lost bilateral symmetry and returned to a radially symmetrical body plan. However, only adult starfishes and sea urchins are radially symmetrical. The larval stage remains bilaterally symmetrical and is characterized by cephalization. Other echinoderms, the sea cucumbers, have regained bilateral symmetry in the adult. Thus the phylum has been characterized by multiple instances of the acquisition and loss of bilateral symmetry and cephalization.

Mollusks represent another group in which cephalization has been lost and regained. For example, **bivalves** are not particularly cephalized (although some scientists have argued that they are "all head"). However, as with the echinoderms, certain mollusks regained cephalization. In particular, the appropriately named cephalopods (the group that includes the squid and octopus) are characterized by an advanced degree of cephalization. Their sense organs, including well-developed eyes and a brain, are concentrated in a distinct head region. Interestingly, as with vertebrates, the evolution of an advanced degree of cephalization in cephalopods was associated with the evolution of a predatory lifestyle.

bivalves mollusks that have two shells

The Origin of the Head

Although cephalization appears to have evolved multiple times, in the last ten years molecular biological work implies that the distinction between head and the rest of the body may actually be quite ancient. In particular, certain genes expressed only in the head region appear to determine the boundary between head and trunk. These genes are present in diverse animal phyla, including arthropods, chordates, and annelids (other groups have yet to be studied). This broad distribution of the multiple genes indicate that they may have been present in the common ancestor of most animals. Studies of the hydra have shown that it too possesses some of these same genes, suggesting that the distinction between head and trunk is rather ancient in the animal kingdom because the hydra is a member of a primitive lineage (the cnidarians). SEE ALSO Body Plan.

Jennifer Yeh

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Cephalochordata

notochord a rod of cartilage that runs down the back of chordates

lancelet a type of primitive vertebrate

brackish a mix of salt water and fresh water

The cephalochordates are the closest living relatives of the vertebrates. The group derives its name from the **notochord** that extends far forward into the head (farther than the brain, in contrast to vertebrates). The most famous representative of the group is *Branchiostoma lanceolatus* (also known as *Amphioxus*, or **lancelet**). There are about twenty-five living species of cephalochordates. All adults are small, fishlike animals that are rarely longer than 5 centimeters (2 inches). Cephalochordates live in shallow marine or **brackish** water all over the world. They can actively swim around, but most of the time are sedentary, buried in sand.

Swimming and burying are accomplished through an interaction between the notochord (stabilizing element and anchor point for muscles) and large blocks of muscle segments along the body wall. Unlike the vertebral column of vertebrates, the notochord is an elastic, flexible rod. It prevents the body from shortening when the muscles contract, causing it to bend sideways instead. This creates an undulating (wavy) body movement much like that of fishes. However, poor fin development makes cephalochordates relatively inept swimmers, and as a consequence they spend most of their time (except when they disperse and reproduce) buried in sand with only their front end exposed.

pharyngeal having to do with the tube that connects the stomach and the esophagus

When they are buried, their head sticks out to filter out food particles from the water. In this process, water is driven through the mouth opening into the mouth cavity and back out into the environment through **pharyngeal** gill slits. In the process, food particles suspended in the water are caught in a sheet of mucus that covers the inside lining of the pharyngeal slits. Cephalochordates may have up to 200 pharyngeal gill slits, making their filter feeding very efficient. The slits are separated from one another by so-called gill bars, which are supported by cartilage rods. During the evolution of vertebrates (about 500 million years ago) from a cephalochordate-like ancestor, these cartilage rods eventually gave rise to the jawbones of vertebrates.

Cephalochordates have a closed circulatory system (the blood is enclosed in blood vessels) but lack a central pump (heart). Instead, the blood is propelled by pulsation (rhythmic contraction and relaxation) of several blood vessels. The blood contains no pigments or cells and is thought to function largely in nutrient distribution rather than in gas exchange and transport. The central nervous system of the cephalochordates is very simple. A dorsal nerve cord extends through the length of the body, giving rise to segmentally arranged nerves. No brain is detectable. The skin is rich in sensory nerve endings that probably help produce a sense of touch and are important for burrowing. A number of cephalochordates have some photosensors near the front and back ends of their body, but in general (unlike vertebrates) they lack any eyes or organs to sense gravity.

Cephalochordates reproduce by releasing their eggs and sperm into the water, where they are fertilized externally. The fertilized eggs develop into free-swimming larvae that drift in the water for up to 200 days, feeding on plankton and other suspended matter, before settling down as adults. SEE ALSO Phylogenetic Relationships of Major Groups.

Kathrin F. Stanger-Hall

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Cestoda

The class Cestoda consists of long, flat, ribbonlike worms that are commonly called tapeworms. Tapeworms are **obligatory parasites**, ones that cannot survive independent of a host, that live in the intestines of vertebrate hosts. They form an extremely varied group, and nearly every vertebrate species is associated with a different parasitic cestode. Most cestodes make use of one or more intermediate hosts to bring them into the body of the ultimate host. Some cestodes can achieve impressive lengths—worms of up to 15 meters (50 feet) have been observed.

obligatory parasites an animal that can only exist as a parasite

Characteristics of Cestodes

All tapeworms share a body plan. At the front end is a head region called the scolex. The scolex maintains a hold on the host's digestive tract and has many suckers and hooks for this purpose. The scolex also contains the tapeworm's sense organs, which consist primarily of cells sensitive to touch and chemical stimuli, as well as the modest concentration of nervous tissue that makes up the tapeworm brain.

The scolex is followed by a short neck region and a trunk, which is divided into a series of segments known as proglottids. New proglottids are produced in the neck region. As these form, older proglottids are pushed back toward the rear of the animal. The proglottids house the reproductive organs, which mature gradually as proglottids move to the back.

The scolix, or head region, of an adult pork tapeworm. The scolix is used to hold onto the host's digestive tract; it also contains the tapeworm's sense organs.

Tapeworms are **hermaphroditic**, so that each proglottid includes both male and female **gonads** and generates both sperm and eggs. A tapeworm can reproduce sexually, either through self-fertilization or cross-fertilization with another tapeworm, or asexually, by breaking off proglottid segments at the end of the trunk. These reproductive traits are admirably adapted to reproduction in an environment (in the body of a host) in which worms are not guaranteed to encounter individuals of the same species.

Proglottids and fertilized eggs exit the host's digestive tract along with the host's excrement. In most tapeworm species, eggs or proglottids are first ingested, or taken in, by an intermediate host, often an arthropod or a different vertebrate species. The cestode may develop into a larval form or may become temporarily dormant within the intermediate host. The ultimate host becomes infested with the cestode when it consumes an infested intermediate host.

Because of the cestodes' parasitic lifestyle, certain organ systems are unnecessary. The most obvious of these is the digestive tract, which is absent from the group. Because cestodes live in an environment that is not only rich in nutrients, but one in which the nutrients are already well processed, further digestion is unnecessary. Instead, food absorption occurs over the entire surface of the cestode body, in an ectodermal, or skin, layer known as the integument. The integument is covered with tiny projections called mitotrichia, which increase the surface area available for absorption.

hermaphroditic having both male and female sex organs

gonads the male and female sex organs that produce sex cells

Subclasses of Cestodes

Cestodes are divided into two subclasses, Cestodaria and Eucestoda. Cestodaria is a small subclass of relatively small tapeworms that are parasites to elasmobranch fishes (sharks, rays, and chimeras). The trunks of cestodarians are not segmented into proglottids. The rear of the body includes a small sucker. Eucestoda is a much more diverse group, and includes all other cestodes. Eucestodes are characterized by the presence of proglottids. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Jennifer Yeh

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Chitin

Chitin is a major constituent of the exoskeleton, or external skeleton, of many arthropods such as insects, spiders, and crustaceans. Exoskeletons made of this durable and firm compound support and protect the delicate soft tissues of these animals, which lack an internal skeleton. Chitin is a **polysaccharide**, a type of carbohydrate that has a basic structure of a repeating chain of sugar molecules. Chitin is analogous in structure to cellu-

polysaccharide a class of carbohydrates that break down into two or more single sugars

The exoskeleton of the Cayman Islands stone crab is made up, in part, of the polysaccharide chitin.

lose, the compound that provides structural support to plant tissues. In addition to being found in arthropod exoskeletons, chitin is also found in the cell walls of some species of fungi.

Chitin does not work alone in forming exoskeletons. It is associated with a number of proteins, including an elastic, rubberlike substance called resilin. The identity and nature of these proteins determines whether the exoskeleton will be rigid, like a beetle's shell, or soft and flexible like the joints of a crab leg. Chitin also associates with nonprotein compounds, such as the calcium carbonate that is part of the shells of crustaceans such as crabs, lobsters, and shrimp.

Animals that wear their skeletons on the outside are relatively inflexible because of their armor rigidity. Arthropods can bend their limbs or the segments of their body only at the joints, where the exoskeleton is thinner. Therefore, it is important that the composition and character of the exoskeleton complement the anatomy it covers and the overall ecology of the organism.

Chitin confers a number of protective benefits to animals with exoskeletons. As well as defining the basic shape of the animal, the tough shell that encases arthropods protects the wearer from **dessication**, or dehydration. This particular function is essential to terrestrial arthropods, which may perish if too much water is lost from their blood and body tissues. Shells also provide effective protection against some predators.

dessication drying out

Chitinous exoskeletons must be molted, or shed, as the animal grows because the rigid shell does not expand with the rest of the body. After the old shell is cast off, a new, larger exoskeleton is secreted by glands in the epidermis. Newly molted individuals are particularly vulnerable to attack because they have little protection while they wait for their new shells to harden.

chitinous made of a complex carbohydrate called chitin

Exoskeletons would be impractical for larger animals because chitin is not strong enough to protect and support them. Land-dwelling invertebrates, who do not benefit from the buoyant support of water, are limited in size because as an exoskeleton gets larger, it becomes thicker and heavier. These animals would not be able to move very well under the weight of this protective armor. SEE ALSO Bone; Keratin.

Judy P. Sheen

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Chondrichthyes

The class Chondrichthyes consists of the cartilaginous fishes, including sharks, batoids (rays, skates, guitarfish, and sawfishes), and chimaeras, or ratfishes. A diverse group comprising more than 700 species, Chondrichthyans are found throughout the world's oceans and in some freshwater environments. The group as a whole is characterized not by mineralized bone but by a skeleton of soft, flexible **cartilage** lined with hard tissue. Chondrichthyans lack the air-filled swim bladder found in most bony fish, and therefore must swim continuously to stay afloat. Buoyancy is assisted by light oils in the liver, which can comprise up to 25 percent of a shark's total body weight.

cartilage a flexible connective tissue

Chondrichthyan males have a pelvic clasper, a specialized organ used in mating. Unlike most bony fishes, all chondrichthyans have internal fertilization. Reproduction can be **oviparous** (laying eggs, notably the "mermaid's purses" found on beaches), **viviparous** (live-bearing), or **ovoviviparous** (eggs carried within the mother).

oviparous having offspring that hatch from eggs external to the body

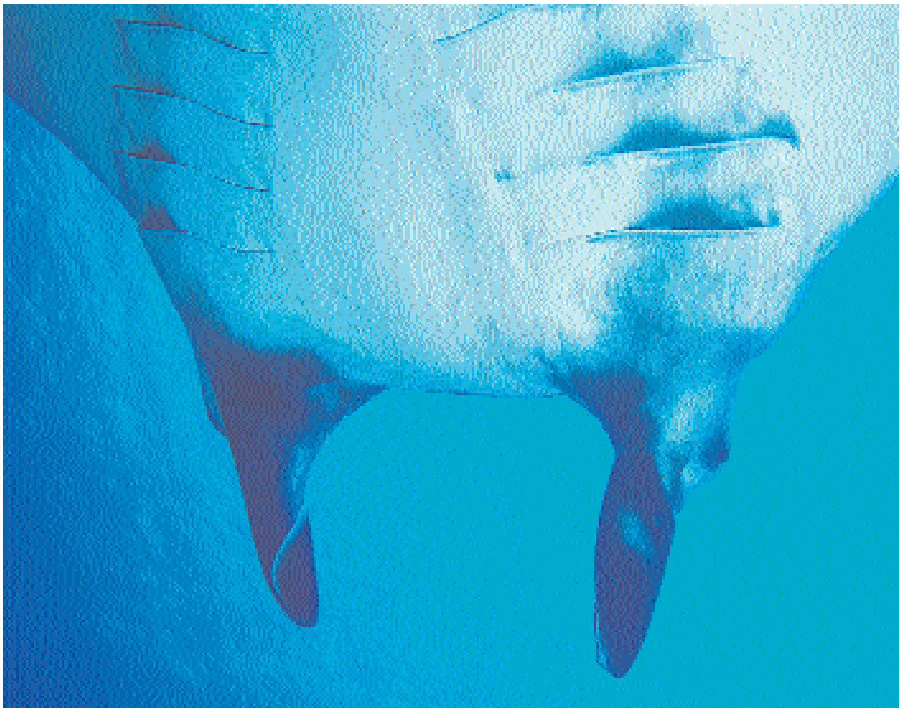
viviparous producing living young (instead of eggs) that were nourished by a placenta between the mother and offspring

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

placoid scales scales composed of three layers and a pulp cavity

The physiology of Chondrichthyan is of interest to cancer researchers because the cartilage of chondrichthyans contains substances known to inhibit the growth of tumors, and cancer is extremely rare in sharks. The group is characterized by **placoid scales** (also called dermal denticles, or skin teeth), with a structure similar to teeth consisting of an outer enamel layer, dentine, and an inner pulp cavity. As the animal grows, the skin surface is expanded by the addition of more scales rather than by the growth of individual scales. The teeth themselves are simply modified placoid scales; sharks have several rows of teeth, with replacement teeth always developing behind the frontmost rows of functional teeth. In some species, an individual can shed more than 30,000 teeth in its lifetime.

