

ENVIRONMENTAL BIOLOGY FOR ENGINEERS AND SCIENTISTS

DAVID A. VACCARI

Stevens Institute of Technology

PETER F. STROM

Rutgers, The State University of New Jersey

JAMES E. ALLEMAN

Iowa State University

 **WILEY-
INTERSCIENCE**

A JOHN WILEY & SONS, INC., PUBLICATION

**ENVIRONMENTAL BIOLOGY
FOR ENGINEERS AND
SCIENTISTS**

ENVIRONMENTAL BIOLOGY FOR ENGINEERS AND SCIENTISTS

DAVID A. VACCARI

Stevens Institute of Technology

PETER F. STROM

Rutgers, The State University of New Jersey

JAMES E. ALLEMAN

Iowa State University

 **WILEY-
INTERSCIENCE**

A JOHN WILEY & SONS, INC., PUBLICATION

Copyright © 2006 by John Wiley & Sons, Inc. All rights reserved

Published by John Wiley & Sons, Inc., Hoboken, New Jersey
Published simultaneously in Canada

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording, scanning, or otherwise, except as permitted under Section 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the Publisher, or authorization through payment of the appropriate per-copy fee to the Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, (978) 750-8400, fax (978) 750-4470, or on the web at www.copyright.com. Requests to the Publisher for permission should be addressed to the Permissions Department, John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, (201) 748-6011, fax (201) 748-6008, or online at <http://www.wiley.com/go/permission>.

Limit of Liability/Disclaimer of Warranty: While the publisher and author have used their best efforts in preparing this book, they make no representations or warranties with respect to the accuracy or completeness of the contents of this book and specifically disclaim any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives or written sales materials. The advice and strategies contained herein may not be suitable for your situation. You should consult with a professional where appropriate. Neither the publisher nor author shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

For general information on our other products and services or for technical support, please contact our Customer Care Department within the United States at (800) 762-2974, outside the United States at (317) 572-3993 or fax (317) 572-4002.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic formats. For more information about Wiley products, visit our web site at www.wiley.com.

Library of Congress Cataloging-in-Publication Data:

Vaccari, David A., 1953–

Environmental biology for engineers and scientists / David A.

Vaccari, Peter F. Strom, James E. Alleman.

p. cm.

Includes bibliographical references.

ISBN-13 978-0-471-72239-7 (cloth : alk. paper)

ISBN-10 0-471-72239-1 (cloth : alk. paper)

1. Biology--Textbooks. I. Strom, Peter F. II. Alleman, James E.

III. Title.

QH308.2.V33 2005

570--dc22

2005008313

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

At the conclusion of this project, my feelings are well expressed by the last lines of *Huckleberry Finn*:

... and so there ain't nothing more to write about, and I am rotten glad of it, because if I'd 'a' knowed what a trouble it was to make a book I wouldn't 'a' tackled it, and I ain't a-going to no more.

Dedicated to Liana and Carlo
D.A.V.

During the course of working on this book, and despite all the hours wrapped into its effort, my family learned a lot about the vital essence of life and the gifts we've all been given to share and treasure.

Dedicated to Carol, Amy, Matthew, Alison, Paul, and Elizabeth
J.E.A.

Dedicated to the environment, and to all those, past, present, and future, who make it worth caring about, especially to Daryl, Russell, Sue, Jean, and Arthur.

P.F.S.

CONTENTS

Preface	xix
1 Perspectives on Biology	1
1.1 Why Environmental Engineers and Scientists Should Study Biology,	1
1.2 Present Perspectives on Environmental Engineers and Scientists,	2
1.3 Past Perspectives on Environmental Engineers and Scientists,	5
1.4 Ambiguity and Complexity in Biology,	6
1.5 Conservation and Environmental Ethics,	9
1.6 Guidelines for Study,	13
Problems,	14
References,	15
2 Biology as a Whole	16
2.1 What Is life?,	16
2.2 The Hierarchy of Life,	18
2.3 Evolution,	21
2.4 Taxonomy,	26
2.5 Interaction of Living Things with the Environment,	30
2.6 Brief History of Life,	33
Problems,	34
References,	34
3 The Substances of Life	35
3.1 Basic Organic Chemical Structure,	35
3.2 Chemical Bonding,	36
3.3 Acid–Base Reactions,	38
3.4 Physicochemical Interactions,	40

3.5	Optical Isomers, 41	
3.6	The Composition of Living Things, 44	
3.6.1	Carbohydrates, 44	
3.6.2	Lipids, 47	
3.6.3	Proteins, 51	
3.6.4	Nucleic Acids, 58	
3.6.5	Hybrid and Other Compounds, 61	
3.7	Detection and Purification of Biochemical Compounds, 62	
	Problems, 63	
	References, 64	
4	The Cell: The Common Denominator of Living Things	65
4.1	Prokaryotes and Eukaryotes, 66	
4.2	The Biological Membrane, 67	
4.3	Membrane Transport, 69	
4.4	Eukaryotic Cell Structure and Function, 72	
4.5	Cell Reproduction, 74	
	Problems, 79	
	References, 79	
5	Energy and Metabolism	80
5.1	Bioenergetics, 80	
5.1.1	Some Basic Thermodynamics, 80	
5.1.2	Oxidation–Reduction, 85	
5.1.3	Phosphate Compounds and ATP, 86	
5.1.4	Reaction Coupling, 87	
5.2	Elementary Kinetics, 88	
5.3	Enzyme Kinetics, 90	
5.3.1	Single-Substrate Kinetics, 91	
5.3.2	Multiple Substrates, 95	
5.3.3	Effect of pH, 96	
5.3.4	Effect of Temperature, 97	
5.3.5	Other Considerations, 98	
5.4	Biochemical Pathways, 98	
5.4.1	Glycolysis, 98	
5.4.2	Fermentation, 99	
5.4.3	Respiration, 101	
5.4.4	Oxidation of Fats and Amino Acids, 105	
5.4.5	Photosynthesis, 106	
5.4.6	Biosynthesis, 113	
	Problems, 114	
	References, 115	
6	Genetics	116
6.1	Heredity, 116	
6.1.1	Mendel’s Experiments, 118	

6.1.2	Sex Chromosomes, 120	
6.1.3	Genetic Disease, 121	
6.2	Molecular Biology, 122	
6.2.1	Protein Synthesis, 124	
6.2.2	Gene Regulation, 126	
6.2.3	Mutations, 129	
6.2.4	DNA Repair, 130	
6.3	Genetic Engineering, 131	
6.3.1	DNA Analysis and Probes, 132	
6.3.2	Cloning and Recombinant DNA, 135	
6.3.3	Polymerase Chain Reaction, 136	
6.3.4	Genetic Engineering and Society, 137	
6.4	Genetic Variation, 138	
6.5	Sexual Reproduction, 140	
	Problems, 141	
	References, 142	
7	The Plants	143
7.1	Plant Divisions, 144	
7.2	Structure and Physiology of Angiosperms, 146	
7.2.1	Water and Nutrient Transport, 146	
7.2.2	Plant Growth and Control, 150	
7.2.3	Plant Nutrition, 153	
	Problems, 153	
	References, 154	
8	The Animals	155
8.1	Reproductive Strategies, 155	
8.2	Invertebrate Phyla Other Than Arthropods, 158	
8.3	Mollusks, Segmented Worms, Arthropods, 160	
8.3.1	Mollusks, 160	
8.3.2	Annelids, 160	
8.3.3	Arthropods, 161	
8.3.4	Lesser Protostomes, 165	
8.4	Deuterostomes (Starfish, Vertebrates, etc.), 166	
8.4.1	Echinoderms, 166	
8.4.2	Chordates, Including the Vertebrates, 166	
	Problems, 172	
	Reference, 172	
9	The Human Animal	173
9.1	Skin, 174	
9.2	Skeletal System, 175	
9.3	Muscular System, 176	
9.4	Nervous System, 178	
9.4.1	Nerve Signal Transmission, 178	

- 9.4.2 Synaptic Transmission, 179
- 9.4.3 Nervous System Organization, 180
- 9.5 Endocrine System and Homeostasis, 184
 - 9.5.1 Homeostasis, 184
 - 9.5.2 Hormones, 186
- 9.6 Cardiovascular System, 190
- 9.7 Immunity and the Lymphatic System, 193
- 9.8 Respiratory System, 196
- 9.9 Digestion, 199
- 9.10 Nutrition, 203
- 9.11 Excretory System, 207
- 9.12 Reproduction and Development, 211
 - 9.12.1 Prenatal Development, 214
- Problems, 216
- References, 216

10 Microbial Groups 217

- 10.1 Evolution of Microbial Life, 218
- 10.2 Discovery of Microbial Life, 219
 - 10.2.1 Antonie van Leeuwenhoek, 219
 - 10.2.2 Spontaneous Generation and the Beginnings of Microbiology, 220
 - 10.2.3 Virus Discovery, 223
 - 10.2.4 Discovery of Archaea, 223
- 10.3 Diversity of Microbial Activities, 223
 - 10.3.1 Energy Sources, 224
 - 10.3.2 Carbon Source, 224
 - 10.3.3 Environmental Preferences, 225
- 10.4 Microbial Taxonomy, 226
 - 10.4.1 Basis of Identification, 226
 - 10.4.2 Prokaryotic “Species”, 227
 - 10.4.3 Naming of Microorganisms, 228
 - 10.4.4 Characterization of Prokaryotes, 230
- 10.5 Bacteria, 241
 - 10.5.1 Aquificae, 245
 - 10.5.2 Xenobacteria, 245
 - 10.5.3 Thermomicrobia (Including Green Nonsulfur Bacteria), 245
 - 10.5.4 Cyanobacteria: Blue-Green Bacteria (Formerly, Blue-Green Algae), 246
 - 10.5.5 Chlorobia: Green Sulfur Bacteria, 246
 - 10.5.6 Proteobacteria, 248
 - 10.5.7 Firmicutes: Gram Positives, 258
 - 10.5.8 Planctomycetacia, 262
 - 10.5.9 Spirochetes, 263
 - 10.5.10 Fibrobacter, 264
 - 10.5.11 Bacteroids, 264
 - 10.5.12 Flavobacteria, 264
 - 10.5.13 Sphingobacteria, 265

- 10.5.14 Fusobacteria, 265
- 10.5.15 Verrucomicrobia, 265
- 10.6 Archaea, 265
 - 10.6.1 Korarchaeota, 265
 - 10.6.2 Crenarchaeota, 265
 - 10.6.3 Euryarchaeota (Including Methanogens), 266
- 10.7 Eukarya, 267
 - 10.7.1 Protozoans, 268
 - 10.7.2 Algae, 271
 - 10.7.3 Slime Molds, 279
 - 10.7.4 Fungi, 281
- 10.8 Noncellular Infective Agents: Viruses, Viroids, and Prions, 285
 - 10.8.1 Viruses, 286
 - 10.8.2 Viroids and Prions, 288
- Problems, 288
- References, 288

11 Quantifying Microorganisms and Their Activity

290

- 11.1 Microbial Composition and Stoichiometry, 290
 - 11.1.1 Elemental Makeup, 290
 - 11.1.2 Growth Factors, 293
 - 11.1.3 Molecular Makeup, 294
- 11.2 Microscopy, 294
 - 11.2.1 Light Microscopes, 295
 - 11.2.2 Electron Microscopes, 298
- 11.3 Sampling, Storage, and Preparation, 299
 - 11.3.1 Sampling, 299
 - 11.3.2 Storage, 299
 - 11.3.3 Preparation, 300
- 11.4 Determining Microbial Biomass, 300
 - 11.4.1 Measurements of Total Mass, 300
 - 11.4.2 Measurements of Cell Constituents, 301
- 11.5 Counts of Microorganism Numbers, 302
 - 11.5.1 Direct Counts, 303
 - 11.5.2 Indirect Methods, 305
 - 11.5.3 Relationship between Numbers and Mass, 310
 - 11.5.4 Surface Area/Volume Ratio, 311
- 11.6 Measuring Microbial Activity, 311
 - 11.6.1 Aerobic Respiration, 312
 - 11.6.2 Anaerobic Systems, 314
 - 11.6.3 Enzyme Activity, 315
- 11.7 Growth, 315
 - 11.7.1 Exponential Growth, 315
 - 11.7.2 Batch Growth Curve, 320
 - 11.7.3 Death, Viability, and Cryptic Growth, 325
 - 11.7.4 Substrate Utilization, 327
 - 11.7.5 Continuous Culture and the Chemostat, 329

- 11.7.6 Environmental Factors, 336
- 11.7.7 Inhibition, 338
- Problems, 340
- References, 340

12 Effect of Microbes on Human Health

342

- 12.1 Microbial Colonization of Humans, 342
 - 12.1.1 Abnormal Microbial Infection, 343
- 12.2 Waterborne Diseases, 354
 - 12.2.1 Types of Water, 355
 - 12.2.2 Sources of Contamination, 355
 - 12.2.3 Routes of Infection, 356
 - 12.2.4 Fecal–Oral Route, 357
 - 12.2.5 Modern and Recent Outbreaks, 362
- 12.3 Foodborne Diseases, 364
 - 12.3.1 Bacterial Food Poisoning, 365
 - 12.3.2 Bacterial Infections, 366
 - 12.3.3 Other Agents, 367
- 12.4 Air-Transmitted Diseases, 368
 - 12.4.1 Pneumonia, 368
 - 12.4.2 Other Streptococcal Infections, 368
 - 12.4.3 Tuberculosis, 369
 - 12.4.4 Influenza, 370
 - 12.4.5 Diphtheria and Whooping Cough (Pertussis), 370
 - 12.4.6 Meningococcal Meningitis, 371
 - 12.4.7 Histoplasmosis, San Joaquin Valley Fever, and Aspergillosis (Respiratory Mycoses), 371
 - 12.4.8 Hantavirus Pulmonary Syndrome, 371
- 12.5 Vector-Transmitted Diseases, 371
 - 12.5.1 Malaria, 372
 - 12.5.2 Trypanosomiasis (African Sleeping Sickness), 372
 - 12.5.3 Plague, 373
 - 12.5.4 Typhus Fever, 373
 - 12.5.5 Rocky Mountain Spotted Fever, 373
 - 12.5.6 Lyme Disease, 373
 - 12.5.7 Dengue, 374
 - 12.5.8 Yellow Fever, 374
 - 12.5.9 Rabies, 374
 - 12.5.10 West Nile Encephalitis, 374
- 12.6 Sexually Transmitted Diseases, 374
 - 12.6.1 Syphilis, 375
 - 12.6.2 Gonorrhea, 375
 - 12.6.3 Chlamydial Infections, 375
 - 12.6.4 AIDS, 375
 - 12.6.5 Genital Herpes and Warts, 376
 - 12.6.6 Trichomoniasis, 376
 - 12.6.7 Yeast Infections, 376

- 12.7 Other Diseases Transmitted by Contact, 376
 - 12.7.1 Tetanus, 376
 - 12.7.2 Gangrene, 376
 - 12.7.3 Trachoma, 377
 - 12.7.4 Bacterial Conjunctivitis, 377
 - 12.7.5 Anthrax, 377
 - 12.7.6 Leprosy, 377
 - 12.7.7 Athlete's Foot and Ringworm, 377
 - 12.7.8 Hepatitis B, 378
 - 12.7.9 Ebola, 378
- 12.8 Control of Infection, 378
 - 12.8.1 Physical Steps to Prevent Transmission, 378
 - 12.8.2 Immunity and Vaccination, 379
 - 12.8.3 Antibiotics and Antitoxins, 381
- 12.9 Indicator Organisms, 382
 - 12.9.1 Physical-Chemical Indicators, 382
 - 12.9.2 Microbiological Indicators, 382
- Problems, 385
- References, 385

13 Microbial Transformations

387

- 13.1 Carbon, 389
 - 13.1.1 Carbon Reduction, 391
 - 13.1.2 Carbon Oxidation, 396
 - 13.1.3 Carbon in Environmental Engineering and Science, 397
- 13.2 Nitrogen, 414
 - 13.2.1 Nitrogen Reduction, 417
 - 13.2.2 Nitrogen Oxidation, 421
 - 13.2.3 Nitrogen in Environmental Engineering and Science, 424
- 13.3 Sulfur, 429
 - 13.3.1 Sulfur Reduction, 430
 - 13.3.2 Sulfur Oxidation, 432
 - 13.3.3 Sulfur in Environmental Engineering and Science, 432
- 13.4 Iron, 435
 - 13.4.1 Iron Reduction, 436
 - 13.4.2 Iron Oxidation, 436
 - 13.4.3 Iron in Environmental Engineering and Science, 437
- 13.5 Manganese, 439
 - 13.5.1 Manganese Reduction, 439
 - 13.5.2 Manganese Oxidation, 439
 - 13.5.3 Manganese in Environmental Engineering and Science, 439
- Problems, 441
- References, 441

14 Ecology: The Global View of Life

442

- 14.1 Flow of Energy in the Ecosystem, 443
 - 14.1.1 Primary Productivity, 444

- 14.1.2 Trophic Levels, and Food Chains and Webs, 446
- 14.2 Flow of Matter in Ecosystems, 451
 - 14.2.1 Sedimentary Cycles, 453
 - 14.2.2 Carbon Cycle, 454
 - 14.2.3 Hydrologic Cycle, 456
 - 14.2.4 Nitrogen Cycle, 457
 - 14.2.5 Sulfur Cycle, 460
 - 14.2.6 Phosphorus Cycle, 462
 - 14.2.7 Cycles of Other Minerals, 463
 - 14.2.8 System Models of Cycles, 464
- 14.3 Factors that Control Populations, 466
 - 14.3.1 Limiting Factors and Interactions, 466
 - 14.3.2 Resources and Environmental Conditions, 468
 - 14.3.3 Tolerated Range of Factors, 469
 - 14.3.4 Species Interactions, 470
- 14.4 Populations and Communities, 472
 - 14.4.1 Growth Models: Temporal Structure of Populations, 472
 - 14.4.2 Species Richness and Diversity: Synoptic Structure of Communities, 484
 - 14.4.3 Development and Succession: Temporal Structure of Communities, 486
 - 14.4.4 Distribution vs. Abundance: Spatial Structure of Communities, 488
- 14.5 Humans in the Balance, 490
- 14.6 Conclusion, 492
- Problems, 492
- References, 494

15 Ecosystems and Applications

- 15.1 Terrestrial Ecosystems, 496
 - 15.1.1 Forest Nutrient Cycles, 499
 - 15.1.2 Soil Ecology, 500
- 15.2 Freshwater Ecosystems, 506
 - 15.2.1 Aquatic Environments, 507
 - 15.2.2 Biota, 508
 - 15.2.3 Succession in Lakes, 520
 - 15.2.4 Microbial Loop, 522
 - 15.2.5 River Productivity, 523
 - 15.2.6 Nutrients and Eutrophication in Lakes, 526
 - 15.2.7 Organic Pollution of Streams, 530
- 15.3 Wetlands, 536
 - 15.3.1 Hydric Soils, 538
 - 15.3.2 Hydrophytic Vegetation, 540
 - 15.3.3 Wetlands Animals, 543
 - 15.3.4 Hydrology and Wetlands Ecology, 545
 - 15.3.5 Wetlands Nutrient Relationships, 546
 - 15.3.6 Major Wetland Types, 546