These fishes are often thought of as primitive compared to bony fishes and land-based vertebrates. Many chondrichthyans, however, have evolved sophisticated adaptations that have made them successful predators over a wide range of habitats. The senses of active predators, including many sharks,



The Atlantic manta ray, a member of the Chondrichthyes batoid subgroup. Manta rays are the largest rays, attaining widths of about 7 meters (23 feet).

are especially well developed. A keen sense of hearing allows sharks to locate prey from as far away as 250 meters (800 feet). They are particularly sensitive to low-frequency vibrations such as those emitted by injured animals. Sound is detected through the ears and through the **lateral line**, a series of fluid-filled canals along the head and sides of the body that contain sensory cells sensitive to vibrations. As in many **nocturnal** mammals, the inside of a shark's eye is covered with a **tapetum**, a membrane that reflects light back into the eye, making it easier to see in dim light. Unlike most fishes, sharks can reduce and expand their pupils. In some species, the eyes are protected during feeding by the nictitating membrane, a structure similar to an eyelid. The Elasmobranchi group has external nostrils on the lower side of the body; because of them, sharks can detect tiny concentrations of substances such as blood, which allows them to scent prey from distances of several hundred feet. Finally, sharks can detect electrical signals via the ampullae of Lorenzini, which are specialized organs distributed over a shark's head that detect changes in electrical currents. Sharks use these to sense the electrical fields emitted by the heart and muscles of their prey.

lateral line a row of pressure sensitive sensory cells in a line on both sides of a fish

nocturnal active at night

tapetum a reflective layer in the eye of nocturnal animals

The class Chondrichthyes includes two major groups: the Elasmobranchi (sharks, skates, and rays) and the Holocephali (chimaeras or ratfishes). Elasmobranchs are further divided into selachians (sharks) and batoids (rays and their relatives). The earliest evidence of Chondrichthyes in the fossil record is from the Devonian, the so-called Age of Fishes, from 350 to 400 million years ago.

Selachians (Sharks)

There are approximately 350 species of sharks. They are characterized by a heterocercal tail (the upper half being longer than the lower half), five to seven gill slits for respiration, and a rounded body tapered at both ends.

Sharks are among the most misunderstood of all creatures. Popular culture has exaggerated beyond reason the danger posed by sharks to humans. The California coastline, with a high density of both human and great white shark populations, averages only one shark-related fatality every eight years. There is little evidence that sharks prey on humans for food. A disproportionate number of shark attacks occur near seal and sea lion rookeries, and surfers, whose paddling resembles the behavior of a seal on the surface, are more likely to be attacked than scuba divers. These factors indicate that sharks may be mistaking humans for seals or other large marine prey. Spearfishers carrying wounded fish are also at greater risk of shark attack; the vibrations of a thrashing fish may attract sharks, so one's catch should always be immobilized. Over half of total shark attacks appear to be misdirected territorial or courtship displays, with a characteristic motion preceding the attack: the shark shakes its head from side to side and swims back and forth erratically, with its head pointed up. Most sharks that attack humans are mackerel sharks, including the great white sharks (*Lamnidae*) and requiem sharks (*Carcharhinidae*); sharks in these families feed on large fish or marine mammals. Requiem sharks include the tiger shark and the bull shark, which feed primarily on other sharks. Hammerhead sharks (*Sphyrnidae*) specialize in attacking stingrays.

CHIMAERAS, OR RATFISHES

Chimaeras—also knows as ratfishes—possess unusually large heads with deep, well-developed eyes. They also have a mouth that resembles a rabbit's inside which rest grinding, plate-like teeth.

The plankton-feeding whale sharks (*Rhincodontidae*) are the world's largest fishes, with lengths of up to 18 meters (60 feet). Other huge plankton feeders include the aptly named megamouths (*Megachasmidae*) and basking sharks (*Cetorhinidae*). These sharks swim with their mouths open, straining plankton through modified structures associated with the gills.

While the larger sharks are better known to the general public, smaller species are far more diverse and abundant. The *Squalidae* include the spiny dogfish, which feeds mainly on invertebrates; it is a favorite candidate for inclusion in a fish and chips dinner and for classroom dissection. Another member of the *Squalidae*, the diminutive (four-inch) cookie-cutter shark, apparently uses the light-producing organs arrayed around its body to mimic a school of small fish. This attracts large fish, which the cookie-cutter shark then attacks, cutting out a round portion of flesh with specially modified teeth. Saw sharks (Pristiophoridae) use a long snout lined with sharp teeth to slash their way through schools of fish; they then return to feed on wounded fish and any detached pieces they may find. The angel shark (*Squatinidae*) resembles a ray but can be distinguished by gill openings on the side of the head rather than on its bottom and by the fact that the pectoral fins are not attached to the side of the head as they are in batoids.

Batoids (Rays, Skates, Guitarfishes, and Sawfishes)

The 470 species of this diverse group of fishes have in common a flattened body with expanded pectoral fins fused to the head (the "wings" in rays). Batoids are distributed throughout the world's oceans and in some tropical freshwater environments.

Sawfish (*Pristidiformes*) can exceed 7 meters (23 feet) in length; they have a long snout lined with sawlike teeth and capture prey like the saw sharks described above. Guitarfish or shovelnose rays (*Rhinobatiformes*) are characterized by a long, thick body and relatively narrow pectoral fins; they feed mainly on invertebrates on the sandy bottom. Skates (*Rajiformes*) are found mostly in deep water; they, too, feed on invertebrates and are distinguished by a series of thorns on the tail.

The order Myliobatidiformes contains several types of ray. The large eagle rays (*Myliobatidae*) have strong, muscular pectoral fins for rapid swimming. Manta rays (*Mobulidae*) are the largest rays, attaining widths of about 7 meters (23 feet); like the largest sharks, they bear specialized mouthparts for feeding on plankton. Stingrays (*Dasyatididae*) have a tail ending in a flexible, whiplike section that is equipped with one or more poisonous spines. Persons wading on a sandy bottom, particularly in calm water, often run the risk of stepping on a stingray and being stung as a result; one should always shuffle one's feet while walking on a sandy substrate. These animals almost never sting unless provoked; attack is often preceded by a warning stance where the tail is brought forward over the body.

This bottom dweller ratfish surveys pieces of the Titanic wreckage, most likely looking for its next meal of mollusks.

Torpedo rays (*Torpediniformes*), also known as electric rays or numbfishes, have evolved modified muscles that function as electric organs. The largest electric rays can produce up to 200 volts of electricity in a single discharge. Several species are found exclusively in fresh water.

Holocephalans (Chimaeras, or Ratfishes)

The approximately twenty-five species of ratfishes are mostly bottom dwellers in some of the deeper marine habitats. They feed primarily on mollusks and other invertebrates in the substrate, crushing hard shells with their flat teeth. Ratfishes are characterized by a large head and eyes and by a long, slender tail. They have an **operculum**, a hard, bony layer of tissue covering the gills, found in many bony fishes but absent in all other chondrichthyans. SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

operculum a flap covering an opening

Gil G. Rosenthal

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Chordata

Human beings are chordates—of the phylum chordata—and so are all other vertebrates, or animals with a spinal column. In addition, there are two invertebrate groups of chordates: the urochordates and the cephalochordates.

The Urochordata (e.g., tunicates) and Cephalochordata (e.g., lancelets) were the earliest chordates to evolve, and they provide a link between invertebrate and vertebrate animals. However, as different as these organisms are from each other and from vertebrate chordates, they all share the following characteristics that identify them as chordates (and distinguish them from all other invertebrate animals): a notochord, a dorsal hollow nerve cord, and pharyngeal gill slits. Many adult vertebrates have no notochord or pharyngeal gill slits, but these structures can nevertheless be found in their embryos.

The notochord is a long, elastic rod that provides structural support to the chordate body. In cephalochordates it prevents the body from shortening when muscle fibers in the body wall draw together, causing a bending from side to side and propulsion of the animal. In most vertebrates (except some fishes), bony vertebrae develop around the nerve cord and the notochord, and the vertebral structures largely replace the notochord in most adult vertebrates. However, some adult vertebrates may retain remnants of the notochord (e.g., the gelatinous disks between the vertebrae of humans). The dorsal hollow nerve cord is a key element of the chordate nervous system and is present in all chordates. In vertebrate embryos it develops into the **spinal cord** and the brain.

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

The pharyngeal pouches with gill slits originally evolved as filter-feeding devices and can still be found as such in invertebrate chordates. During some point in their development all chordates still exhibit them. However, among the vertebrates only fish retain pharyngeal gill slits as adults. The cartilage-based rods that support the gill bars (the solid areas between the gill slits) in invertebrate chordates gave rise to the vertebrate jaw during vertebrate evolution, completely changing the feeding method in this group of animals. Subsequently, some of the bones in the vertebrate jaw evolved into middle-ear bones in amphibians, reptiles, birds, and mammals; these bones assisted in the transmission of sound and hearing when early vertebrates moved from life in the water onto land.

The first chordates appear as fossils in rocks from the Cambrian period. These rocks are approximately 570 million years old.

Vertebrates differ greatly from other chordates in size and activity level, and the evolution of their distinctive characteristics is largely correlated with this difference. Vertebrates actively move around looking for food. This led to the concentration of sense organs at the front end of the body and an accumulation of nerve cells (i.e., a brain) to process all the sensory information. The need for more efficient movement led to the evolution of a stronger support system (vertebral column), a bony skeleton, and four limbs to support the body on land.

Today the vertebrates, with nearly 43,000 living species, are the most diverse group of all chordates. All vertebrate species can be grouped into seven different classes: Agnatha (jawless fishes), Chondrichthyes (cartilaginous fishes), Osteichthyes (bony fishes), Amphibia (amphibians), Reptilia (reptiles), Aves (birds), and Mammalia (mammals). SEE ALSO PHYLOGENETIC RELATIONSHIPS OF MAJOR GROUPS.

Kathrin F. Stanger-Hall

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Circadian Rhythm

The circadian rhythm describes the internal biological clock that controls an organism's daily activity cycles. It is well-known that in many species, activity does in fact follow daily patterns. This applies to activities such as feeding or sleeping, as well as to physiological attributes such as metabolic rate, body temperature, blood pressure, and **hormone** levels. Most animal and plant species have daily rhythms and even fairly simple creatures like bacteria have been known to have natural daily cycles.

hormone a chemical signal secreted by glands that travel through the bloodstream to regulate the body's activities

Experiments in which organisms are placed in constantly light or constantly dark environments frequently indicate that daily periodicity in activity patterns persists even when the normal day-night cues from sunlight are removed. These circadian rhythms are important in allowing for the timing of important daily activities.

Circadian Cycles

Circadian rhythms typically describe a twenty-four-hour cycle that corresponds to the length of the day on Earth. However, for almost all species, the "natural" cycle is either a little shorter or a little longer than twenty-four hours. This explains the origin of the term "circadian" rhythm: *circa* means "about" and *diem* refers to "day." Thus, circadian means "about a day."

Changing light cues from the external environment allow organisms to adjust their natural body clocks and conform to a twenty-four-hour day. Research on circadian rhythms in humans has shown that the human body naturally drifts toward a twenty-five-hour cycle in constant-light conditions.

The ways in which circadian rhythms are controlled vary among biological organisms. In many vertebrate species, circadian rhythms are controlled by the hormone melatonin. Melatonin production follows a daily cycle, high during the night hours and low during daylight hours. (Because increased levels of melatonin production cause sleepiness, it is sometimes used as a sleeping aid.) Melatonin is produced by endocrine cells in the pineal gland, which is located in the central part of the brain. Ultimately, melatonin cycling responds to light cues from the environment.

In some species, such as certain fishes and lizards, a minute hole in the otherwise bony skull allows light to pass directly to the pineal gland. In this way, the pineal gland receives direct information from the external environment on day-night cycles. However, direct exposure of light to the pineal gland is not necessary. In birds, photoreceptors in the eyes as well as in the brain are responsible for transmitting signals to the part of the brain that controls circadian rhythms.

In mammals, the eyes alone appear to be responsible for photoreception related to circadian cycles. This involves a special pigment (a light-absorbing molecule) called crytochrome that is present in mammalian eyes. Crytochrome is distinct from the pigments that are responsible for vision, and is also found in a different part of the retina. In certain cases of blindness, the circadian rhythm is not disrupted because the parts of the retina that contain crytochrome are intact.

Patterns of long- and short-term hibernation—exhibited here by a nesting dormouse—are often the product of circadian rhythm, an internal "biological clock" that controls many organisms' activity cycles.

Problems Linked to Circadian Rhythm

Circadian rhythms impact everyday human life in many ways.

Jet lag. Jet lag, which can be the result of travel across several time zones, is caused by discrepancies between an individual's internal clock and signals provided by the external environment. The body generally adjusts to jet lag over the course of a few days as it is exposed to daylight patterns in the new time zone. Working the night shift can also be problematic for humans, because humans are naturally **diurnal**, that is, active during the day and asleep at night. Data indicate that the majority of industrial accidents occur at night, when the body is programmed to slow down in preparation for sleep.

diurnal active in the daytime

Seasonal affective disorder (SAD). Seasonal affective disorder (SAD), which can result in extreme depression during the winter months, may also be related to the operation of circadian clocks. SAD strikes when the days are short and light is scarce. SAD is particularly common at high latitudes, where the days are particularly short during the winter. Short light cycles are likely to disrupt the circadian clock, although the link to depression has not been demonstrated. Regular exposure to artificial bright lights is often effective in treating SAD.

Sleep disorders. Certain sleep disorders, not surprisingly, are related to problems with circadian rhythms. Older people, for example, produce less melatonin. This may be linked to the sleeping patterns associated with age, such as insomnia, early rising, and sleepiness during the day. Delayed sleep phase syndrome (DSPS), which has also been linked to old age, is a more serious problem that causes people to want to sleep from early morning to noon, instead of during more typical night hours.

Circadian rhythms are only one example of the broader category of biological rhythms. Biological rhythms range widely in duration, with circadian rhythms being among the shortest. Other biological activities follow longer cycles, such as lunar cycles, or even periods of several months or a year. The menstrual cycle and seasonal mating activity are examples of processes that occur cyclicly, but over a longer time period. SEE ALSO Diurnal; Nocturnal.

Jennifer Yeh

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Circulatory System

Every living organism on Earth, from amoebas to redwoods to whales, has a circulatory system—a means of gathering and transporting nutrients and collecting and removing waste products.

Plants have an elegant system of strawlike tubes called phloem and xylem, which stretch from the roots to the topmost leaves. Stomata, tiny evaporative holes in the leaves, create suction that steadily draws water up the xylem from the roots, allowing plants hundreds of feet tall to circulate nutrients without a pump.

All cells of the simplest animals, such as single-celled amoebas and multicellular flatworms, are close to the surface. In these cells, nutrients wash through the cell fluid, and wastes pass out through a porous outer membrane between the cell and its environment. The cells of larger animals are buried many layers deep, so these animals require a system that connects each cell to the outer world. This system, which consists of the fluid that carries nutrients through vessels that reach every part of the body and the mechanism that powers the flow of nutrients, is called the circulatory system.

The simplest form of circulatory system is an open circulatory system. In an open circulatory system, blood flows through a network of open tubes and hollow spaces, and the movement of the animal itself keeps the blood flowing. In more complex systems, blood is pumped through the body by contractions of the blood vessels. Invertebrates, such as insects and other **arthropods**, have a central blood vessel that runs down the length of the back. A series of bulbous pumping centers slowly squeeze the blood through a maze of hollow spaces around the body past all the organs.

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

Vertebrates, including amphibians, reptiles, birds, and mammals, have increasingly complex, closed circulatory systems. Closed circulatory systems consist of an intricate network of vessels filled with blood that delivers nutrients, regulates internal temperature, and takes away waste products. The system is powered by the heart, a muscular pump that never stops working, which continually circulates the blood through the body.

A radiograph of a normal coronary artery. The elastic walls of the arteries stretch open to allow the blood to flow in, then squeeze back together to force it along.

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

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

antibodies proteins in the plasma produced by B cells and plasma cells in reaction to foreign substances or antigens

In all vertebrates, the heart is made of involuntary muscle tissue, but the structure is very different in each group. Fish have a two-chambered, single-pump heart. Amphibians have a three-chambered heart that also acts as a single pump. Birds and mammals have a more sophisticated four-chambered, double-pump heart design. One chamber sends blood to the **lungs** to be purified and reoxygenated, the other sends the enriched blood out into the body. Interestingly, the human embryo goes through every stage of circulatory development, from a passive single-celled heart to a two-, three-, and four-chambered heart.

In adult humans, the circulatory system consists of blood, the heart, and a network of vessels through which the blood travels. Blood is plasma (a watery liquid) that contains billions of molecules of sugars, proteins, **hormones**, **antibodies**, and gases. The heart is a strong, muscular, double pump that pushes the blood continuously and automatically around the body through roughly 100,000 kilometers (62,000 miles) of arteries, veins, and capillaries. It takes the blood about one minute to complete a circuit around the body, and this happens about 1,000 times a day.

The human circulatory system has two loops. The shorter pulmonary circulation goes from the lower-right chamber of the heart (the ventricle) through the pulmonary artery to the lungs and back to the upper-left chamber (the atrium) through the pulmonary vein. From there, the newly oxygenated blood descends into the left ventricle through a one-way valve and is pumped into the longer systemic circulation through the main artery of the body, the aorta. The spent blood travels back to the right atrium in two main veins. The superior vena cava drains the upper body, the head, neck, and arms. The inferior vena cava handles the lower body. From the right atrium, the blood flows through the relaxed one-way valve into the right ventricle. Then another pulse of the powerful heart muscle closes the valve and spurts the blood into the pulmonary artery, beginning the cycle again. The sound known as the heart "beat" is the sound of the valves between the atria and ventricles and between the ventricles and arteries as they snap shut to keep the blood from flowing backward.

A healthy, relaxed, adult heart beats about seventy times a minute, pumping blood under high pressure into the thick-walled arteries. The elastic walls of the arteries stretch open to allow the blood to flow in, then squeeze back together to force it along. Arteries branch into narrower and more muscular arterioles. Arterioles branch into finer and finer capillaries, thin-walled, hairlike vessels that interact with surrounding body cells to exchange nutrients and wastes. Capillaries then enlarge into venules, which merge into veins, and carry the spent blood back to the heart. After the blood has traveled through the capillary network the pressure is greatly reduced, and the veins can afford to be much thinner than arteries with weaker muscle fiber. Small, one-way valves inside the veins keep the blood moving against gravity toward the heart.

As well as delivering the supplies that keep cells functioning, the bloodstream regulates body temperature by dissipating heat that builds up in the organs. The contraction or dilation of surface capillaries allows more or less heat to escape the system, depending on whether the body is too hot or too cold. The bloodstream also contains disease- and infection-fighting antibodies.

The lymphatic system is a one-way independent drainage network of fine capillaries primarily involved in fighting disease and infection. White blood cells used in neutralizing bacteria collect in lymph glands. Then normal muscle movement and one-way valves keep the lymph flowing toward the chest, where it drains into two large veins and reenters the blood stream. SEE ALSO Blood.

Nancy Weaver

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Classification Systems

There are more than five million different species on Earth. While each species represents the end point of a unique evolutionary path, biologists do not treat each one as completely unrelated to the others. Instead, they have created biological classification systems, or taxonomies, to reflect similarities and differences among species. A taxonomy is hierarchical, meaning that groups, or **taxa**, are themselves members of larger groups. For example, birds and mammals are grouped together as vertebrates because they both have backbones. Jellyfish do not belong to the vertebrate taxon because they lack backbones. However, birds, mammals, and jellyfish all belong to the taxon Animalia.

taxa named taxonomic units at any given level

The fundamental group in a biological **taxonomy** is the species. The most widely accepted definition of a species is "a group of actually or potentially interbreeding natural populations that are reproductively isolated from (unable to mate with) other such groups." In the eighteenth century, a Swedish naturalist named Linnaeus developed a biological taxonomy called "binomial nomenclature." Linnaeus grouped very similar species together into genera (singular, genus). Thus, every species is known by two labels: the name of the genus to which it belongs, and a specific modifier to distinguish it from other species in the genus (e.g., *Homo sapiens*).

taxonomy the science of classifying living organisms

Today, species are organized into groups at many levels higher than genus, including family, order, class, phylum, and kingdom. Systematists, who are biologists specializing in taxonomy, have developed two different methods to organize these groups: cladistics, which considers **phylogeny** (evolutionary history), and numerical phenetics, which considers phenotypic (outwardly observable) similarity. Cladists group taxa according to how long ago they diverged from a common ancestor, using only characteristics that provide information about phylogeny. They group together taxa that are closely related. Pheneticists group taxa according to their overall similarity in appearance, using as many characteristics as possible, regardless of phylogeny. These methods contradict one another when closely related groups appear to be very different. For example, crocodiles are more closely related

phylogeny the evolutionary history of a species or group of related species to birds than to turtles, snakes, or lizards, but look more like turtles, snakes, or lizards than like birds.

Systematists now use molecular techniques to analyze protein and DNA sequences for information on relatedness and similarity. Data at the level of molecules have the advantage of being more easily quantifiable, or reducible to numbers, than much phenotypic data. Furthermore, certain types of DNA and protein are thought to evolve at constant rates over long periods of time, providing "**molecular clocks**" for establishing phylogenetic relatedness. However, the accuracy of these "clocks" is difficult to determine without independent knowledge of phylogeny, such as a detailed fossil record.

molecular clocks using the rate of mutation in DNA to determine when two genetic groups spilt off

While there remains considerable debate over the merits of the various taxonomic methods, there is no doubt about the scientific importance of biological classification. Suppose we want to know how flight evolved. Taxonomic methods tell us that bats, birds, and insects each evolved flight independently. Thus, any other characteristics that bats, birds, and insects share can tell us something about the evolution of flight in general. Without a taxonomy, we might assume that flight evolved just once, making it difficult to draw any conclusions. A more pressing reason to develop taxonomies is the rapid loss of biological diversity, since conservationists may prefer to focus their efforts on unique species with few close relatives, rather than on species that are more similar to others. Taxonomies can help them prioritize the species that are least replaceable. SEE ALSO KINGDOMS OF LIFE; LINNAEUS, CAROLUS; PHYLOGENETIC RELATIONSHIPS OF THE MAJOR GROUPS.

Brian R. West

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Cnidaria

Cnidaria is one of the more primitive animal phyla. It includes aquatic organisms such as jellyfish, sea anemones, corals, and hydras. Most cnidarians are marine, although a few, such as the well-known hydra, are freshwater species.

Characteristics of Cnidarians

All cnidarians are characterized by **radially symmetric** body plans, rather than the bilaterally symmetric body plans that are found in most other animal phyla. Although cnidarians are more advanced than sponges (phylum Porifera) in that they possess distinct tissue layers, they lack many of the features of more advanced animal phyla, such as internal organs and central nervous systems. Most cnidarians possess tentacles, and many also have nematocysts (specialized stinging cells). Both are involved in feeding.

radially symmetric wheel-like symmetry in which body parts radiate out from a central point

Cnidarians are characterized by the presence of three tissue layers, an outer protective epidermis, a middle layer called the mesoglea, and an inner layer called the gastrodermis, whose function is primarily digestive. The mesoglea of cnidarians is not as highly developed as the **mesoderm** of other animal groups, being primarily gelatinous with only a few fibrous or amoeba-like cells.

Cnidarians possess only one digestive opening, which serves as both the mouth and the anus. This opening is surrounded by tentacles and leads to an internal digestive cavity called the **gastrovascular cavity**.

Cnidarians feed using tentacles that are embedded with stinging nematocysts. The nematocysts are springing barbs with small hairlike triggers that are activated by contact with prey. Most nematocysts require stimulation in more than one sensory mode before they will fire. For example, a nematocyst may respond only if there is mechanical stimulation from physical contact with the prey as well as chemical stimulation signaling the presence of suitable prey. As nematocysts fire, barbs unfold and become embedded in the tissue of the prey. At the same time, the nematocysts inject the prey with an immobilizing toxin through a long hollow thread within the barb. Once the prey item has been captured and subdued, tentacles are used by the cnidarians to bring the prey item into the gastrovascular cavity. Within the gastrovascular cavity, the food item is broken into small particles by digestive enzymes secreted by gastrodermal cells lining the cavity. The minute particles are then taken in by the gastrodermal cells, and digestion is completed in digestive vacuoles (small cavities) within these cells. The indigestible remnants of the prey are expelled from the mouth of the gastrovascular cavity.

Like other cnidarians, this sea anemone features a radially symmetric body plan and tentacles used in the feeding process. Sea anemones are anthozoans, existing only in the polyp form.

One hypothesis about the origin of nematocysts suggests that they were **prokaryotic endosymbionts** which lived within **eukaryotic cells** as **mutualists** (mutualisms are **symbiotic relationships** between individuals of two different species, in which members of both species derive benefits from the relationship), the same way organelles (specialized parts of cells) such as **mitochondria** and chloroplasts are believed to originate.

mesoderm the middle layer of cells in embryonic cells

gastrovascular cavity a single cavity where digestion occurs

prokaryotic endosymbionts single-celled organisms that lack a true cell nucleus that live inside of other cells

eukaryotic cells cells containing a membrane-bound nucleus and membrane-bound organelles

mutualists a symbiotic relationship where both organisms benefit

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

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

Unlike more advanced animal phyla, cnidarians lack a central nervous system. Instead, their nerves are organized in nerve nets that cover the entire body. Impulses spread slowly out from the point of stimulation along the nerve net. Some cnidarians, such as jellyfish, have more complicated arrangements of nerves that allow for more complex responses to stimuli as well as more effective patterns of movement.

Cnidarians also lack certain tissue types found in other animal phyla, such as true muscle cells. However, they do have fibers that can contract and therefore can be used in capturing prey and in moving about.

Major Groups of Cnidarians

Cnidarians are divided into three major classes. These are the Hydrozoa (hydras and other colony-forming species), the Scyphozoa (jellyfish), and the Anthozoa (sea anemones and corals).

Hydrozoa. The best-known member of the Hydrozoa is the hydra, a freshwater species. However, the hydra is not a typical hydrozoan. For example, the hydra has only a polyp stage, for example, whereas most hydrozoans have a biphasic (two-stage) life cycle that alternates between a sedentary polyp stage and a mobile, bell-shaped medusa stage. The hydra is not strictly sedentary; it moves in a very unusual way, by turning somersaults. In addition, most hydrozoans are colonial, with each colony arising from the asexual budding of a single individual. Members of a hydrozoan colony have interconnected gastrovascular cavities, and the fluid in this cavity is circulated by cells with long, beating **flagella**. There is typically some degree of division of labor within the colony. Usually, there are feeding polyps, which possess tentacles and nematocysts (stinging cells), and reproductive polyps, which continually bud off tiny mobile medusas. The medusas swim by tightening and relaxing cells within the bell, and are also scattered by prevailing water currents. Medusas release sperm and eggs directly into the water, where fertilization occurs. The **zygote** (fertilized egg) develops into what is called a planula larva—the larvae of cnidarians. The larva ultimately settles to the substrate (rocky bottom of the ocean), finds something to anchor to, develops a mouth and tentacles, and becomes a polyp that subsequently buds to form a new colony.

flagella cellular tails that allow the cell to move

zygote a fertilized egg

Scyphozoa. The Scyphozoa includes the well-known jellyfish. In this group, the polyp stage is far less significant than among the Hydrozoa, since the medusa stage is dominant. Scyphozoan medusas grow to sizes considerably larger than those found among the Hydrozoa. They range in size from a few centimeters to over 2 meters across. The nervous systems of jellyfish are also more developed than those of other cnidarians. Instead of a simple nerve net, they have a nerve ring around the edge of the bell portion of the medusa. **Neurons** throughout the rest of the body connect to this ring. This organization allows for faster conduction of impulses from one side of the body to the other, which in turn allows the jellyfish to swim with coordinated contractions of the entire bell.

neurons nerve cells

Anthozoa. The Anthozoa includes the sea anemones and the corals. These species lack the medusa stage altogether, and exist exclusively in the polyp form. Anthozoans tend to have more highly developed contractile cells (cells capable of contracting) than other cnidarians, as well as a more highly developed, thicker mesoglea, which often forms a fibrous connective tissue. Corals secrete a hard, limy skeleton and can form huge reefs, such as the Great Barrier Reef off the coast of Australia. Coral reefs are an impressive ecosystem, one of the most diverse and productive on Earth. SEE ALSO Phylogenetic Relationships of Major Groups.