15.3.7	Wetland Law and Management, 549	
15.4	Marine and Estuarine Ecosystems, 552	
15.4.1	Productivity and Nutrients, 553	
15.4.2	Marine Adaptations, 557	
15.4.3	Marine Communities, 558	
15.4.4	Adverse Impacts on Marine Ecosystems, 562	
15.5	Microbial Ecology, 564	
15.6	Biological Effects of Greenhouse Gases and Climate Change, 567	
15.7	Acid Deposition, 569	
15.8	Endangered Species Protection, 571	
	Problems, 574	
	References, 575	
16	Biological Applications for Environmental Control	577
16.1	Wastewater Treatment, 580	
16.1.1	Process Fundamentals, 582	
16.1.2	Attached-Growth Systems, 586	
16.1.3	Suspended-Growth Systems, 600	
16.1.4	Stabilization Lagoon Systems, 618	
16.1.5	Constructed Wetland Systems, 623	
16.2	Sludge Treatment, 633	
16.2.1	Anaerobic Digestion, 636	
16.2.2	Aerobic Digestion, 646	
16.2.3	Composting, 652	
16.3	Potable Water Treatment, 659	
16.4	Water and Wastewater Disinfection Treatment, 662	
16.5	Solid Waste Treatment, 668	
16.6	Air Treatment, 671	
16.7	Soil and Groundwater Treatment, 675	
16.7.1	Phytoremediation, 675	
16.7.2	Bioremediation, 684	
	Problems, 699	
	References, 702	
17	The Science of Poisons	704
17.1	Mechanisms of Toxicity, 705	
17.2	Abiotic Factors That Affect Toxicity, 708	
17.3	Individual Variability, 711	
17.4	Toxic Effects, 712	
17.4.1	Biochemical and Physiological Effects, 713	
17.4.2	Genotoxicity, 714	
17.4.3	Mutagenesis, 714	
17.4.4	Teratogenesis, 714	
17.4.5	Carcinogenesis, 715	
17.4.6	Histological Effects, 720	
17.4.7	Effects on Particular Organs or Organ Systems, 721	
17.4.8	Effects at the Individual Level, 729	

- 17.4.9 Effects at the Ecological Level, 730
- 17.4.10 Microbial Toxicity, 731
- Problems, 732
- References, 732

18 Fate and Transport of Toxins 734

- 18.1 Physicochemical Properties, 734
- 18.2 Uptake Mechanisms, 742
- 18.3 Absorption and Routes of Exposure, 743
- 18.4 Distribution and Storage, 746
- 18.5 Biotransformation, 747
 - 18.5.1 Phase I Reactions, 748
 - 18.5.2 Phase II Reactions, 750
- 18.6 Excretion, 753
- 18.7 Pharmacokinetic Models, 755
 - 18.7.1 Dynamic Model and the Half-Life, 758
 - 18.7.2 Steady-State Model and Bioaccumulation, 760
 - 18.7.3 Equilibrium Model and Bioconcentration, 761
 - 18.7.4 Food Chain Transfer and Biomagnification, 763
 - 18.7.5 Multicompartment Models, 764
- 18.8 Effect of Exposure Time and Mode of Exposure, 765
- Problems, 767
- References, 768

19 Dose–Response Relationships 770

- 19.1 Tolerance Distribution and Dose–Response Relationships, 772
- 19.2 Mechanistic Dose–Response Models, 776
- 19.3 Background Response, 777
 - 19.3.1 Low-Dose Extrapolation, 777
 - 19.3.2 Thresholds, 780
- 19.4 Interactions, 780
 - 19.4.1 Nonadditive Interactions, 783
- 19.5 Time–Response Relationship, 785
- 19.6 Other Measures of Toxic Effect, 785
- Problems, 786
- References, 787

20 Field and Laboratory Toxicology 788

- 20.1 Toxicity Testing, 788
 - 20.1.1 Design of Conventional Toxicity Tests, 789
 - 20.1.2 Test Duration, 789
 - 20.1.3 Selecting Organisms, 790
 - 20.1.4 Toxic Endpoint and Other Observations, 792
 - 20.1.5 Route of Administration and Dosage, 792
 - 20.1.6 Number of Organisms Per Test, 793
 - 20.1.7 Other Experimental Variables, 793

- 20.1.8 Conventional Toxicity Tests, 794
- 20.1.9 In Situ Measurement of Conventional Toxicity, 796
- 20.1.10 Occupational Monitoring, 797
- 20.1.11 Population and Community Parameters, 797
- 20.1.12 Testing for Carcinogenicity and Teratogenicity, 797
- 20.1.13 Mutagenicity Testing and In Vitro Tests, 798
- 20.1.14 Extrapolation from Animals to Humans, 799
- 20.2 Epidemiology, 800
- Problems, 802
- References, 802

21 Toxicity of Specific Substances 803

- 21.1 Metals, 803
- 21.2 Pesticides, 807
 - 21.2.1 Toxic Effects, 808
 - 21.2.2 Ecosystem Effects, 811
- 21.3 Hydrocarbons, Solvents, PAHs, and Similar Compounds, 813
- 21.4 Halogenated Organics, 819
- 21.5 Air Pollutants, 824
- 21.6 Water Pollutants, 827
- 21.7 Toxicity to Microbes, 829
- 21.8 Ionizing Radiation, 831
 - 21.8.1 Dosimetry, 834
 - 21.8.2 Radiation Exposure and Risks, 837
- Problems, 840
- References, 840

22 Applications of Toxicology 842

- 22.1 Risk Assessment, 842
 - 22.1.1 Human Health Risk Assessment, 843
 - 22.1.2 Ecological Risk Assessment, 847
- 22.2 Toxicity Reduction Evaluation, 850
- Problems, 852
- References, 853

Appendixes 855

- A** Physicochemical Properties of Common Pollutants, 856
- B** Biodegradability of Common Pollutants, 862
- C** Toxicological Properties of Common Pollutants, 867
- D** Standards for Exposure to Common Toxic Pollutants, 876
- E** Ambient Air Quality Standards, 878
- F** Unit Conversions and Physical Constants, 879

xviii CONTENTS

G The Elements, 883

H Periodic Table of the Elements, 884

Index

885

PREFACE

This book was originally developed to introduce environmental engineers to biology. However, we have realized that it will also fulfill a need for environmental scientists who specialize in nonbiological areas, such as chemists, physicists, geologists, and environmental planners. Much of what we say here about engineers applies also to these other specialists as well.

Those people coming from a biological science background might be surprised to discover that most engineers and many chemists and physicists do not have a single biology course in their bachelor's degree programs. Even environmental engineering students often receive only a brief exposure to sanitary microbiology, with a vast range of biological issues and concerns being neglected almost completely. Environmental chemists may study aquatic chemistry with little knowledge of biological activity in the aquatic system, and meteorologists studying global warming may have only a rudimentary understanding of the ecosystems that both affect and are affected by climate. However, the growth of the environmental sciences has greatly expanded the scope of biological disciplines with which engineers and scientists need to deal. With the possible exceptions of biomedical and biochemical engineering, environmental engineering is the engineering discipline that has the closest connection with biology. Certainly, it is the only engineering discipline that connects with such a wide range of biological fields.

The need to make engineers literate in biological concepts and terminology resulted in the development of a new graduate-level course designed to familiarize them with the concepts and terminology of a broad range of relevant biological disciplines. The first one-third of the semester introduced basic topics, covering each of the general biology topics in the first 10 chapters of the book. A college-level general biology text was used for this portion of the course, but no single text provided adequate coverage of the range of topics presented in the other chapters. This is the focus of and motivation for this book, which covers a much wider range of biology than has traditionally been taught to environmental engineers and scientists. Our intent in doing so is to strike off

in a new direction with the approach to be used for training environmental professional in the future.

Specialists in every field have learned not to expect their colleagues trained in other areas to have certain basic knowledge in their own areas. This book aims to break one of these barriers of overspecialization. The objectives of a course based on this book will have been met if an engineer, chemist, or geologist who studied it is meeting with a biologist to discuss a situation of environmental concern, and the biologist at some point turns and says: "How did you know that?" It should not be a surprise that any well-educated person possesses some specialized knowledge outside his or her own profession.

The information herein is not limited to what environmental engineers or scientists "need to know" to do their jobs. The nonbiologist may occasionally need to read technical material written by biologists and should not be confused by the use of terminology standard to such material. Engineers and scientists who may eventually move to management positions of diversified organizations should be especially concerned about this.

A secondary need that this subject meets is the necessity for any technically literate person to be familiar with biology. Exposing nonbiologists to this field broadens their knowledge of the living world around them and of their own bodies. The biologically literate engineer or scientist will better understand and cope with the impact of technologically driven changes in the world. This understanding should encompass not only environmental issues such as pollution effects, ecosystem destruction, and species extinction, but also issues bearing on agriculture and medicine. Rapid progress in genetic engineering and medical technology makes it more essential to have such an understanding because it forces many societal and individual choices.

No single book can completely cover all biological topics relevant to environmental engineers and scientists. By design, this book has more information than could be covered in a single semester. Students should leave a course with a sense that there is more to know. It also gives students and instructors the choice of which topics to explore in more detail.

The first nine chapters are intended for use as a study guide and a summary of information that otherwise would have been learned in a course in general biology. Thus, they could be skipped in a course for, say, environmental science students who have already taken general biology. The rest of the chapters contain information that is specific to environmental applications. In broad terms, the important areas are traditional sanitary microbiology (health and biological treatment), ecology, and toxicology.