Jennifer Yeh

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Coevolution

As organisms evolve to take better advantage of their surroundings, they may come into competition. A predator may compete with its prey, or two species eating the same plant may compete with one another to find it. With only a limited amount of resources to go around, living things have to adapt not only to climate, geography, and other slow-changing variables but also to the more rapid evolutionary changes undertaken by their competitors. Although change in climate can be seen as a comparatively slow change, one's living competitors are constantly evolving, and this requires that both parties keep on their respective toes: Fighting for resources can be a never-ending battle, and evolution ensures that the playing field is rarely level. However, evolution does not necessary breed outright competition, as it is also possible for two species to enter a mutually beneficial relationship whereby they help each other. No species lives in a vacuum, and potential interactions with one's neighbors can be beneficial, costly, or both. The chart below details the possible outcome of species interactions.

Note that predation does not differentiate lions eating antelopes from antelopes eating grass—both are predators eating prey, and prey does not have to possess a backbone or sturdy legs. In each case, both predator and prey can respond evolutionary to one another, and those changes may be physiological or behavioral. The antelopes can evolve to run faster. The lions might respond by evolving to run faster too. The grass, although it cannot run away, can evolve to taste bad to discourage antelopes from eating it. This might force the antelopes to find another type of grass, or their taste buds might change. When two (or more) species begin to respond evolutionarily to one another, this is called "coevolution."

Nature offers countless examples of coevolution. Many of these result from predator-prey interactions. Prey may evolve camouflage defenses, which require that predators become progressively better at detecting them. Walking sticks, for example, are insects that closely resemble twigs and are therefore frequently overlooked by predators. Because walking sticks are difficult to detect, their predators must have more acute vision and a greater ability to discern them from the inedible wood they mimic.

Predators, too, may employ camouflage to position themselves closer to prey. Yellow crab spiders reside in yellow flowers, patiently waiting for tasty insects to land on the flower looking for nectar. Such prey finds a nasty surprise instead. Scorpion fish, an extremely toxic species of fish found in temperate and tropical oceans, closely resemble the rock-covered sea floor.

Species A	Species B	Result
0	0	"Neutralism." The species do not interact.
+	0	"Commensalism." One species benefits from, but does not harm the other.
+	-	"Predation" or "parasitism." One species benefits at the cost of the other.
-	-	"Competition." Both species compete for the same resource.
+	+	"Mutualism." Both species derive benefits from the relationship.

Possible outcome of species interaction.

When inattentive prey drifts too close to the lurking scorpion fish, it swiftly gets eaten.

As one species in such a relationship grows more and more camouflaged, the other must get better at detection. More complex camouflage structures result for one, and a more refined nervous system and perhaps keener vision, smell, or hearing develop for the other. The driving forces for these adaptations are the other species, not temperature, geography, or any other variables.

polymorphisms having two or more distinct forms in the same population

Experiments suggest that camouflage is an effective tactic prey can use to confound predators. Theodore D. Sargent and the team of Alexandra T. Pietrewicz and Alan C. Kamil showed in 1981 that blue jays had a difficult time detecting underwing moths (*Catocala*) resting on certain backgrounds. The moths have wing patterns that blend in with tree bark, provided that they are oriented on the bark properly. Slight variations in the moths' wing patterns are called **polymorphisms**. If consistently shown just one polymorphism, blue jays became quite effective at detecting it even when a moth was on tree bark and oriented correctly. But if the blue jays saw different polymorphisms in random order, they never learned. Thus, in this evolutionary arms race, the blue jays have evolved the ability to detect subtle camouflage, but only one type at a time. Adapting to this ability by introducing a polymorphism enables the moths to defeat the blue jays' learning and detection abilities.

The ability of predators to detect hidden, or cryptic, prey can be found elsewhere. For example, John L. Gittleman and P. H. Harvey showed in 1980 that chicks were able to learn to discern camouflaged prey in a comparatively small number of trials. Predators may get better at identifying prey through a variety of mechanisms. They may get better at detecting camouflaged prey against a specific background or they may restrict their searches to more limited areas. In response, prey become more and more devious in their disguises, and each species can exhibit enormous evolutionary pressure on the other as they interact more frequently and grow increasingly adept at duping the other.

Relationships among Species

How do such relationships start? Imagine a worm that can partially conceal itself from its predator, a blue jay. Given that a blue jay has to look for any worm it eats, extra time spent looking for that hidden worm may well be wasted. In a limitless universe of worms, with half being concealed and the other half being unconcealed, the blue jays will never bother to identify the concealed ones, because it will be far easier to just pluck up the easily visible ones. As such, the concealed worms gain a selective advantage over the obvious ones.

But suppose the obvious worms all get eaten up. Then the blue jays have to start eating concealed worms, which they cannot find nearly as fast. So blue jays with better sensing abilities will tend to eat more, grow healthier, and reproduce more. Before long, with an abundance of blue jays with keen vision, the partially concealed worms will start to become scarce, unless they can better conceal themselves.

Two species may sometimes enter into a mutually beneficial relationship whereby they help each other, a situation illustrated by this yucca moth pollinating a yucca flower.

With a small advantage, that of partial concealment on the part of the worms, an evolutionary arms race has been created. The worms get better and better at hiding, and the blue jays get better and better at finding them. In a competitive world, this arms race can be seen everywhere. For example, trees grow taller to get more sunlight than their neighbors. Their neighbors, in response, grow taller too. For all this growing, however, the amount of sunlight reaching the trees does not change: They are expending increasing amounts of energy competing for the same, unchanging supply of a resource.

Competition of such intensity can be costly. To describe this phenomenon, Leigh van Valen coined the term "Red Queen Principle" in 1973. This term comes from an observation made by the Red Queen in Lewis Carroll's *Alice in Wonderland*. Alice and the Queen had been running furiously but could not go anywhere. The Queen told Alice, "Here, you see, it takes all the running you can do to keep in the same place. If you want to go somewhere else, you must run at least twice as fast as that!"

The Red Queen principle suggests that competing species may have to allocate more and more resources into fighting one another for a modest or negligible increase in benefit. As each side grows leaner and faster and better able to fight the other, the balance between competitors can be maintained. However, what is to be said of uneven matches? The struggle between bacteria or viruses and mammals is seriously lopsided. Bacteria, as parasites, can infect mammals and live off of them. A long-lived mammal, such as a human, may take twenty years or longer to go from birth to reproducing age, whereas the infecting bacteria may be able to reproduce within a matter of hours. With a faster generation time and many more **mutations** when they reproduce, bacteria can adapt to different environments and evolve much more quickly. Given this discrepancy, one might be tempted to think that competition between organisms with disparate generation times might always go to the ones that can evolve more quickly. In scenarios like that of lions and antelopes, it seems like an even match. But when bacteria tussle with humans, one might initially think the bacteria should always win.

mutations abrupt changes in the genes of an organism

The Evolutionary Struggle

Fortunately for humans, this is not always so. While the evolutionary arms race gives rise to new structures with which one fights the enemy, it can also give rise to structures that get around the problem of slower generation times. An internal simulation of evolution is an incredibly intricate structure, and it helps illustrate the heights of complexity that an evolutionary arms race can produce. The mammalian immune system has devised a number of strategies that closely resemble a tightly controlled simulation of evolution: The mechanism that generates antibodies (and T-cell receptors) recombines genes far more quickly than does the conventional method of mammalian reproduction. These genes, designed to recognize fast-changing bacterial and viral invaders, can change as fast as their competition.

Like all evolution, bacterial mutations must be beneficial for the bacteria to survive. The genes encoding antibodies do not particularly affect the survival of antibody-generating cells (B cells). But for the system to be effective, the body wants only the cells possessing the genes that can catch up with the bacteria. Thus, after creating an isolated scheme to accelerate mutation of specific genes, the body must create selective pressures to guarantee that it gets only the ones it wants. It does this, too, in the lymph nodes. By keeping little pieces of the bacteria around, the body can select only the B cells that best recognize the invader and discard the rest. Thus, even with lengthy generation times and low mutational rates for the rest of their **genomes**, mammals are able to simulate the conditions of rapid turnover and high mutational rates inside their own bodies to combat invaders with the same characteristics. Stronger and faster muscles are different manifestations of the arms in question, as is the antibody system. One set makes the organism go faster, and the other makes it selectively evolve faster.

genomes the sum of all genes in a set of chromosomes

Selectively speeding up evolution is not necessarily restricted to organisms that need to catch up to their competitors. The butterfly genus *Heliconius* boasts brightly colored wings and produces foul-tasting chemicals to discourage predators. Once a predator eats a *Heliconius* butterfly, it quickly learns to avoid butterflies with similarly idiosyncratic markings. But what if a butterfly that is not *Heliconius* can mimic the colors on *Heliconius* wings? This mimic can enjoy the reputation of being poor prey without actually having to manufacture the foul-tasting components itself.

Of course, this mimicry does not help *Heliconius*. If a predator comes upon a mimic and finds it tasty, it becomes more likely that a *Heliconius* might be eaten later, foul taste or not. This is another form of an evolutionary arms race: The mimic gets an advantage at *Heliconius*' loss. Such mimicry, when a nontoxic species tries to look like a toxic one, is called Batesian mimicry. It is fairly common in the insect world: For example, the hornet moth (*Sesia apiformis*), the wasp beetle (*Clytus arietis*), and the hoverfly (*Syrphus ribesii*) all have the same characteristic stripes as the common wasp (*Vespula vulgaris*), but only the common wasp has that painful stinger. Each one of the stingerless species usurps an ornery reputation from the common wasp, and as predators learn to eat them, the common wasp suffers more predation.

There are a few potential responses to these Batesian mimics. The predator could get better at discerning mimics from the real thing. As the predator gets better, the mimics too will get closer and closer to the real thing to fool the predator. Alternately, the original, toxic species could change its markings, forcing the mimics to change as well. If the mimics and the toxic species have roughly the same mutation rates and generation times, these changes might proceed at the same rate.

Heliconius has come up with a different strategy. It has evolved a select toolbox of wing patterns from which to choose during development. This pattern tactic resembles the rapid evolution enjoyed by the mammalian immune system—*Heliconius* can quickly change its wing pattern over a few short generations rather than taking a long time. Its mimics, on the other hand, must slowly evolve to get that precious wing pattern and thus avoid their predators without having to taste toxic.

Mutualism

Not all coevolution needs to be adversarial. Flowers are a coevolutionary adaptation for pollination. Many plants have flowers that are tailored to the needs of a specific insect or bird or bat. Flowers are designed to catch the eyes of certain animals, and the nectar inside is meant to appeal to particular tastes. Bees cannot see red but readily pick up blue, green, yellow, and ultraviolet. Butterflies have decent vision but a poor sense of smell, so they tend to pollinate brightly colored but odorless flowers.

Other structures can keep the relationship between a plant and its pollinator very close. For example, certain flowers have parts designed specifically for the length of a moth's tongue, and only that certain moth species can drink the nectar inside. Common snapdragons are designed so that the flower opens when an object the exact weight of a bumblebee lands on it.

These adaptations are mutually beneficial. The animal provides the plant with pollination, which means the plant can reproduce. The plant provides the animal with nectar, which can feed and sustain the animal. To ensure reliable pollination, the plant evolves to become more and more recognizable by its pollinator, and, conversely, the pollinator gets a steady food source. Each side grows stronger and can reproduce more under the part-

This bumblebee was attracted to the bright yellow of this flower. The nectar the bee takes away from the flower will be used to create honey, and the pollen the bee carries will fertilize the next flower, thereby helping the flowers to reproduce.

nership. In such cases, coevolution is an enormous asset to the species involved.

Coevolution of two organisms, therefore, aptly demonstrates that evolution does not have to respond exclusively to nonliving forces. Slight pressure from a competitor, or an ally, can redirect a species. Some pressures, such as predatory ones, can cause the species to invest more in camouflage, detection, or muscle and speed. Others, such as ones that lead to mutualism, may promote structures that will help a species more closely work with its partner, like a plant with its pollinator. Also, different strategies can lead to the bending of the rules, such as getting around the problem of evolution rates. As organisms come into close contact with another, a coevolutionary strategy is the most efficient path to success. SEE ALSO BEHAVIOR; BEHAVIORAL ECOLOGY.

Ian Quigley

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Colonization

Colonization occurs when a species enters and spreads into a new geographic area or habitat. This process involves both the initial entry, or invasion, into the new area by the species and its successful establishment there, which includes finding adequate resources for growth and reproduction. Less commonly, the term may be used when a parasite enters into and spreads inside a host or when a gene enters into and spreads within a new population.

The process of colonization is intensively studied along with theories of island biogeography because islands are discrete, measurable areas where colonization occurs. Island biogeography is the study of the dynamics that effect populations of isolated areas, and that encompasses the entire process of colonization. Island biogeography theories can be divided into three types. The first relates to habitat diversity and focuses on the suitability of the new habitat for the invading species. The second pertains to equilibrium, or the balance of colonization of the new habitat and its rate of extinction. The third concerns itself with the balance between colonization of the new habitat and speciation within it, and employs an evolutionary approach to examine it.

Increased habitat diversity is the most basic explanation to support the well-documented fact that as the area of land under study increases the number of species present increases. An organism that arrives to colonize a new area will need to find an appropriate habitat, or environment, in which to live. For example, a bird that uses large trees in which to nest will not be able to colonize a grassland. The proper habitat is of critical importance for the success of a colonizer, and even small differences in environmental factors such as soil type or humidity contribute to the success or failure of a new colonist.

A second theory of island biogeography is equilibrium theory. It explains the balance that is reached between colonization and extinction. The amount of colonization depends on the distance between the source of the colonizers and the new habitat. For example, the diversity of species on islands is greater when the islands are closer to the mainland than when they are farther away. The obvious reason is that the process of invasion, or the initial journey to the island, is more difficult when the distance is greater. The ease of the journey is different for different taxa, as birds may have no problem flying to an island whereas ground mammals would find it nearly impossible. Extinction is also known to occur faster on smaller islands because the available space fills up more quickly and competition drives some species to extinction.

Sometimes a new colonist finds abundant resources and little competition and is therefore highly successful and potentially free to evolve to take advantage of all the newly available untapped resources. In these cases, the evolutionary process impacts the colonizers faster than invasions of new species.

Examples of this situation can be found on remote islands such as the Hawaiian islands, where there are many closely related species of fruit fly that occur nowhere else. In this case, an ancestor was probably blown into the new habitat, where it established itself and had many generations of progeny, each of which ultimately invaded new habitats or neighboring islands that were free from competition. The new habitats were isolated enough from the founder population so that the invaders evolved into new species. SEE ALSO MIGRATION.

Jean K. Krejca

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Communication

The world is full of sights, sounds, and smells that organisms use to communicate with each other. Because humans are diurnal (active during the day) and have well-developed eyes and ears, we tend to think of communication in terms of vision and **acoustics**. However, other animals, plants, fungi, and even microorganisms can communicate, and do so using a variety of different methods. Communication is defined as any signal from one organism that influences the behavior of another organism. The type of signaling an organism uses depends on the reception abilities of the receiver.

acoustics a science that deals with the production, control, transmission, reception, and effects of sound

Nocturnal animals use sound and smells to communicate with each other, flowers attract pollinators by smell and sight, microorganisms communicate through touch and chemicals, and aquatic organisms can use electricity.

Communication between different individuals enhances the chances of survival by the sender. The sender may successfully defend a territory, thus ensuring a food supply, or successfully attract a mate, thus increasing reproductive success. Parents communicate with offspring, increasing the probability that the offspring will mature and reproduce.

While the sender of a signal usually benefits, predators have learned to exploit these signals. The calls of male Tungara frogs can be received by bats. Fireflies have learned to prey on other fireflies by mimicking mating signals. There are five modes of communication used by animals: visual, acoustic, chemical, tactile, and electrical.

Visual

infrared an invisible part of the electromagnetic spectrum where the wavelengths are shorter than red. Heat is carried on infrared waves

Visual communication is transmitted by light, ranging from **infrared** to ultraviolet, and is detected by photoreceptors. Only vertebrates and arthropods have photoreceptors advanced enough to be useful in communication. In vertebrates, the receptors are located in the retina of the eye, but in arthropods, they are encased in each of the miniature "eyes" that form their compound eyes. The eyes of arthropods and vertebrates are very different, having independent evolutionary origins. In general, vertebrates have sharper vision than arthropods, but this clarity is due to the larger size of vertebrates rather than a more advanced eye.

aposematic coloration a bright coloration in animals with physical or chemical defenses that act as a warning to predators

Some visual signals are exhibited simply through color patterns. One example is **aposematic coloration**, in which an animal advertises that it is toxic, distasteful, or otherwise dangerous, through bright colors. Like many signals, aposematic coloration can be deceitful. Coral snakes and scarlet king snakes have yellow, red, and black bands, but only coral snakes are venomous. King snakes mimic coral snakes in order to appear venomous and escape predation. Similarly, a group of harmless flies is marked with yellow and black banding, mimicking the various bees and wasps that actually do pose a danger.

Sometimes visual cues evolve when other forms of communication are ineffective. The semaphore frog in Borneo lives on rocks next to raging waterfalls, so the normal croaks and whistles of frog communication would be ineffective. This species has instead evolved visual signaling, which involves flashing white-spotted feet.

Visual signals, which are most effective in daylight, are usually used by diurnal animals. However, some insects, such as the familiar firefly, have evolved ways to communicate visually in darkness. Male fireflies flash bioluminescent abdomens in a particular pattern, hoping to elicit a similar flash sequence in some female on the ground. After receiving a signal, the male will join the female and mate. One genus of firefly, *Photurus*, has discovered the flash signal of a different genus, *Photinus*. *Photurus* females mimic *Photinus* females, calling in the *Photinus* males. When the male of the wrong species arrives expecting a mate, the female eats him.

Acoustic

Acoustic signals are produced in a variety of ways, from striking objects to vibrating vocal cords. A sound is heard when vibrations in air or water are detected by mechanoreceptors, which vibrate in response. In mammals, reptiles, birds, and amphibians, the receptors are located in the inner ear. Arthropod receptors are variable, and may be found on the legs, thorax, or abdomen. The only fishes that can detect sound are those with modified flexible air sacs.

A meadow firefly flashes a particular bioluminescent pattern in the hope of eliciting a similar flash sequence in some female on the ground.

Since sound is carried farther in water than in air, aquatic mammals can communicate over great distances. Orcas (so-called "killer whales") use an elaborate system of cries to establish dominance, find offspring and mates, and even express contentment. Each pod of orcas develops its own dialect of cries, allowing pod-mates to recognize each other.

Birds use songs to declare territories and enhance their chances of survival by reducing harmful encounters with birds of the same species. When male birds establish territories for the mating season, they often come to physical blows with each other to defend their boundaries. Once the territory has been settled, the birds reinforce their boundaries by singing rather than fighting. If a bird ceases calling, other birds will immediately take over the space.

Chemical

Most organisms can use molecules to communicate. Animals concentrate chemical receptors in the nose, mouth, and antennae. Vertebrates have the most developed senses of smell and taste because the receptors are kept moist and isolated. Plants cannot sense chemical signals in the same way that animals do, but plants do emit them in abundance. For example, pine trees emit terpenes, sharply odoriferous chemicals that communicate distastefulness to herbivorous insects. This signal is an allomone, a term for any chemical used to communicate between members of different species.

Chemicals that communicate between members of the same species are called **pheromones**. Female moths use these powerful signals to attract mates. Male moths, with their fantastically plumed antennae, are able to detect just a few molecules in a square kilometer (approximately 0.4 square miles). Honeybees use pheromones in conjunction with visual cues to communicate to other workers where food sources are located. Mammals rub scent glands on objects to mark their territories, and on each other during the mating season to act as **aphrodisiacs**.

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

aphrodisiacs substances or objects that are thought to arouse sexual desire

Tactile

Touch is detected by **proprioceptors** on pliable body surfaces of the receiver. Proprioceptors respond to temporary changes in the shape of the surface or the movement of sensory structures such as hairs, whiskers, and bristles. Structures that have a large number of receptors are tactile organs. Human fingertips are tactile organs, having about 100 receptors per square centimeter (0.15 square inch). The tentacles of octopuses, antennae of some insects, and bills of sandpiper birds are also tactile organs.

proprioceptors sense organs that receive signals from within the body

Touch is a less informative means of communication than sight, sound, or chemicals, but can be crucial. Male and female crane flies must touch legs before either animal will accept the other as a mate, and human infants must be held and cuddled to develop properly and to recover more quickly from illness.

Electrical

Communication by electrical current has evolved only in fishes, but within this group it has arisen several times independently. The fish generate an electrical charge in specialized cells called electrocytes. Electrocytes are arranged in columns and surrounded by insulating cells. Electric eels can generate charges up to 720 volts, but these strongly electrical fish use their charge to capture prey, rather than for communication.

Weakly electric fish, such as skates and knifefishes, evolved the use of their signals for social communication because they are either active at night or in murky water. Electrical signaling is highly versatile. A single fish can communicate territory boundaries, advertise for a mate, or show aggressiveness just by changing the strength and pattern of pulses. Wave fish use their signals to establish a social hierarchy. Dominant fish reinforce their position by matching their charge frequency to submissive wave fish, forcing the submissive fish to shift their frequencies away. Male Nile fish spend days building a suitable nest and then send out invitations to females by emitting pulses of electricity.

Communication is essential to any form of social interaction, and so all living things have developed some way to transmit and receive information. The few examples provided in this article do not come close to demonstrating the diversity of communication that exists in the natural world. SEE ALSO Acoustic Signals; Aposematism; Courtship; Vocalization.

Jes Marie Creech

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Community Ecology

Community ecology is the study of the organization and functioning of communities of organisms. As populations of species interact with one another, they form biological communities. A community of organisms consists of all the interacting populations of the species living within a particular area or within a particular habitat. Community ecology also studies the relationships of the members of a community to their environment. Community ecology is usually subdivided according to habitat or **biome**. Typical habitats include forest, grassland, desert, and stream or lake environments.

biome a major type of ecological community

The Trophic Pyramid

All biological communities have a similar structure called a trophic pyramid. Each pyramid contains four or five levels. Food energy is passed from one level to the next along a food chain. Since energy is lost to heat at each level in the pyramid, it takes many organisms at a given trophic level to support those in the next level up. The base of the pyramid in every biological community is composed of species called autotrophs, organisms that harvest sunlight (or in rare cases, heat) directly through photosynthesis (or chemosynthesis). All other organisms in the pyramid are called heterotrophs.

A food chain typically contains four or five links, from autotrophs, through grazers and other herbivores, then culminating with a carnivore as top predator. Many animals, however, eat more than one species. Also, animals may eat different foods at different stages of their growth. Many animals eat both plants and other animals and therefore feed at more than one trophic level. Consequently, food chains are usually interconnected into highly complex food webs.

In addition to eating one another, species also compete for resources and interact in other ways within a community. Nontrophic relationships between species are as important as food chains and food webs in shaping the organization of biological communities.

Ecological Succession

Through the process of ecological succession, communities are constantly changing. Disturbances to communities may be local, such as a tree falling and opening the canopy to allow more sunlight, or widespread, such as fires and storms. Whether local or general, each disturbance creates an opportunity for a new species to colonize that region. These new species can alter the biological structure of the community and create an environment that is suitable to other new species. By this process, the community evolves over time.

In some environments, succession eventually produces a stable community dominated by a small number of species. This is called a climax community. The web of biological interactions has become so intricate and interconnected that no other species can successfully compete for food resources. In other environments, small disturbances produce communities that are a diverse mix of species. Some tropical forests contain hundreds of thousands of species within a square kilometer. When a tree dies and falls, the dense canopy is opened and new space is available for different species to take root. Some coral reefs contain thousands of different species, and whichever species is able to rapidly colonize a new disturbance patch will be successful.

Ecological Niches

The way of life of an organism is shaped by its environment and by its interactions with other organisms through the processes of evolution. The role an organism plays in its relation to other species and its environment

Competition plays an important role in community interaction and ecology. This Kirtland's warbler, for example, may be forced to compete with other birds to preserve its nesting site.

is known as its ecological niche. The niche of an organism includes what it eats, how it obtains food, where in the environment it lives, what temperature it prefers, how much light it can tolerate, and many other factors.

Guilds

Some similar species have evolved strategies that allow them to allocate resources in a way that avoids competition. For example, different species of warblers that prey on the same species of insects may forage at different levels in the same trees. A group of organisms that share a common food resource is called a guild. Guild members may have strong interactions with each other but only weak interactions with other members of the community. In the American Southwest, birds, rodents, and ants constitute a guild that competes for the same seeds. Whereas birds exploit temporary patches of seeds, rodents and ants are permanent residents. Ants generally take smaller seeds than rodents. In East Africa, communities of animals form a guild of grazers. First, elephants and buffalo eat the tall, coarse grasses and then move on. They are able to consume large quantities of this low-nutrition food source. Zebras follow along behind the elephants, reducing the plant **biomass** even more. The zebras are followed by a still smaller animal, the wildebeest, which selects among the lower growing plants that remain after the zebras have fed. Finally, the smallest grazers, such as Thompson's gazelles, are able to reach the young, protein-rich sprouts of grass missed by the wildebeest.

biomass the dry weight of organic matter comprising a group of organisms in a particular habitat

Interactive Relationships

The interactive relationships that arise between populations of different species form the interactive web of communities. These interactions range from antagonistic to cooperative and have positive, negative, or neutral effects on the species involved. In antagonistic relationships the interaction is detrimental to individuals of either one or both species; in **commensal** relationships (commensalism) one species benefits while the other remains unaffected; and in **mutualistic relationships** (mutualism) both species benefit.

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

mutualistic relationships symbiotic relationships where both organisms benefit

The organization and stability of biological communities results from the mix of these different kinds of interaction.

There are many different kinds of interspecific interactions within an ecological community. These relationships between species are not static; they evolve as natural selection continually shapes and reshapes them. The complex relationships between prey and predators, for example, are snapshots of one instant during the evolution of interactions. As interactions between species evolve, the nature of relationships may shift. Nineteenth-century British naturalist Charles Darwin called this ever-changing mix of species and their interactions the "entangled bank" and stressed its importance in the evolutionary process. While antagonistic relationships, such as predator-prey or parasite-host, are the most dramatic kinds of relationships, other forms of interaction such as mutualism or commensalism are just as important.

Mutualism. This is a relationship where both participants in the interaction receive benefit. For example, plants are hosts for insects that pollinate them or eat their fruit and for microorganisms that attach themselves to their roots. Mutualistic associations between animals and microorganisms are an important part of the structure of communities. Most animals rely on the microorganisms in their gut to properly digest and metabolize food.

Parasitism. This is possibly the most common way of life in nature. Parasitic organisms may account for half of all living species. The majority of species of wasps are tiny parasites that lay their eggs on a specific host organism. Some wasps are parasitic on plants, some are parasitic on insects, some even parasitize other wasps! The larvae hatch and burrow into the host species. As it is consumed from the inside out, the host species survives long enough to allow the larvae to mature.

Antagonism. Antagonism is a form of relationship where one species benefits and the other is harmed. Grazing, parasitism, and predation are examples of antagonistic relationships. While we generally think of grazers as large herbivores, a grazer is defined as any species that moves from one organism to another, feeding on part of each without actually killing it outright. Grasshoppers are grazers that jump from plant to plant, chewing a portion of the leaves of each one they visit. Some caterpillars are grazers that crawl from one plant to another during development rather than remain as parasites on an individual plant. The grazing lifestyle differs from the parasitic lifestyle in a few important ways. Individuals can vary their diets with different foods. Also, because grazers do not remain attached to a single individual for long periods, their victims do not have time to develop induced specialized defenses, such as an immune response that a host can develop against a parasite.

Predation. This form of relationship differs from both parasitism and grazing. In predation, the victims are killed and often consumed immediately. Predators therefore differ from parasites and grazers in their effects on the dynamics of populations and the organization of communities. As with parasitism and grazing, predation is an interaction that has arisen many times in many taxonomic groups worldwide.

Competition is an important form of interaction in communities in which neither species benefits. In competitive interactions, species evolve either to avoid each other, to tolerate the presence of the other, or to aggressively exclude the other.

Species compete for almost every conceivable kind of resource. Birds compete for nesting sites. Male birds compete for preferred sites to defend as territories for attracting females. While species compete for many resources at the same time, there is often a single resource, called the limiting resource, that is in scarce supply. This resource restricts the growth of each species. In deserts, water is often the limiting resource.

Commensalism. In this kind of interaction, one species benefits and the other is unaffected. For example, cattle egrets (*Bubulcus ibis*) forage around the feet of cattle. The grazing behavior of the cattle stirs up many small insects and other arthropods that the cattle egrets eat. The cattle egrets receive a benefit, but there is no indication that the cattle are affected in any way.