To play to the strengths of engineers, mathematical techniques are emphasized, as this was the initial focus of the book. Examples include population dynamics, microbial growth kinetics (focusing on batch systems, and stopping with the chemostat, short of treatment process models), pharmacokinetic models of toxicity, ecosystem modeling, statistical approaches to epidemiology, and probabilistic modeling of bioassay data. Other specialists, including biologists, could benefit from this treatment, as biology is becoming more and more quantitative. Nevertheless, the mathematical discussions can be skipped if time does not permit their development.

Familiarity with basic environmental concepts is assumed, such as the sources and types of pollutants, an understanding of acid–base relationships, oxygen demand, and other basic chemistry concepts.

There is sufficient information in this book for a two-semester course. We recognize that many programs have only a single semester to devote to this topic. Therefore, we

offer the following as an outline on which to base such a course. The balance of the book will then be supplementary and reference material that instructors may draw from based on their special interests. The instructor may also consider assigning a research paper to be based on a topic from the book not included in the course.

Topic	Chapters/Sections
1. Introduction: the study of biology; complexity; ethics; biological hierarchies, evolution, taxonomy, interactions in biology	Chaps. 1 and 2
2. Biochemistry: organic structure and physicochemistry, carbohydrates, proteins, lipids, nucleotides The cell: structure and function, membranes	Chaps. 3 and 4
3. Metabolism: enzyme kinetics, glycolysis, fermentation, respiration	Secs. 5.1–5.3, 5.4.1–5.4.3
4. Genetics: heredity, DNA replication, protein synthesis, mutations and DNA repair, polymerase chain reaction	Secs. 6.1.1, 6.2, 6.3
5. Plant and animal taxonomy: including the fungi Human physiology: respiratory system, endocrine system, excretory system	Secs. 7.1, 8.1, 8.4.2, 9.1, 9.8, 9.11, 9.12
6. Microbes: stoichiometry, metabolism, classification, pathogenesis	Chaps. 10, 12
7. Microbial growth kinetics	Chap. 11
8. Biogeochemical cycles: nitrogen cycle reactions, etc.	Chap. 13
9. Ecology: energy pyramid, food web, biogeochemical cycles, population growth, diversity	Chap. 14
10. Ecosystems: forest, soil, aquatic, wetlands, microbial	Secs. 15.1–15.3, 15.5
11. Biological pollution control: activated sludge, anaerobic digestion	Chap. 16
12. Toxicology: mechanisms, effects, carcinogens, organ effects	Chap. 17
13. Fate and transport: uptake, absorption, distribution, biotransformation, excretion	Secs. 18.1–18.6
14. Dose–response: extrapolation, toxicity testing	Secs. 19.1–19.4, 20.1
15. Toxicity: effects of specific substances	Secs. 21.1–21.4

ACKNOWLEDGMENTS

Support for the lost productivity that resulted from writing this book came from two main sources: Stevens Institute of Technology, and my wife, Tien-Nye H. Vaccari. Without the support of both, this book would not have been finished. Moreover, without the encouragement of B. J. Clark, it would not have been started. B.J. was the first person other than the authors to recognize the need that this book would fulfill. Appreciation is also due to my relatives and friends in and around Castelgomberto, Italy, where the book got a good start under the most agreeable of situations. I also appreciate the help I received from Dina Coleman, Patrick Porcaro, James Russell, Alison Sleath, Zhaoyan Wang, and Sarath Chandra Jagupilla.

D. A. VACCARI

1

PERSPECTIVES ON BIOLOGY

Before immersing ourselves in the subject of environmental biology, in this chapter we consider factors to motivate, facilitate, and provide a context for that study. Thus, we start by discussing reasons, history, mindsets, and ethics that can guide our approach to the subject.

1.1 WHY ENVIRONMENTAL ENGINEERS AND SCIENTISTS SHOULD STUDY BIOLOGY

For an environmental scientist, the answer to the question posed in the title of this section is fairly evident. However, for environmental engineers it is worthwhile to consider this in more detail. For example, environmental engineers need to know a broader range of science than does any other kind of engineer. Physics has always been at the core of engineering, and remains so for environmental engineers concerned with advective transport (flow) in the fluid phases of our world. The involvement of environmental engineers with chemistry has increased. Formerly, it was limited to chemical precipitation and acid–base chemistry in water, and relatively simple kinetics. Now it is necessary also to consider the thermodynamics and kinetics of interphase multimedia transport of organics, the complex chain reaction kinetics of atmospheric pollutants or of ozone in water, and the organic reaction sequences of pollutant degradation in groundwater. In a similar way, the role of biology in environmental engineering has burgeoned.

Traditionally, the biology taught to environmental engineers has emphasized microbiology, because of its links to human health through communicable diseases and due to our ability to exploit microorganisms for treatment of pollutants. Often, there is a simple exposure to ecology. However, the ecology that is taught is sometimes limited

to nutrient cycles, which themselves are dominated by microorganisms. As occurred with chemistry, other subspecialties within biology have now become important to environmental engineering. Broadly speaking, there are three main areas: microbiology, ecology, and toxicology. The roles of microbiology are related to health, to biological pollution control, and to the fate of pollutants in the environment. Ecological effects of human activity center on the extinction of species either locally or globally, or to disturbances in the distribution and role of organisms in an ecosystem. Toxicology concerns the direct effect of chemical and physical pollutants on organisms, especially on humans themselves.

This book aims to help students develop their appreciation for, and awareness of, the science of biology as a whole. Admittedly, applied microbiology is often included in many environmental engineering texts, focusing on disease transmission, biodegradation, and related metabolic aspects. However, little if any material is provided on the broader realm of biology in relation to environmental control. Such an approach notably overlooks a considerable number of important matters, including genetics, biochemistry, ecology, epidemiology, toxicology, and risk assessment. This book places this broad range of topics between two covers, which has not been done previously.

There are other factors that should motivate a study of biology in addition to the practical needs of environmental engineers and scientists. The first is the need to understand the living world around us and, most important, our own bodies, so that we can make choices that are healthy for ourselves and for the environment. Another is that we have much to learn from nature. Engineers sometimes find that their best techniques have been anticipated by nature. Examples include the streamlined design of fish and the counter-current mass-transfer operation of the kidney. An examination of strategies employed by nature has led to the discovery of new techniques that can be exploited in systems having nothing to do with biology. For instance, the mathematical pattern-recognition method called the *artificial neural network* was inspired by an understanding of brain function. New process control methods are being developed by reverse-engineering biological systems. Furthermore, there may be much that engineers can bring to the study of biological systems. For example, the polymerase chain reaction technique that has so revolutionized genetic engineering was developed by a biologist who was starting to learn about computer programming. He borrowed the concept of iteration to produce two DNA molecules repeatedly from one molecule. Twenty iterations quickly turn one molecule into a million.

Engineers can also bring their strengths to the study of biology. Biology once emphasized a qualitative approach called **descriptive biology**. Today it is very much a quantitative science, using mathematical methods everywhere, from genetics to ecology. Finally, it is hoped that for engineers the study of biology will be a source of fascination, opening a new perspective on the world that will complement other knowledge gained in an engineering education.

1.2 PRESENT PERSPECTIVES ON ENVIRONMENTAL ENGINEERS AND SCIENTISTS

Science is defined as “knowledge coordinated, arranged, and systematized” (Thatcher, 1980). The *McGraw-Hill Dictionary of Science and Engineering* (Parker, 1984) defines **engineering** as “the science by which the properties of matter and the sources of power in nature are made useful to humans in structures, machines, and products.”

Thus, engineering is defined as one of the sciences. Yet in the professional world, those who classify themselves as scientists and those who call themselves engineers seem to distinguish themselves from each other. To be sure, engineers study the sciences relevant to their disciplines, although not as deeply as scientists might prefer (the subject of this book being an instance of this). On the other hand, wouldn't scientists benefit from a better understanding of how to apply engineering analysis to their fields? For example, aren't mass and energy balances or transport phenomena useful for analyzing the multiplicity of phenomena affecting a laboratory experiment?

The following comparison of engineers' and scientists' approaches were obtained from the authors' observations, plus informal discussions with science and engineering practitioners. They reflect the perception of differences between engineers and scientists, not necessarily reality. They certainly do not apply to all. A common complaint to be heard from a scientist about an engineer is that the latter "wants to reduce everything to a number" and tends not to look at the system holistically. This may be due to the basic function for which an engineer is trained—to **design**: that is, to create an arrangement of matter and energy to attain a goal or specification, using the minimum amount of resources. Ultimately, this is reduced to such things as how big, how much, or for how long an arrangement must be made. An engineer designing an in situ groundwater bioremediation project uses models and design equations (and judgment) to determine flow rates, well locations, nutrient dosages, duration of treatment, and finally, the financial resources needed to eliminate a subsurface contaminant.

However, nonquantitative factors may be just as important to the success of a project. Are microorganisms present that are capable of utilizing the contaminant? In fact, is the contaminant biodegradable at all? Are the by-products of the biodegradation process more or less toxic than the starting material? Although such considerations are taught in engineering courses, a quick look at homework and exams shows that the emphasis is on the "single-valued outcome," the bottom-line answer.

Paradoxically, there is also a sense in which an engineer's approach is *more* holistic than a scientist's. To make a problem tractable, the scientist may simplify a system, such as by considering it as a *batch* or *closed system*: one in which material cannot cross the boundary. Alternatively, a scientist may restrict systems to be either constant temperature or adiabatic (insulated): a reaction in a beaker, microbial growth in a petri dish, or a laboratory ecosystem known as a **microcosm**. An engineer deals more often with flow or open systems. He or she will literally turn on the pump, adding and removing material and energy. The underlying process is the same from a scientist's point of view. However, the study of open systems is dealt with much more often in engineering courses than in science courses. This study enables scientific principles to be applied more directly to real problems in industrial or environmental situations.