The richness and ubiquity of interactions among populations of organisms demonstrate that the characteristics of all species have been influenced by the interaction with other species. Species have coevolved with each other. Predators have evolved along with their prey. Parasites evolve with their hosts. Rarely is only one interaction responsible for the evolution of a species, however. More common is a sort of diffuse coevolution where the traits of a single species are influenced by interactions with many other species. Such diffuse coevolution may prevent a sort of evolutionary "arms race," where predator and prey become ever faster or stronger. SEE ALSO Coevolution; Ecology; Ecosystem; Habitat.

Elliot Richmond

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Comparative Biology

Under this scientific method, biologists formulate hypotheses, or predictions, from an existing body of knowledge and then test their hypotheses through experiments. Experiments range from simple to complex, and can be performed on a computer, in a laboratory setting, or outdoors. Technological developments during the twentieth century—including high-speed computing, DNA sequencing, and a wide array of visualization techniques—have opened the door to many exciting lines of biological investigation. Biologists are constantly developing new techniques to test increasingly complex questions, and have even designed experiments to re-create natural events such as hurricanes, forest fires, and floods.

The scientific method can be applied to many, but not all, types of scientific inquiry. Experimental methods cannot directly test hypotheses con-

cerning the processes of evolution because these events took place over the course of millions of years, under environmental conditions that are as difficult to define as they would be to recreate. Biologists must therefore rely on a comparative method to deduce how evolutionary events created the patterns of animal diversity that exist today.

One such pattern involves how animals living in similar environments have evolved similarities in particular traits. For centuries, biologists have been interested in how such characteristics adapt the animals to their surroundings and ecological role. A biologist studying the adaptive significance of a morphological trait, such as fur coloration, will look at animals living in similar environments to search for patterns linking this trait with environmental factors such as plant types and density.

A comparative framework can be used while looking at different types of traits, whether they are **genetic**, **morphological**, **behavioral**, or **ecological** in nature. In setting up a comparison, the biologist must be familiar with the evolutionary relationships of the animals in question. For many groups of organisms, these relationships have been described through a branch of biology called phylogenetics. The product of a phylogenetic analysis is called a **phylogeny**, which is a hypothesis about relationships between organisms. Phylogenies can be constructed using a combination of genetic, morphological, and behavioral traits. These phylogenies can describe relationships at various levels: gene, species, genus, and so on.

After the biologist selects the level at which she will make a comparison, she uses a number of criteria, or standards, to decide whether the structure to be examined in each organism is **homologous**. When judging morphological structures to be homologous, criteria may include their position and developmental origin. Function is not a reliable indicator of homology because similar functions may be formed by dissimilar structures (e.g., a bird's wing as opposed to a bat's wing). Such structures would be the result of convergent evolution, and would be called analogous rather than homologous (same function, different structure). The criteria differ for judging homology in other types of traits. For example, judging homology in behavioral traits would require examination of genetic origins and behaviors that may represent a transition between two behaviors that are of interest.

When the biologist maps homologous traits onto the phylogeny and examines the evolutionary relationships between groups sharing similar traits, the patterns revealed may provide clues about how various traits evolved. Biologists may examine, for instance, the correlation, or connection, between the presence of the trait and the environmental or genetic factors that may cause this trait to be expressed. The scientist uses statistical methods to determine whether or not the correlation he has found between the trait of interest and the factors occurred as the result of a random process. If the scientist determines that the patterns were not created randomly, then he concludes that the trait is an adaptation.

A comparative framework is invaluable while studying evolutionary relationships of various animals, and while looking at how traits evolved. However, the comparative method is also useful in cases where the investigator does not need to create a historical, or evolutionary, context. If a biologist

genetic relating to an organism's genetic make-up

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

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

ecological relating to an organism's interaction with its environment

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

homologous similar but not identical is interested in only the function of a particular structure, and not in how it evolved, she may decide to make comparisons of the same structure in more distantly related animals.

For example, a biologist interested in the functions of morphological traits might be interested in how flight structures differ in birds and bats. He knows that wings evolved independently in birds and bats because a published phylogeny indicates that many bird and bat ancestors did not fly. Rather than assume that wings evolved in the most recent common ancestor of bats and birds, and was subsequently lost later on in many groups of reptiles and mammals (the closest living relatives to birds and bats), it is assumed that wings evolved twice. The functional morphologist uses the knowledge that bird and bat wings evolved independently to help direct future research. SEE ALSO Adaptation; Biological Evolution.

Judy P. Sheen

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Competition

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

Populations of animals are controlled by many factors. **Natural selection** is a broad term that describes one effect of these controls on population. For example, one form of population control that can result in natural selection is competition.

intraspecific involving members of the same species

There are a number of essential resources upon which animals' lives depend. Whenever these resources are limited, animals are forced to compete for survival. Competition can be **intraspecific**, between the same species, or interspecific, between different species. Since resources are rarely abundant in any given environment, competition can be fierce. Three resources that animals are likely to complete for are space, water, and food.

Competing for Space

The availability of space is a primary consideration in any habitat. The actual territory in which an animal lives is vitally important since an animal's environment must be able to support the needs of each species. All animals must have enough room for feeding, reproducing, and exercise in order to live comfortably.

Along with the amount of space, some animals require a particular terrain, such as the prairie dog. A prairie dog colony must have enough flat and fairly soft earth in which the animals can build elaborate tunnel systems. If the soil is too rocky, the prairie dogs cannot build their brooding dens and escape tunnels.

Similarly, some birds require lots of open sky in which to perform their courtship flights. Without these elaborate flights the birds do not become stimulated to reproduce. If the terrain does not permit the birds to move in wide-open spaces, the birds' chances of successful reproduction in that habitat are reduced.

Competing for Water

Another important resource that animals compete for is access to water. Most animals require a particular amount of water everyday, which they may use as drinking water, or to contribute to their overall health. In general, animals must maintain a certain moisture balance in order for their tissues to work properly. When animals do not have enough to drink their bodily tissues become dehydrated and cannot function properly. Organs, such as kidneys, stop working, resulting in death.

Using larger bodies of water for bathing purposes is another common use of water as a resource. For instance, overheating in elephants is a problem usually countered by cool baths in rivers or mud. When water becomes scarce in the dry season, competition between individual elephants or between elephants and other species can reach a dangerous peak.

Finally, **aquatic** animals are especially vulnerable when the water level of their environment drops. Fish living in the shrinking rivers and streams are easy prey for birds when the waters become so shallow that they are easily seen. The fish will compete for choice hiding spots from hungry predators, with the unlucky losers being eaten, therefore removing their genetic material from the gene pool.

aquatic living in water

Competing for Food

Food is one of the most basic resources over which individuals compete. In extreme cases where animals have gone for long periods without enough food to sustain them, individuals will compete, sometimes to the death, for mere scraps of food. Animals that practice a high level of parental care have to carefully balance finding enough food for both themselves and their offspring. When food is scarce, the parent may go for months without eating but will rarely risk their own death for the sake of their young. Usually, by the time the parent is in danger of starvation the resources for the young will have already been exhausted and the young will have already died.

Examples of competition for water can be found in many nature videos. Parched elephants threaten thirsty lions for limited water in rivers. Baby elephants may get trampled in the rush for water and space in the limited water pools. Even crocodiles find competition as they march to a new water hole only to find resistance from crocodiles already in residence.

The reason the parent allows its young to die is motivated by the parent's instinct to survive. Once the offspring dies the parent is free to readopt food-finding methods that might lead it farther from the nest or den where its young were kept. The parent is driven to preserve its genetic information by remaining healthy enough so that it can reproduce again, hopefully when there is more food available.

Sometimes species will compete for more than one resource at a time. Competitions for territory and food are easily seen in interactions between ants. On one hand, the social structure of the colony is an amazing example of how the members of a species cooperate and specialize for the benefit of all. The queen lays the eggs and produces the offspring. Workers attend to the maintenance and growth of the colony. Soldier ants defend the colony against invaders. The area around an ant colony, however, is often lacking in food after a few seasons of food gathering and resource use.

Some colony members will forage beyond their usual boundaries and encounter ants from another colony. This will immediately set off a warning throughout both colonies. Soldiers and workers rush out of the two

Competition for food and territory is a highly visible component of ant interaction. For example, if ants from one colony invade the space of another colony, the results often mean war over the disputed area.

colonies to fight each other for the contested territory and food resources. The success of one or both of the colonies may be at risk, and the death toll for each colony can be high. Even colonies of the same species will war against one another. If one species enters the colony area of another, the two colonies may suffer serious battle losses.

Strategies to Avoid Competition

Although competition between animals can be seen in a variety of situations, many species have developed elaborate strategies to avoid competition. It is not the habit of any species to try and obliterate another. Confrontations occur as a last resort. Without this avoidance of direct competition there would be very few stable communities.

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

More often, the sharing of resources is achieved between species in a habitat. Scientists often refer to the sharing of resources as "**niche** partitioning." In niche partitioning animals tend to use different parts of a resource without coming into direct competition with one another. For instance, grazing animals in parts of Africa come in all sizes. The smaller Thompson's gazelles eat grass that grows close to the ground. Zebras and wildebeests consume the tall grasses and shrub food. The giraffe has a long neck enabling it to browse far above the ground. While all of these animals use plants as a food resource, none come into direct competition with one another. As a result, they **coexist** peacefully and reduce confrontation.

coexist live together

Many species of birds and monkeys in rain forests also partition resources. Some are specialized for feeding on fruit from lower branches of trees nearer the forest floor, while others are able to exploit food items found in the top or canopy region of the forest.

It is only when resources are limited that one observes any actual competition. Even then animals will often find a unique solution to the problem. For example, barnacle colonies exist in competition with other animals for limited space on rocks and hard surfaces in the oceans. While the larvae are free-swimming and float as part of the planktonic community throughout their juvenile stage, the adults need a firm surface to anchor and construct hard permanent shells. From within these shells they extend feathery feeding appendages that sweep food particles from the ocean currents.

Barnacles exploit unique measures in order to avoid the fierce competition from ocean-dwelling **filter feeders** (such as corals, anemones, and limpets) for ocean floor space. Instead of competing, many form colonies on the tough skins of whales. They hitchhike around the sea feeding on food suspended in the water surrounding the whale. It is very common to find whales with large colonies of barnacles on their snouts and jaws. Even ships are suitable landing places for the barnacle larvae. Barnacle colonies can become so large on the bottoms of ships that the ships must be removed from the water and the barnacles scraped off to keep the ship moving smoothly through the water.

filter feeders animals that strain small food particles out of water

Ecological competition is a fascinating and varied topic in biology. Scientists are always discovering new ways in which animals compete with one another. Even more interesting is the way in which they reduce or eliminate competition. Humans can learn a great deal from how animals coexist with one another. SEE ALSO Aggression; Populations.

Brook Ellen Hall

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Competitive Exclusion

The competitive exclusion principle states that two species that occupy the same biological niche cannot coexist. Another way of expressing this idea is that "complete competitors" cannot coexist. That is because when two species occupy precisely the same niche, and compete for precisely the same resources, one species will inevitably be better at exploiting those resources than the other. The more effective species will outcompete the other and eliminate it from the habitat. The competitive exclusion principle was first stated in this form in 1934 by G. F. Gause, although other biologists, starting as early as Charles Darwin, appear to have had similar thoughts.

The competitive exclusion principle is actually a µtheoretical result derived from mathematical equations for competition called the Lotka-Volterra equations. However, there appears to be empirical, or factual, support for the idea as well. Studies of coexisting species always show that they differ in at least one important aspect of their niche. In one famous study, Robert MacArthur examined the habitat use of five species of coexisting forest

COMPETITIVE EXCLUSION PRINCIPLE

This principle defines the concept that when populations of two different species compete for the same limited resources, one species will use the resources more efficiently than its competitor. This provides the more efficient species with a reproductive edge, so that the second species will eventually be eliminated.

warblers and found that each species foraged for food on a different part of the tree.

Similar studies of lizards of the genus *Anolis* suggest that in this group, species that are found in the same place tend to be of different sizes, prefer to forage at different branch heights, or use branches of different thicknesses. In certain large lakes of the African Rift Valley, several hundred species of cichlid fish may coexist. Studies of these species suggest that each is specialized to exploit a different food resource.

Competition between species is an interspecific interaction (that is, one that occurs between individuals of different species) that harms both players involved. Consequently, species tend to evolve in such a way as to avoid competition. When two competing species coexist in the same habitat, they tend to shift their niches in such a way as to overlap less. The niche that a species is able to exploit in the absence of any competitors is called its fundamental niche. The resources that are actually exploited by a species in a specific habitat represent its realized niche. The realized niche is always smaller than the fundamental niche and a subset of it.

character displacement a divergence of overlapping characteristics in two species living in the same environment as a result of resource partitioning

If competition occurs over long periods of time, **character displacement** may occur. Character displacement describes a situation where two species are more morphologically different in habitats where they coexist than in habitats where they do not coexist. Character displacement is often interpreted as evidence for past (and perhaps continuing) competition. Character displacement has been observed among species of *Anolis* lizards as well as among the Galapagos finches. SEE ALSO COMPETITION.

Jennifer Yeh

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Conservation Biology

Conservation biology is the study of the biological diversity—biodiversity for short—of Earth. Biodiversity is the variety of different living creatures, both plants and animals. Conservation biology is a relatively new field of study, having its start in the 1980s. It applies the principles of many sciences in order to preserve biodiversity throughout the world.

While at the end of the twentieth century the number of described species was about 1.7 million, estimates put the total number of species at 5 to 30 million. Many scientists believe that Earth is experiencing the greatest episode of mass extinction since the extinction of the dinosaurs 65 million years ago. Current rates of species extinctions throughout the world are believed to be 50 to 100 times greater than rates prior to human impact. In tropical forests, the extinction rates are believed to be 1,000 to 10,000 times higher than the expected rate. Given the current rates of extinction, by the year 2020, 30 to 70 percent of the world's

As part of a conservation biology tracking project, a research biologist puts an eartag on a sedated bobcat.

species will be extinct. This crisis is thought to be due largely to human activities. Human population reached 6 billion in September 1999. Every day, this number increases by an estimated 250,000 (an extra 87 million people per year). This huge human population is straining Earth's natural resources in many ways.

The leading factor in the increasing rate of species extinctions has been the human destruction of natural areas where plants and animals live. Since 1950, one-third of the world's forests have been destroyed. Loss of tropical rain forest is estimated at an acre every second. It is estimated that humans consumed one-third of the world's natural resources during the period 1970 to 1995. It has also been estimated that the United States, with only about 5 percent of the world's population, consumes 25 percent of the world's resources and generates 25 to 30 percent of the world's waste.

Other human activities that are increasing species extinctions are the pollution of the environment and the overexploitation of animals, such as whales and tigers, that have commercial value.

There are many reasons to conserve and protect biodiversity. New species could provide new food sources for humans. Genes from wild plants are used to improve food crops. New plants and animals can be used as **biological control** agents to control pests. Nearly all the medicines used today were derived from plants or animals, and other species may provide important new medicines. Plants and animals carry out many functions in the environment that are critical to humans. For example, bees and bats pollinate flowering plants, and green plants provide oxygen.

biological control the introduction of natural enemies such as parastites, predators, or pathogens as a method of controlling pests instead of using chemicals

There are other less practical reasons to preserve biodiversity. Plants and animals are beautiful and interesting. Humans gain much pleasure and peace of mind interacting with the natural world. In addition, there is the argument that all species have value regardless of their worth to humans.

Denise Prendergast

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Constraints on Animal Development

Within a given taxon, development generally results in the production of individuals that are recognizable as members of that specific group. Vertebrate embryos can be recognized as such early in development, regardless of whether they will later become fish, birds, or mammals. Humans nearly always have the same number of fingers and toes at birth (rare exceptions do exist, however), and, although there are slight variations in the size and shape of digits and limbs from one individual to the next, they are recognizable as human features (for example, wings, hooves, and fins never appear in humans). Normal development seems to follow the same pathway, and resulting variation is limited. This is because developmental constraints favor certain outcomes and prevent others. Developmental constraints are any aspects of a developmental system that increase the probability of a particular outcome and limit the production of variable **phenotypes**. Just as natural selection favors change to suit environment (adaptation and convergent evolution), developmental constraints limit adaptation and favor conservation of the morphology, or form, of animals. The internal organization of living organisms limits the range of possible phenotypes on which natural selection can operate. Developmental mechanisms are fundamental in generating diversity. At the same time, they impose constraints on the direction of evolutionary change.

phenotypes the physical and physiological traits of an animal

Developmental Mechanisms

Because of the particular pattern of embryonic development characteristic of a given species, some structural patterns are more likely to form than others. The probability that a mutation will result in a potentially functional

Mutations, such as the blue pigment in this green frog's skin, may take place late in the developmental cycle. Late-developing mutations are more likely to benefit an organism's ability to function in its environment.

body form depends on when the mutation is expressed. Mutations that act on early development are likely to have drastic effects on phenotype because normal development of later structures depends on that of earlier structures, a phenomenon known as **epistasis**. Drastic changes early in **ontogeny** are unlikely to result in benefits to the organism and in fact are usually lethal. In contrast, mutations that are expressed late in development are less likely to disrupt the developmental process and more likely to result in functional phenotypes that would benefit the organism.

epistasis a phenomenon in which one gene alters the expression of another gene that is independently inherited

ontogeny the embryonic development of an organism

morphogenesis the development of body shape and organization during ontogeny

Morphogenesis includes those processes of development that produce the final form of the organism. Anything that alters the final form through evolutionary time must do so through alterations in development. Yet development is a very tightly integrated process in which it is difficult to change one thing without adversely affecting many other things.

Constraints on Development

Regardless of the direction and magnitude of external selective pressure, it may be impossible for the organism to change because of internal constraints. Natural selection might not favor even seemingly adaptive changes because of trade-offs among developmental costs because of pleiotropy, the action of genes in multiple tissues that may be otherwise unrelated. Pleiotropy can result in constraints in which no possible genetic change can produce beneficial morphological change without causing other undesirable changes. Groups of characters may also be associated because of pleiotropy, resulting in suites of characters that are inherited together. In this case, change in one character is impossible without change in the others.

Constraints on development can be generally classified as structural or **phylogenetic**. Structural constraints can be physiological, cellular, genetic, metabolic, or mechanical. For example, the respiration rate across cell membranes presents physiological limits to cellular surface-to-volume ratios, and

phylogenetic relating to the evolutionary history of species or group of related species mechanical constraints limit how long or thin a limb can be and still support the weight of the organism.

Cellular constraints are limits to rates of cell division, secretion of cell products, and cell migration and/or metabolic efficiency. Metabolic constraints such as the maximum rate of respiration limit the abundance of tissues that have high rates of oxygen consumption. Functional constraints arise in embryos as the organ systems responsible for functions such as feeding and respiration become functionally connected.

Limits to the maximum rate of mutation and recombination that reduce the potential rate of evolutionary change are one form of genetic constraint. The other is a form of historical constraint. Some genes are highly conserved, occurring in many species and higher taxonomic units, because they are involved with fundamental aspects of development.

Phylogenetic constraints (also called historical constraints) are reflected in differences among species that result from having different patterns of descent. Phylogenetic constraints are one reason why variation associated with the production of a given baüplan (body plan) is minimal. Therefore, development of the baüplan may be canalized (guided or controlled) by both structural and historical aspects of genetic constraints. SEE ALSO Allometry; Body Plan; Morphology; Phylogenetics Systematics.

Andrew G. Gluesenkamp

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Continental Drift

If you have ever looked at a map of the Atlantic Ocean, you have probably noticed that the coastlines of Africa and South America seem to fit together like pieces of a jigsaw puzzle. The fit between the two coastlines is even better when the edges of the continental shelf are compared. For many years, scientists thought this was just a coincidence, because no one could think of a way that the continents could slide around.

Evidence for Continental Drift

Evidence that South America and Africa might once have been joined to each other came from the research of the German geographer, Alexander von Humboldt. Von Humboldt traveled throughout South America, Africa, and other parts of the world, collecting plant and animal specimens and studying geography and geology. He observed many similarities between

South America and Africa in addition to the apparent fit of continental coastlines. For example, von Humboldt noticed that the mountain ranges near Buenos Aires, Argentina, match mountain ranges in South Africa.

Other mountain ranges in Brazil extend to near the seashore and stop. Similar mountain ranges begin at the corresponding seashore in Ghana in Africa. All of these mountain ranges appear to have the same age and to be formed of the same kinds of rock. The rock strata in these and other mountain ranges would match perfectly if the coastlines of the two continents were lined up. Von Humboldt also observed similar patterns among mountain ranges in Europe and North America.

Von Humboldt and other naturalists also noticed many similarities among fossils of plants and animals on either side of the Atlantic. Although fossil species in eastern South America are somewhat different from fossil species in western Africa, their similarities are often striking. Before long, similarities across other oceanic gaps were observed. Plant and animal fossils found in India, for example, are often remarkably similar to those found in Australia.

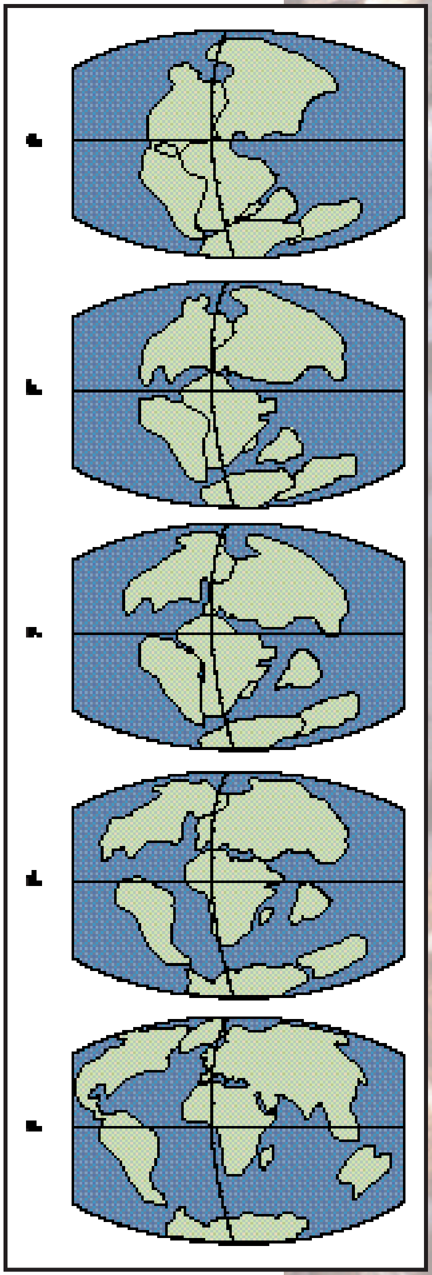
Another important piece of evidence was discovered in the early twentieth century. When molten lava freezes, it preserves traces of Earth's magnetic field. Basalt, which freezes deep underground, also records Earth's magnetic field at the time the basalt cooled. Measurements of the direction of Earth's magnetic field from many different rocks of different ages on different continents indicate either that Earth's magnetic poles have moved all over the planet or that the continents themselves have moved.

Continental drift was first proposed in 1908 by American geologist Frank B. Taylor. However, Taylor's paper was mostly ignored and soon forgotten. Then a German meteorologist, Alfred Wegener, began working on a theory of continental drift. By 1912 Wegener had developed a theory suggesting that continental rocks were stronger and lighter than seafloor rocks. He also suggested that the seafloor rocks were like very thick tar. He concluded that the stronger continents were able to drift around on the weaker seafloor rocks.

Furthermore, Wegener thought the continents had once been part of a single large land mass, which he called Pangaea. Initially, he asserted, the original land mass had broken into two parts, two supercontinents, which he called Gondwanaland and Laurasia. Over millions of years, he suggested, Gondwanaland had broken apart into South America, Africa, India, Australia, and Antarctica, while Laurasia separated into North America and Eurasia.

Unfortunately, Wegener could not suggest any mechanism that would have caused the continents to break apart and move around in this way. In contrast to Taylor's experience, Wegener's theory was met with rejection and open hostility by other scientists, probably because Wegener was a meteorologist, not a geologist.

In the mid 1930s, however, Wegener's ideas were resurrected and rehabilitated. Scientists had discovered a ridge down the middle of the Atlantic seafloor through which hot lava was flowing upward and spreading outward. Stripes of lava on either side of this ridge were progressively older



a) Pangaea at end of Permian; b) Pangaea breaks up at the end of Triassic; c) End of Jurassic; d) End of Cretaceous; e) Today. Redrawn from Matthews, 1981.

the farther away they were from the ridge. This pattern of stripes of lava strongly suggested to the scientists that the floor of the Atlantic Ocean was getting steadily wider. The discovery of this spreading of the seafloor, along with other discoveries, eventually led to the modern theory of **plate tectonics**.

plate tectonics the theory that Earth's surface is divided into plates that move

Plate Tectonics

Wegener's idea of continental drift had the continents floating around on semisolid oceanic rock. In contrast, plate tectonics suggests that Earth's entire crust is composed of a number of large plates that are in constant motion relative to each other. Some plates are sliding under other plates, some are sliding past each other, others are pulling apart, and still others are colliding. Each of these types of interactions produces unique geological consequences. The Himalayas are formed as two continental plates collide. Along the northwest coast of North America, an oceanic plate is sliding under the North American plate. The resulting geological characteristic is a chain of volcanoes. As one plate is forced under the other, friction causes enormous amounts of heat that builds up until a volcano forms and erupts. Earthquakes are often the result of sudden movement of two adjacent plates. The plates "lock up" until enough force is generated to break them apart, causing the quake. One of the world's most famous earthquake zones, the San Andreas Fault, lies at the boundary of the Pacific and the North American plates.

After being initially rejected and ridiculed, the concept of continental drift (and plate tectonics) is now widely accepted as one of the fundamental unifying ideas of geology. This shift in thinking among geologists depended not only on the discovery of an adequate explanation for continental movement (seafloor spreading, rifts, and trenches) but also on the discovery of more and more similarities between continents.

Evolution and Biological Diversity

Early explorers, mapmakers, and traders were often accompanied on their travels by naturalists (people who studied all the natural sciences). These naturalists made two striking observations. They found that fossils of exactly the same plants and animals were located on continents that are separated by thousands of miles of oceans. For example, the tropical fossil fern, *Glossopteris*, was found in South America, Africa, India, and Australia. Similarly, fossils of the land vertebrate, *Kannemeyrid*, were found in Africa, North and South America, and Asia.

While the ancient fossils on different continents were often similar or identical, the exploring naturalists were finding out that living plants and animals on the different continents were often very different. The naturalists were discovering whole new groups of animals and plants on nearly every island and continent they visited. Most biological species seemed to be unique to the region or continent in which they were found. How could these seemingly contradictory observations be reconciled? Plate tectonics provided the answer. When the different land masses were connected, the same or closely related plants and animals inhabited each. After the land masses were separated, the different populations were geographically isolated from each other by great distances of ocean. Life on the different con-

A marsupial is a member of the mammalian subclass Metatheria, which includes a wide variety of mammals that give birth to undeveloped young. The young complete their development outside the mother's body, attached to a nipple. Most marsupials have a pouch that covers the nipples and protects the young while they are developing.

tinents had apparently evolved into different species, because the populations were isolated from each other by such great distances.

It is possible to correlate, or link, the breakup of the continents with the types of animals found on each. The longer the period of separation, the more differences between species were found. For example, all of the indigenous (native) mammals found in Australia are marsupials. There are no naturally occurring **placental** mammals. This suggests that Australia broke away before placental mammals had evolved. In geographic isolation from the rest of the world, Australia's mammals were able to evolve into many highly sophisticated forms found nowhere else.

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

Has the diversity of life on Earth increased as a result of the breakup of the supercontinents? This idea was first proposed in 1970 by the American geologists James W. Valentine and Eldridge M. Moores. They suggested that the diversity of life increased as continents broke up and moved apart and decreased as land masses moved together and joined.