An engineer may be more likely to draw conclusions inductively from previous cases to find solutions to a problem. On the other hand, a scientist prefers to avoid assumptions and to base decisions on case-specific information only. For example, in examining a contaminated landfill, an engineer expects it to be similar to others in his or her experience, until information to the contrary appears. A scientist may be more deductive and may be reluctant to proceed until a thorough study has been conducted. The former approach is more economical, except when unanticipated problems arise. The latter approach is more rigorous but may sometimes be impractical because of cost. One must decide between the risk of overlooking unexpected problems vs. that of experiencing "paralysis by analysis."

A scientist is looking for knowledge; an engineer is looking for solutions. Thus, when an engineer is done with his or her work, a problem has been solved. When a scientist is done, there may be more questions than before.

Engineers are trained to consider the cost-effectiveness of their actions. Economic feasibility may be farther down the list of a scientist's priorities. Some engineers are more willing to make environmental trade-offs; an environmental scientist prefers to "draw the line" against any environmental costs. If wetlands would be destroyed by a project, an engineer may weigh it against the value of the project. If the project is important enough, the value of the wetlands may be compensated for by mitigation or by replacement methods. A scientist may accept the necessity of this, but may still consider the loss of the original wetlands a tragedy.

The tasks of both scientists and engineers are to explain (analyze), predict (forecast), and prescribe (design). A scientist needs to know about all of the individual phenomena that may affect a system and how they are related. An engineer often depends on having a mathematical model to represent the phenomena. If such a model can be created, engineers can produce quantitative results. However, science comes into play again when the limitations of the model are considered. These include extreme conditions where assumptions of the model may be violated and effects of phenomena (and every system will have such phenomena) that are not amenable to mathematical modeling.

For example, suppose that an industry that uses well water from a shallow aquifer is having problems with iron in the water. After use, the water is contaminated with biodegradable organics and ammonia and is treated in a lagoon system before discharge to surface water. In considering the pollutional inputs to the system and an analysis of the groundwater, a scientist, might identify the problem as being due to a recycling effect where some of the water seeps from the lagoon into the soil, whereupon microbially mediated nitrification consumes some of the alkalinity in the water, lowering the pH, dissolves iron from the soil, and then is again taken up in the well. The scientist might then prescribe a long-term solution involving adding alkalinity to the water after use. An engineering approach might be to model the system using acid-base chemistry to predict the effect of the nitrification on the effluent, followed by groundwater flow and water quality modeling to predict the water quality at the well. The model could be used to determine the alkalinity dosage required, leading to a design for the treatment process.

This process started with a scientific analysis and continued with engineering methods. Now, suppose further that after implementation, the lagoon effluent being discharged to the surface water is found toxic to fish. Again, a scientific analysis is called for: a toxicity identification evaluation (TIE). It may be found that at the higher pH, more of the ammonia in the effluent is in non-ionized form, which is more toxic to fish than is the ammonium ion. No one will doubt that science and engineering cannot be divorced from each other, but the better that engineers and scientists understand each other's disciplines, the better the outcome will be.

The engineering approach can be fruitful for scientific inquiry. Consider the problem of explaining why multicellular life-forms evolved. A biologist may think first of survival, fitness, and adaptation. An engineering approach might focus on considerations of energy efficiency and the effect of area/volume ratio on mass and energy transfer between the organism and the environment. Both approaches are valid and contribute to understanding.

Engineers and scientists have much to learn from one another, which they do by working together. In addition, both will profit from a direct study of each other's disciplines.

There are many instances in this book of mathematical or engineering analysis applied to biology. These should help convince engineers that biology really is a “hard” science. By learning and applying knowledge of biology, engineers can help convince scientists that engineering isn’t always simplification and abstraction—that they can take into account the full complexity of a system. At the same time, engineers should be humble about their capability. The following statement by LaGrega et al. (2001) with respect to toxicology should be true of other biological disciplines as well: “What is the single, most important thing for an engineer to know about toxicology? The engineer cannot and should not practice toxicology.” Still, the more the nonspecialist understands, the better his or her decision making will be.

1.3 PAST PERSPECTIVES ON ENVIRONMENTAL ENGINEERS AND SCIENTISTS

Environmental biology is not a unified discipline. Almost every chapter in this book could constitute a different field with its own history. What we can describe here is a bit of history of the development of the associations that have formed between biology and environmental engineers.

Barely a century ago, environmental and sanitary issues were largely the domain of scientists rather than engineers. In fact, long before the practice of environmental engineering had ever been conceived, physicists, chemists, and biologists were already hard at work investigating a range of pollution problems that they recognized as a serious threat.

These sorts of concerns about procuring clean waters and discarding wastes safely had actually been documented and addressed for at least two millennia. However, by the time that Charles Dickens had written his classic, *A Tale of Two Cities*, the “worst of times” had truly befallen most industrialized countries. Humankind’s waste emissions had finally overtaxed nature’s assimilatory capacity, and the telltale signs were readily evident. Skies were blanketed with coal smoke and soot, rivers were befouled with a sickening blend of filth, and waste piles offered frightful opportunities for the dissemination of disease.

In the latter half of the nineteenth century, the heightened level of pollution brought by the Industrial Revolution triggered a response from scientists, whose contributions continue to this day. For example, one of England’s leading chemists, Edward Frankland, routinely monitored water quality changes in the Thames River, and his microbiologist son, Percy, tried to resolve the bacterial reactions found in sewage. John Tyndall, a renowned physicist, focused a considerable amount of his talent on air quality and contaminant analysis problems. Charles Darwin’s eminent friend and staunch supporter, Thomas Huxley, played a major role in the cause of sanitary reformation as a practical extension to his expertise in biology.

The roots of our modern practice of environmental engineering sprang largely from the sciences. These investigators were not motivated by regulatory requirement, legal threat, or financial gain. Instead, their fledgling efforts were effectively compelled by personal concerns about an environment whose quality had already deteriorated seriously. These scientists had been trained to appreciate the balance of nature and were duly concerned about the stress imposed by a rapidly escalating range of pollution problems. It was the field of biology, however, which truly gave these yesteryear environmental efforts their

highest motivation. Biologists working at the end of the nineteenth century demonstrated successive refinements in their sense of awareness and appreciation for the technical importance of the environmental problems that they faced.

The connection between biology and environmental engineering is best demonstrated by tracing the academic lineage extending beyond Thomas Huxley's seminal work with sanitary health. Although apparently self-educated, Huxley was a preeminent leader in the emerging field of biology late in the nineteenth century and gained worldwide recognition for his forceful backing of Charles Darwin's evolutionary theories. Having been invited to present the opening speech for Johns Hopkins University's inaugural ceremony in 1894, he used the opportunity to recommend one of his students H. Newell Martin, as chairman of the first biology department in the United States. Under Martin's leadership, students were imbued with an inherent sense of "environmental" concern. For William Sedgwick, this issue became a lifelong cause. After receiving his doctorate, Sedgwick joined the biology program at Harvard, where he introduced a radical new focus on sanitary matters. Together with his own student, George Whipple, he then cofounded public health programs at Harvard and the Massachusetts Institute of Technology (MIT), which in the coming years would lead formatively to distinct academic offerings in public health, sanitation, and industrial hygiene. At much the same time, Sedgwick and Whipple created a technical program at MIT that dealt with the applied aspects of sanitary science, thereafter known as the first-ever environmental engineering program.

1.4 AMBIGUITY AND COMPLEXITY IN BIOLOGY

Often in fields such as physics or engineering it is possible to identify all the variables that affect a process (in terms of a model). In fact, the number of variables can be reduced to a minimum by the use of dimensional analysis, producing a set of dimensionless numbers that describe a situation completely. In biology, it is more common for there to be unknown influences and obvious gaps in our knowledge. Consequently, many biological "facts" are conditional—answers often have to be prefaced with "it depends..." or important questions may be totally lacking an answer. Despite the recent explosion of knowledge in chemical genetics, we still cannot give a satisfactory explanation of how an embryonic cell "knows" to grow into part of a fingertip and not a hair follicle. We need to have a certain humility in our studies:

In school we start each course at the beginning of a long book full of things that are known but that *we* do not yet know. We understand that beyond that book lies another book and that beyond that course lies another course. The frontier of knowledge, where it finally borders on the unknown, seems far away and irrelevant, separated from us by an apparently endless expanse of the known. We do not see that we may be proceeding down a narrow path of knowledge and that if we look slightly left or right we will be staring directly at the unknown. (Gomory, 1995)

Few appreciate the difficulty of making ironclad distinctions in the study of biology. Actually, the same is true for all fields, although it is perhaps more apparent in biology. In engineering, the mathematical constructions create an abstract ideal out of concepts. When we speak of the velocity of water in a pipe, the idea seems very clear and can be manipulated fairly unambiguously, such as to compute flow or pressure drop. However,

if the turbulent nature of the flow is examined in detail, we find that we need to use probability distributions to describe the velocity, and even that is incomplete. We use the simplified abstraction so often, and with such success, that we often forget the underlying complexity.

In biology, the uncertainties behind the abstractions are often closer to the surface. For example, consider the concept of *species*. We would like to define species such that all living things belong unambiguously to a species. This turns out to be impossible. One definition is that a **species** is a group of organisms that interbreed with each other in nature and produce healthy and fertile offspring. Thus, the horse and the donkey are different species even though they can mate, because all their offspring are infertile. A number of problems occur with this definition. First, not all organisms reproduce by breeding (sexual reproduction). More important for this discussion is that there are populations we would like to define into separate species that can interbreed, such as the domestic dog and the African golden jackal. So perhaps we would alter the definition to include organisms that can *potentially* interbreed. However, there are cases in nature where organism A can breed with B, B with C, C with D, but D cannot breed with A.

Similar problems occur every time we make a classification. The euglena is a single-celled organism that can move at will through its aqueous environment. This motility, together with its lack of a cell wall, would indicate that it should be classified as an animal. However, it has the green pigment chlorophyll, which enables it, like a plant, to capture light energy. Biologists have created a separate category, the protists, in part to eliminate the problem of where to put the euglena. However, some protists, the algae, are very similar to plants; others, such as protozoans, are animal-like. Thus, the classifications lack an iron-clad quality. Textbook definitions sometimes include the word *mostly*, as in “animals are mostly multicellular.”

Whether an organism is single-celled or multicellular is an important characteristic used in classification. However, some may either be at different stages in their life cycle or may simply change in response to environmental conditions. The slime mold is an unusual organism that grows on the forest floor and behaves at one stage as a mass of single-celled protozoans; at another stage the cells fuse into a single supercell with many nuclei; and at yet another stage it forms fruiting bodies on stalks resembling a plant.

Another idea that must be recognized as somewhat arbitrary is the notion of an *event*. This is another kind of useful fiction. In classical science (i.e., other than in quantum mechanics), there are no events, only processes. Consider the “moment of conception,” when a sperm enters and fertilizes an egg. Examined more closely, we must realize that the event consists of a sequence of changes. If we say that fertilization occurs as soon as a sperm penetrates an egg’s cell membrane, we must ask, “penetrates how far?” If, instead, we place the event at the moment that the chromosomes join into a single nucleus, we must ask how complete the joining must be. It is like asking when two asymptotic curves combine. The problem is not that science cannot say when the critical moment occurs. No such moment actually exists.

Another thing that is important to appreciate about biology is that a certain amount of caution is necessary when making predictions or judgments about the validity of reported observations. Living things often surprise and contradict. The following quote by the Dutch biologist C. J. Bregèr (1958) applies as well to biology as a whole: “The insect world is nature’s most astonishing phenomenon. Nothing is impossible to it; the most improbable things commonly occur there. One who penetrates deeply into its mysteries

is continually breathless with wonder. He knows that anything can happen, and that the completely impossible often does.”

There is no perfect way around these difficulties; the complexity of nature sometimes resists our attempts to coordinate, arrange, and systematize it. All life-forms are unique, defying easy classification; so we create a working definition and go on. We must use the distinctions when they are useful and alter them when they’re not.

Biology is also unique in the number of levels of scale that it is necessary to examine in its understanding. In Section 2.2 we describe how living systems can be examined at many levels of detail, from the chemical to the cell to the organism to the ecosystem. Within each level are numerous types of entities (e.g., cells or organisms) and myriad instances of each type. The number of potential interactions is staggering. Sometimes the reductionist approach is appropriate and an individual entity or interaction will be studied almost in isolation. Other times it is necessary to look holistically at the behavior of the group.

It is often the goal of scientific studies to “explain” behaviors observed at one level by looking at behaviors of its component parts. For example, the primary productivity (production of algal biomass) of a eutrophic lake can be predicted by measuring the productivity of individual species cultured in a lab under similar conditions. However, it is often the case that the aggregate behavior of numerous individuals cannot be predicted straightforwardly, even if the behavior of the individuals were well understood. For example, proteins are polymers of 20 different amino acids, in varying sequences. Although the individual amino acids do not function as catalysts, proteins do. A protein is not simply the “sum of its parts.” “New” properties that arise from the interaction of numerous similar parts are called **emergent properties**. A mathematical field of study called **complexity theory** has arisen to study the relation between large numbers of interacting autonomous parts and resulting emergent properties.

A related source of complexity is chaotic behavior. **Chaos** is dynamic behavior characterized by “extreme sensitivity to initial conditions.” Consider the sequence of real numbers, (x_1, x_2, \dots) between 0.0 and 1.0 generated by what is known as the **quadratic iterator**:

$$x_{i+1} = 4x_i(x_i - 1) \quad (1.1)$$

Figure 1.1 shows plots of two such series that start at nearly the same point, 0.9000 and 0.9001, plus a plot of the difference between the two series. Note that after a dozen iterations the two series become uncorrelated. The difference between the two series seems almost random. This demonstrates that although we know the rule generating the data, without perfect knowledge of the initial condition, we cannot predict very far into the future. This extreme sensitivity to initial conditions is also called the **butterfly effect**, after the analogy for chaos in weather systems which states that a butterfly flapping its wings in Beijing can cause a hurricane in New York City two weeks later.

A consequence of chaotic behavior is that extremely complex behaviors can result from very simple rules, as in the example just given. The paleontologist Steven Jay Gould proposed that small mutations can greatly alter body plans, producing great leaps in evolution. The benefit of this for the study of biology is that complex processes do not rule out the possibility of simple explanations. The difficulty is that it places a limit on the reductionist view. Having a high degree of understanding of the dynamics of nerve cells does little to explain how the human brain can so quickly recognize a face or decide on a chess move.

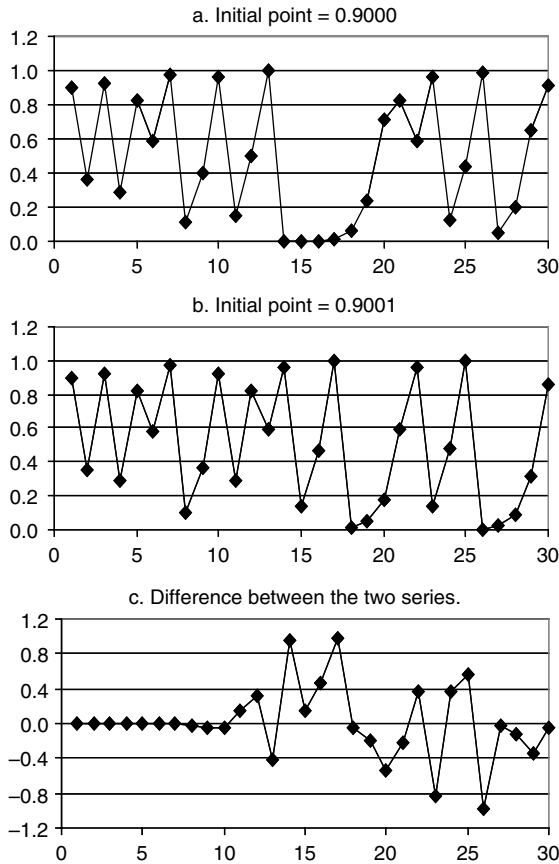


Figure 1.1 Quadratic iterator, illustrating chaotic behavior and extreme sensitivity to initial conditions.

1.5 CONSERVATION AND ENVIRONMENTAL ETHICS

The study of biology helps create an increased appreciation for the natural world. It causes us to question our collective and individual actions that may harm it. However, we seem to be constrained in our concern by our own need for survival. What is needed is an ethic to answer questions such as: How should we value the natural world? What is our place in it? What are our responsibilities toward it?

Why do we pollute, in effect spoiling our own nests? The problem is in a paradox of individual freedom that is called the **tragedy of the commons** (Hardin, 1968):

The tragedy of the commons develops in this way. Picture a pasture open to all. It is to be expected that each herdsman will try to keep as many cattle as possible on the commons. Such an arrangement may work reasonably satisfactorily for centuries because tribal wars, poaching, and disease keep the numbers of both man and beast well below the carrying capacity of the land. Finally, however, comes the day of reckoning, that is, the day when the long-desired goal of social stability becomes a reality. At this point, the inherent logic of the commons remorselessly generates tragedy.

As a rational being, each herdsman seeks to maximize his gain. Explicitly or implicitly, more or less consciously, he asks, “What is the utility to me of adding one more animal to my herd?” This utility has one negative and one positive component.

1. The positive component is a function of the increment of one animal. Since the herdsman receives all the proceeds from the sale of the additional animal, the positive utility is nearly +1.
2. The negative component is a function of the additional overgrazing created by one more animal. Since, however, the effects of overgrazing are shared by all the herdsmen, the negative utility for any particular decisionmaking herdsman is only a fraction of -1 .

Adding together the component partial utilities, the rational herdsman concludes that the only sensible course for him to pursue is to add another animal to his herd. And another. . . . But this is the conclusion reached by each and every rational herdsman sharing a commons. Therein is the tragedy. Each man is locked into a system that compels him to increase his herd without limit—in a world that is limited. Ruin is the destination toward which all men rush, each pursuing his own best interest in a society that believes in the freedom of the commons. Freedom in a commons brings ruin to all.

Morality is about when we should act against our own immediate self-interest. **Ethics** is the study of systems for deciding the morality, or rightness or wrongness, of our actions. **Environmental ethics** is the study of the morality of actions that affect the environment. An understanding of environmental ethics will help us to apply the knowledge and power we gain from our education.

It is a popular saying that one cannot teach someone to be ethical. This is not true. Public educational campaigns are often used with good effect to encourage “right” behavior, such as to institute recycling programs. Furthermore, an understanding of ethical principles can help counter specious or just plain wrong arguments that people sometimes use in support of self-serving actions. Finally, an understanding of ethics can help guide and reinforce those who want to do the right thing.

A **moral principle** is a rule or set of rules used to decide moral questions. Several moral principles have been proposed that are specific to our effect on the environment. A moral principle will not be an infallible guide to behavior. We will still be faced with dilemmas in which each alternative has its own moral cost.