Since 1970 the study of plate activity as a force in the evolution of life has substantially added to our understanding of evolution. For example, during the Permian period (around 286 million years ago), there was a decrease in the variety of species of animals living in the shallow seas around Pangaea. In contrast, when the Atlantic Ocean began to open during the middle Mesozoic era (144 million years ago), the differences between the species living on opposite shores gradually increased. The greater the distance, the smaller the number of families in common. Differences accumulated more rapidly in the South Atlantic than in the North Atlantic, because a land connection between Europe and North America remained until the Cenozoic era (66 million years ago). The opposite happened when North and South America became connected at the **Isthmus** of Panama. In South America, there were many different marsupials and few large predators. After the isthmus emerged, many large herbivores migrated south. They adapted well to the new environment and were more successful than the local fauna in competing for food. Large predators also moved south and contributed to the extinction of at least four orders of South American land mammals. Only a few species, such as the armadillo and the opossum, migrated in the opposite direction. Many of the invading northerners, such as the llama and tapir, died out in North America and are now found only in the south. SEE ALSO Biogeography.

isthmus a narrow strip of land

Elliot Richmond

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Convergence

The term "convergence" is used to describe the presence of a similar feature in two or more taxa that are not closely related. Convergent features evolve independently often as a result of natural selection operating on unrelated taxa that occupy similar environments. The recognition of convergence requires an accurate phylogeny. With a **phylogenetic** hypothesis, **homologous** characters can be distinguished from **analogous** traits. Convergent structures are usually derived from different morphological features or by different developmental pathways (although this is not the case in one special class of convergence described below).

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

homologous similar but not identical

analogous describes a similarity in structures between two species that are not closely related

Convergence can be further broken down into specific phenomena. Analogy describes the convergent modifications of a nonhomologous trait. For example, analogous organs may share a common function but develop from different tissue types in unrelated organisms. The wings of insects and the wings of birds have the same functional role (flight) but they are derived from nonhomologous structures and are structurally very different. Therefore, they are considered analogous structures. The term "parallelism" refers to apomorphic, or derived, traits. Apomorphies are identical traits that are found in different taxa but that do not share a common evolutionary origin. Apomorphies may arise independently (even in closely related taxa) as consequences of similarities in development among species (often due to developmental constraints imposed by similarities in genes that regulate developmental processes). Parallelism differs from other types of convergent evolution in that parallel traits are the product of the same genes and developmental processes operating in different taxa. In this case, convergence is found not only in physical traits but also in the developmental processes that produce them.

A striking example of convergent evolution in animals is the evolution of flight in three different vertebrate taxa: pterosaurs (extinct flying reptiles), birds, and bats. Structural similarities in the wings of each of these groups are indications of common constraints imposed by phylogeny and biomechanics. All vertebrate forelimbs have similar developmental patterns, regardless of whether they will become limbs or wings in the adult. In order to achieve flight, the ratio of the surface area of the wings relative to body mass must be great enough to provide sufficient lift to overcome gravity. Differences among them indicate that in each lineage, unique solutions have evolved under particular historical and functional constraints, resulting in different structural patterns with similar functions. Pterosaurs, like

The Egyptian jerboa is sometimes referred to as a "kangaroo rat" because of its kangaroo-like hind legs, an example of analogous development.

birds, had hollow bones and keeled sterna (breastbones), a short and stout humerus (upper arm bone), and wing fibers that were analogous to bird feathers. The pterosaur wing was supported primarily by an elongated fourth digit. In birds, digits of the forelimb are reduced and the wing is supported primarily by the radius and ulna (bones of the lower arm) and bones of the wrist. Feathers provide rigidity and increased surface area to the wing. In pterosaurs and bats the digits are elongated and provide support for patagia (thin membranes of skin). In birds, feathers provide a unique structural solution to the challenge of flight while elongate digits and patagia have evolved convergently in other groups that lack feathers. SEE ALSO Biological Evolution.

Andrew G. Gluesenkamp

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Courtship

Courtship is a collection of instinctive behaviors that result in mating and eventual reproduction. Courtship is important because it helps to ensure that breeding will occur. Organisms within a species must reproduce successfully in order for the species to survive. Courtship has many other functions, including mate selection, regulation of sexual readiness so that the reproductive physiology of a pair may be synchronized, the reduction of hostility between potential sex partners in territorial animals, and species recognition. Courtship may be rather simple, involving a small number of

A male Australian great bowerbird at his bower, a brightly adorned passage or chamber designed to attract female bowerbirds.

visual, chemical, or auditory stimuli, or it may be a highly complex series of acts involving several types of communication. Some of the most complex courtship behaviors are found in birds.

Mating Systems

In addition to complex courtship patterns, birds also have interesting and varied breeding or mating systems. The most common type of mating system is monogamy, which resembles a traditional human marriage. Ninety percent of birds are monogamous. In this type of mating system, two birds come together or form a pair bond for the procreation of young. The length of the pair bond varies greatly between species and between individuals. A mated pair may remain together for life, as in the case of albatrosses, petrels, swans, geese, eagles, and some owls and parrots. They may remain together for several years, as in the case of American robins, tree swallows, and mourning doves. They may remain together for one year, which is the case with most birds; just for one brood, as is the case with house wrens; or for even shorter periods.

The two birds in a pair are usually faithful to each other during the time that they are together. Pair faithfulness appears to depend on the outward appearance of a bird's mate. This might be a simple matter of recognition. Ringed plovers, for example, establish enduring bonds. In one known instance involving two couples, however, one of the mates in each pair had lost a foot and was rejected by its former mate. Fortunately, the two rejected birds were opposite sexes. They met, paired, and successfully raised normal offspring.

It is difficult to determine, however, the exact nature of the physiological bond that holds a pair together. Other factors may be territory, familiarity with one another, or even something similar to human affection. In fact, it is thought that affectionate bonds actually exist between birds. On two separate occasions, it was observed that the partner of a black duck refused to leave its dying mate when the rest of the flock fled from hunters.

Less common than monogamous pair bonding is polygamy, or the practice of having more than one mate at a time. Polygamy occurs in a wide variety of birds, including peacocks, ostriches, and rheas. Polygamy is usually observed as either polygyny or polyandry. In polygyny, one male mates with two or more females, but the females mate with only one male. The inseminated females incubate their eggs in separate nests and rear their young unassisted by the male. This mating system is most likely to happen when males hold territories that vary greatly in the quality of resources. Important resources may include food, water, and shelter. Females will tend to choose superior males, or those with high-quality territories. If a male in a high-quality territory already has a mate, the new female will usually make a choice to either become his second mate or select a male that holds an inferior territory. If she selects a superior male, both will benefit from increased reproduction. Female marsh wrens sometimes mate with already-mated males, even when bachelor males are available. The number of females mated to each male is related to the amount of growing vegetation in the males' territories, which, in turn, appears to be an indicator of the availability of insect food. Studies of red-winged and yellow-headed blackbirds and indigo and lark buntings also show relationships between territory quality and the likelihood that a male holding a given territory will have more than one mate.

In polyandry, one female mates with two or more males. The word polyandry actually means "many males." This mating system is rare and occurs in less than 1 percent of all bird species—mostly in shorebirds. Polyandry is often accompanied by a reversal of sex roles in which males perform all or almost all of the parental duties. Females in this mating system also compete for mates, such as in the case of the northern jacana, Harris' hawk, acorn woodpecker, and spotted sandpiper.

Other unusual mating systems that birds exhibit are promiscuity, cooperative mating, and lekking. In promiscuous pair bonding, males and females mate indiscriminately. In cooperative pair bonding, two females usually rear broods in the same nest simultaneously, or nonbreeding birds serve as helpers in the nest of one or more breeding pairs. The male is usually not involved in caring for the eggs or the young. A remarkable exception is the American rhea, in which several females lay their eggs—on occasion as many as fifty—in one nest, where the male incubates them by himself. He is also responsible for the care of the young.

In lekking, males engage in communal displays at a traditional site known as a lek. In North America, males of certain members of the grouse family, including prairie chickens, sharp-tailed grouse, and sage grouse, compete for mates at leks.

During these elaborate courtship displays, male birds transmit information by special social signals. They call and inflate brightly colored air sacs on their necks while repeatedly carrying out ritualized dances. Females approach the lek, choose and mate with a male from the display group, and then leave to nest and rear the young alone. Male grouse have a hierarchy and often subdivide territories at a lek, with a dominant male usually holding the most central position and mating with the most females. Lekking species of grouse tend to live in open habitats. Not all lekking bird species live in open areas, however. In the tropics, many forest-dwelling birds such as cotingas, manakins, and hermit hummingbirds display at leks on forest floors.

Courtship Displays

While birds have a wide variety of mating systems, they have an equally vast array of courtship behaviors or displays including dancing, singing, sparring with bills, kissing, caressing, entwining necks, nibbling at each other's feathers, and side-by-side body contact. Some male birds even take on a completely different physical appearance during breeding season, when unique features such as specialized combs, wattles, and pouches appear.

Some aspects of nest building have been incorporated into the displays of some birds. Male and female penguins physically look the same—same size, coloration, and feathers, for example. Male penguins, which are unable to determine sex visually, have adopted a trial-and-error method to solve this problem. In a typical courtship, a male may place a pebble at the feet of another bird. If it is a male, it will start a fight. Females typically ignore the gesture or form a pair bond. The stones may be used later in nest building.

The bowerbirds of Australia and New Guinea (relatives of crows and birds of paradise) provide an example of a special category of courtship display. The males construct special display mounds known as bowers. In an attempt to gain the favor of females, less attractive male bowerbirds build the most elaborate bowers while the more attractive males seem to build less elaborate bowers. One common type of bower architecture consists of two parallel hedges of interlaced grasses or twigs stuck in the ground. In the space between the hedges and interlaced grass or twigs is an area where the male may do some of his displaying.

Another type of bower, called the maypole bower because of its height, is formed from a stack of twigs erected around a vertical sapling or arranged in the form of an open-sided, teepee-like hut whose roof center is supported by a sapling. These bowers are often very large, as many as 3 meters (10 feet) high. The floor under or in front of this type of bower is often cleared of all litter and decorated with colorful objects such as leaves, flowers, fruits, sun-bleached bones, snail shells, parrot feathers, seeds, bits of colored glass, paper, and even jewelry. Some bowerbirds incorporate living orchids into the inner walls of the bower, while others paint the inner walls with mixtures of saliva, grass, or charcoal. One species, the satin bowerbird, paints the mixture onto the walls with a brush of fibers—a rare example of a tool-using animal. This type of bowerbird also has bright blue eyes and favors blue objects. His bower is frequently decorated with blue flowers, blue leaves, and blue-tinted mushrooms. Mating may occur inside the elaborate bowers.

After fertilization, the female builds a nest at a distance and incubates and raises young there. After the young have fledged, she may bring them to the bower where the family engages in a communal display. This may be an imprinting behavior to educate the young in the intricacies of this species' display etiquette. SEE ALSO BEHAVIOR; REPRODUCTION, ASEXUAL AND SEXUAL.

Stephanie A. Lanoue

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Crepuscular

The term "crepuscular" refers to the hours of dawn and dusk. Crepuscular animals include those species that are active at dawn, dusk, or both. Some animals are mistakenly considered to be nocturnal although they are actually crepuscular.

Most crepuscular animals tend to be desert dwellers that remain at rest during the harsh heat of day and the bitter chill of night. Snakes, mice, lizards, and some rabbits use broad daylight and late-night hours for resting in their respective shelters. By mating and foraging for food during the more temperate hours, crepuscular animals are able to conserve precious energy and still pursue those activities that contribute to propagating the species. The saw-scaled adder (*Echis carinatus*) of North Africa, Syria, Iran, and India prospers in arid, sandy regions. During the day, it lies sheltered from the heat under fallen tree trunks or rocks, or flattens its body and digs into the sand by means of its keeled lateral scales.

Not all crepuscular species call the desert their home. Certain deer, snakes, bats, rodents, and opossum tend to be active during early morning and twilight hours because of rhythms of behavior as opposed to environmental controls. The forest musk deer (*Moschus chrysogaster*) lives in the forests and brushlands from the Himalayas to central China. Active in the morning and evening hours, the animal feeds on grass, moss, shoots, twigs, and buds.

Species that find food, avoid predators, and generally maintain body state more effectively during twilight obviously benefit from responding appropriately to different light levels. They may operate most efficiently if they can predict the changes during any twenty-four-hour period by means of an internal clock.

Ann Guidry

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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 triphoshate: 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

amiote: 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 parastites, 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

dessication: 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

euryhaline: 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 agression 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 animals 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 permited

hunting seasons: periods of time during which hunting is permited

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 endrocrine systems

IgA: imunoglobin A; a class of proteins that make up antibodies

IgD: imunoglobin 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 parastic 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 spilt off

molecular clocks: using the rate of mutation in DNA to determine when two genetic groups spilt 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

molted: 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

pedipapls: 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 distrubutions

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 siezing, 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 dimorphorphism 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 eyesm 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: spliting

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
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Tool Use
Water Economy in Desert Organisms

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Aquaculture
Classification Systems
Dinosaurs
Domestic Animals
Farmer
Farming
Selective Breeding
Sustainable Agriculture

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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

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Amphibia
Annelida
Arthropoda
Aves
Cephalochordata
Cestoda
Chondricthyes
Chordata
Cnidaria
Dinosaurs
Echinodermata

Eukaryota
Mammalia
Metazoan
Molluska
Nematoda
Osteicthyes
Platyhelmithes
Porifera
Primates
Prokaryota
Reptilia
Rotifera
Trematoda
Turbellaria
Urochordata
Vertebrata

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Coevolution
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Constraints on Animal Development
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Phylogenetic Relationships of Major Groups
Phylogenetics Systematics
Tetropods—From Water to Land
Xenopus

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Biomechanics
Body Cavities
Body Plan
Bone
Cartilage
Cells
Cephalization
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Echolocation
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Embryonic Development
Feeding
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Gills
Growth And Differentiation of the Nervous System
Homology
Keratin
Locomotion
Mouth, Pharynx, and Teeth
Muscular System
Neuron
Scales, Feathers, and Hair
Sense Organs
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Homeostasis
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Cancer
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Egg
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Molecular Systematics
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Biomass
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Community Ecology
Diversity of Major Groups
Eukaryota
Habitat
Habitat Loss
Habitat Restoration
Zooplankton

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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

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Aposematism
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Burgess Shale and Ediacaran Faunas
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Body Plan
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Diamond, Jared
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Iteroparity and Semelparity
Malaria
Metamorphosis
Parasitism

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Excretory and Reproductive Systems
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Conservation Biology
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Herpetology
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Molecular Biology
Morphology
Mouth, Pharynx, and Teeth
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Physiology
Sociobiology
Taxonomy