What is the basis of moral principles? James Q. Wilson argues that we have inborn “moral senses,” including the senses of sympathy, fairness, self-control, and duty. These senses then propel the development of moral principles. The Harvard biologist Edward O. Wilson postulates that concern for the environment stems from an innate affinity that people have for all living things, a principle he calls the **biophilia hypothesis**. This affinity becomes most apparent when contact with living things is limited. Antarctic researchers who are isolated over the winter must ration time spent in the plant growth chamber. The station’s doctor prescribes such time to treat depression. NASA has conducted experiments in which crews are isolated in closed environmental systems for as long as 90 days to simulate space missions. The crew in one such experiment found that one of their greatest pleasures was growing their small lettuce crop. Planting and harvesting decisions were made only after considerable group discussion, and crew members often enjoyed opening the growth chamber just to look at the plants.

Two basic types of ethics are utilitarian ethics and rights-based ethics. **Utilitarianism** is the principle that rules or acts are moral if they produce the greatest amount of good for all concerned. A problem for utilitarianism is that some may suffer unfairly for the greater

good of the majority. **Rights-based ethics** get around this problem by postulating moral rights that are universal (possessed by all), equal (no one has the right in any greater or lesser degree than another), inalienable (cannot be given up or taken away), and natural (not created by human acts, as are legal rights). A major problem with rights-based ethics is that different rights may conflict, and criteria need to be selected for choosing among them.

Both of the aforementioned types of ethics are focused on needs of individuals and thus are **humanistic**. Some propose a holistic ethic that places value on systems rather than individuals. This approach is used to raise to the level of moral principles ideas such as the diversity and integrity of ecosystems or the sustainability of economic systems.

The Judeo-Christian tradition forms the basis of much of Western thought. Various interpretations have been applied to its view of the relationship between humans and the rest of the natural world. A negative view has been blamed on the biblical injunction to “have dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing that creepeth upon the earth. . . . Be fruitful, and multiply, and replenish the earth, and subdue it: and have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth” Genesis 1:26–28.

However, other passages imply that all of creation has value. Genesis 1:31 states that “God saw every thing that he had made, and, behold, it was very good.” The animals are also commanded to be fruitful and multiply. This leads to the **stewardship** concept, which states that humans have responsibility for the protection of creation. In any case, the Western tradition developed in which humans were viewed as the center and pinnacle of creation, a notion that is called **anthropocentrism**.

Some Asian religions, such as Zen Buddhism, Taoism, and Hinduism (especially the Buddhists), teach unity with nature, including compassion toward other humans as well as animals. For native Americans, unity means an interdependence and kinship between all animals, including humans, and natural systems. They believe that all animals have spirits that deserve respect. Animals can only be killed out of necessity, after which humans have to make apologies and atonement to the spirit of the killed animal. Many tribes also link their identity to prominent landscape features.

The Darwinian revolution dethroned humans from their special position in creation. Instead, they are part of a continuum with the animals, plants, and ultimately with the nonliving chemical world. The other parts of the living and nonliving world are seen as kin, which gives us an incentive to make our ethic include that which is good for them.

The wildlife biologist and amateur philosopher Aldo Leopold (1949) proposed such an ethical system in his book *A Sand County Almanac*. He calls it the **land ethic**. This book is considered the “gospel” of the conservation movement, much as Rachel Carson’s (1962) *Silent Spring* sounded the alarm that stimulated the environmental movement. The idea of a land ethic is developed further by Callicott (1986).

Leopold describes how ethics developed from responsibilities toward other people. Eventually, these responsibilities were expanded to include the family and the clan, and then larger and larger groups, ultimately encompassing all of society. As the boundaries of the community expanded, the inner ones remained. These can be viewed as a concentric hierarchy of responsibilities to larger and larger communities (Figure 1.2): from self to nuclear family, extended family, clan, nation, and all of humanity. A person’s responsibility toward the outer rings does not cancel the inner ones, but rather is layered

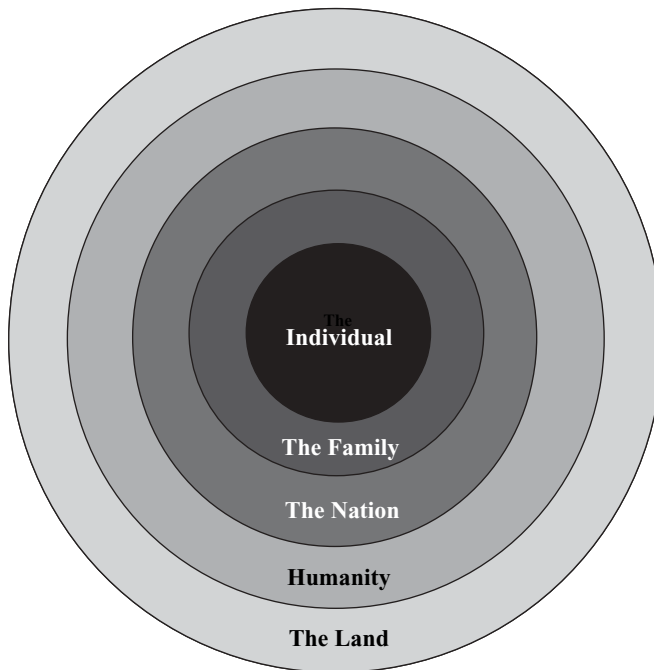


Figure 1.2 Hierarchy of responsibility in the land ethic.

over them. Leopold's contribution was to describe this hierarchy and to extend the idea of community to include the land. By the land he meant not just the soil but the pyramid of energy starting with the soil, to the plants it supports, the herbivores that live on the plants, the predators that depend on all the levels below it, and the organisms of decay that return the nutrients to the soil.

Furthermore, the particular responsibilities due each layer in the hierarchy are different. One does not owe all of humanity the same share of attention and resources that is owed to family members. So what is our responsibility to the land? According to Leopold, human use of the land should preserve and enhance the diversity, integrity, stability, and beauty of the biotic community. This does not prohibit our use of natural resources but requires that we do so in a sustainable way with a minimum of waste.

This leads us to one of the great moral challenges before our society. At the same time that the world's population continues to increase, the per capita use of natural resources is also increasing, and wilderness habitats are continually giving way to human uses. Optimists may expect that continuing technological developments will enable growth to continue. However, eventually we will have to achieve a steady-state condition in which resources are consumed at essentially the same rate at which they are regenerated. Humans have the capacity to plan, so society has the potential to bring about such a steady state without having it imposed by catastrophe. How will such a "sustainable society" look? What will be its population, how much will each person have to eat, and how much will remain of the wilderness and biodiversity that we have today? Although a sustainable society may take generations to become reality, it will never happen unless earlier generations begin to bring it about.

A final note of particular relevance to an engineer or scientist is **professional ethics**, often stated in a **code of ethics**. An example is the code of ethics adopted by the American Society of Civil Engineers, which states their responsibilities to the environment:

- Engineers uphold and advance the integrity, honor, and dignity of the engineering profession by using their knowledge and skill for the enhancement of human welfare.
- Engineers shall hold paramount the safety, health, and welfare of the public in the performance of their professional duties.
- Engineers should be committed to improving the environment to enhance the quality of life.

1.6 GUIDELINES FOR STUDY

In many of the fields of science the task of “coordinating, arranging, and systematizing” the knowledge can be difficult precisely because mathematics cannot easily be applied. Although mathematics has the reputation of being a difficult subject, it is tremendously efficient at compressing information. If a picture is worth a thousand words, an equation is worth a thousand pictures. Consider, for example, the effect of temperature, volume, and composition on the total pressure of a mixture of three solvents in equilibrium with its vapor, or the shape of the cone of depression around a well as it depends on soil permeability and water flow. We cannot easily visualize high-dimensional relationships, so they must be represented by a family of curves. Alternatively, the information could be contained concisely in a single mathematical representation. However, biological systems often are not described so compactly.

This leads us to discuss how to approach the study of biology. The method usually first thought of is to apply memorization. This is laborious and unproductive. It is extremely difficult to keep numerous unconnected facts in your head for any amount of time. The key, then, is to establish connections, to seek out relationships. This recovers some of the efficiency of the mathematical equation. We can think graphically about concepts, mentally plotting developmental trends, sequences, patterns, and networks of relationships.

Make studying an active process by keeping notes: Outline the reading and write lists, even lists of lists, under a unified topic. See if you can create an explanation of the concepts in each section of this book in your own words. If you have trouble with this at some point, you should formulate the difficulty as a question and seek the answer in the references or from your instructor. To learn a complex relationship from a figure such as the oxidation of glucose in Figure 5.5 or the nitrogen cycle in Figure 14.7, try copying it (possibly with less detail), and then try reproducing it again with the book closed.

Create what are known as **concept maps**. These are graphical representations of the relationships among information. For example, Figure 1.3 shows a concept map for science and engineering science topics in environmental engineering education, emphasizing the place of biology and leading to the twin roles of environmental engineers: design and prediction. To create a concept map, start with a list of related concepts. Then, state an **organizing principle**, which is a concept or idea used to arrange and connect items appropriately. The organizing principle behind Figure 1.3 is that connections lead from one topic to others that require their application. Another arrangement of

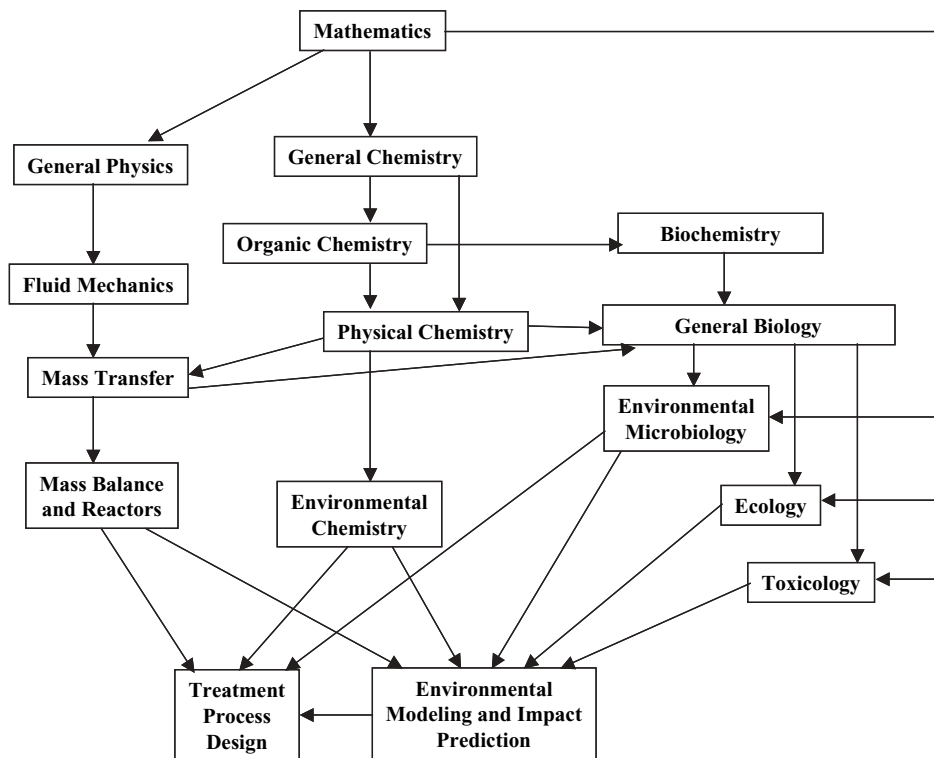


Figure 1.3 Concept map.

the items could have been created using a different organizing principle, for example as the sequence in which the subjects developed historically.

Such data structures organize and compress information, creating a mentally retrievable path to the information when called for. There is no right or wrong way to create structures. As long as it makes sense to you, it's right. The act of creating them results in learning. In addition, this technique is an excellent way to communicate any kind of technical data to others.

Besides the organizing techniques just described, the major activity for the study of biology is simply to read. Read beyond the required material. Seek out the references—these expand and reinforce the basic concepts. Multiple sources of information on the same topics can provide alternative viewpoints that highlight and clarify the key information.

PROBLEMS

- 1.1. Create a concept map using the chapters of this book as a starting list of items to be related. What organizing principle are you using?
- 1.2. How would responsibility to your employer or to your consulting client fit into Aldo Leopold's hierarchy? Where do government regulations come in?

REFERENCES

- Briejèr, C. J., 1958. The growing resistance of insects to insecticides, *Atlantic Naturalist*, Vol. 13, No. 3, pp. 149–155.
- Callicott, J. B., 1986. The search for an environmental ethic, in *Matters of Life and Death*, T. Regan (Ed.), Random House, New York.
- Carson, Rachel, 1962. *Silent Spring*, Houghton Mifflin, Boston.
- Gleick, J., 1987. *Chaos: Making a New Science*, Viking Penguin, New York.
- Gomory, R. E., 1955. The known, the unknown and the unknowable, *Scientific American*, June.
- Gunn, A. S., and P. A. Vesilind, 1988. *Environmental Ethics for Engineers*, Lewis Publishers, Chelses, MI.
- Hardin, Garrett, 1968. The tragedy of the commons, *Science*, Vol. 162, pp. 1243–1248. See also <http://dieoff.org/page95.htm>.
- Kellert, S. R., 1997. *Kinship to Mastery: Biophilia in Human Evolution and Development*, Island Press, Washington, DC.
- LaGrega, M. D., P. L. Buckingham, and J. C. Evans, 2001. *Hazardous Waste Management*, McGraw-Hill, New York.
- Leopold, Aldo, 1949. *A Sand County Almanac*, Oxford University Press, New York.
- Martin, M. W., and Roland Schinzinger, 2005. *Ethics in Engineering*, McGraw-Hill, New York.
- Parker, S. P. (Ed.), 1984. *McGraw-Hill Dictionary of Science and Engineering*, McGraw-Hill, New York.
- Thatcher, V. S. (Ed.), 1980. *The New Webster Encyclopedic Dictionary of the English Language*, Consolidated Book Publishers, Chicago.
- Waldrop, M. M., 1993. *Complexity: The Emerging Science at the Edge of Order and Chaos*, Touchstone Books, New York.
- Wilson, J. Q., 1993. *The Moral Sense*, Free Press, New York.

2

BIOLOGY AS A WHOLE

In this chapter we provide an overview of the broad topic of biology. Much of biological science, as well as the chapters of this book, is *reductionist*. That is, systems are studied by focusing on their component parts. However, in this chapter we examine biology *holistically*, stepping back and looking at concepts that connect all of its disparate components.

The most basic concept, which forms the foundation of the entire structure of biology, is the definition of life. A “vertical” view of the structure generates a hierarchy of scale from biochemical reactions to the ecosystem. A “horizontal” view displays the classifications of living things, the pigeonholes that biologists use to group organisms into species, families, and so on. Connecting the parts of the structure is the theory of evolution, the grand organizing principle that gives the structure resilience, explaining why things are as they are. Finally, stepping back a bit, one can examine the two-way interactions between the structure and its surroundings, the environment.

2.1 WHAT IS LIFE?

First, we must define our subject. *Biology* is the study of living things. What, then, is the definition of *life*? For the most part, none of us would have trouble distinguishing living from nonliving things. Therefore, we will make our definition to include everything we consider to be alive and to exclude the nonliving things. This must be done carefully because we can sometimes find counterexamples to particular rules. Doesn't a crystal grow and possess order? Have you ever seen a polymer solution climbing out of a glass (motility)? Aren't there computer programs that reproduce and evolve? What about virus particles? Viruses are crystalline particles that must take over the cell of an

ordinary organism in order to reproduce. Should we make our definition include them? Even if we do, it turns out that there are infectious agents, viroids and prions, which are even simpler in structure, possibly even single molecules.

It should be obvious that this is one of those somewhat arbitrary questions that often arise in biology. Recognizing this, and also that there may be alternative definitions, let's go ahead and make our definition as best we can:

A living thing is a discrete entity, or **organism**, that has the following characteristics:

- It can **capture useful energy** from its surroundings.
- It can **extract materials** from its surroundings for growth and maintenance of its structure.
- It is **responsive**—it reacts to its surroundings, using energy and material to move or grow.
- It **reproduces**—it generates other organisms like itself, preserving its own characteristics by passing them on to succeeding generations.
- It **adapts** and **evolves**—successive generations can change as the environment changes; individuals exhibit **adaptations**, that is, they are specialized for a particular function in a particular environment.

Other characteristics sometimes mentioned are that life is **orderly** and **complex**; that it is capable of **motility**, or movement, which is a type of response; that it exhibits **development**, in which its complexity increases progressively; and that it has **heredity**, in which its characteristics are passed to its offspring as it reproduces.

So, is a virus alive? It is capable of evolution and reproduction, but it clearly fails in the first two of the criteria above. Strictly adhering to the criteria, the answer would be no. However, this might not be satisfying to some, who feel intuitively that they should be included. It may be that the best answer would be just to say that “viruses have several of the characteristics of living things” and leave it at that. To press the question further may be meaningless. Certainly, the topic of viruses belongs in a book on biology. On the other hand, the line may be drawn to definitively exclude viroids and prions. These may be considered to be chemical substances with infectious behavior.

Textbooks often do not mention at this point in the discussion another criterion for life that is commonly used by biologists:

- All living things are composed of cells.

A **cell** is the smallest entity completely surrounded by a **membrane** and containing a **nuclear region**, which stores the hereditary information used for growth and reproduction, and **cytoplasm**, which is a gel-like substance between the membrane and the nuclear region. With this additional criterion, viruses are clearly excluded, since they lack a membrane and cytoplasm.

Life may also be described in thermodynamic terms. The molecules in any isolated system (a system whose boundaries are sealed to both matter and energy) tend to rearrange themselves by random processes. For such systems of even moderate complexity, of all the possible random arrangements the “orderly” ones are extremely rare. Thus, such systems tend to rearrange into “disordered” systems. This behavior is described by the *second law of thermodynamics*, which states that **entropy**, a measure of disorder, tends to increase *in isolated systems*.

But Earth is not an isolated system. It receives energy in the form of visible and ultraviolet light and emits the same amount of energy to space in the lower-grade form of infrared radiation. As this energy passes through the living world, part of it is used to do the work of countering the increase in entropy on Earth. In fact, living things use energy to cause a local decrease in entropy. The infrared emission to space results in an even greater increase in entropy outside the Earth, so that the total entropy of the universe still is found to increase.

Erwin Schrödinger (1956), developer of the quantum wave equation, described these ideas in a book entitled “What Is Life?”:

Thus a living organism continually increases its entropy—or, as you may say, produces positive entropy—and thus tends to approach the dangerous state of maximum entropy, which is death. It can only keep aloof from it, i.e. alive, by continually drawing from its environment negative entropy—which is something very positive as we shall immediately see. What an organism feeds on is negative entropy. Or, to put it less paradoxically, the essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive.

Later, he continues:

Hence the awkward expression “negative entropy” can be replaced by a better one: entropy, taken with the negative sign, is itself a measure of order. Thus the device by which an organism maintains itself stationary at a fairly high level of orderliness (= fairly low level of entropy) really consists in continually sucking orderliness from its environment. ... After utilizing it they return it in a very much degraded form—not entirely degraded, however, for plants can still make use of it. (These, of course, have their most powerful supply of “negative entropy” in the sunlight.)

This “negative entropy” can be identified with the thermodynamic concept of Gibbs free energy, described in Section 5.1.1.

2.2 THE HIERARCHY OF LIFE

One way to examine living things is to look at them with different degrees of magnification, as it were, from the atomic level to cells, to organisms, to standing back and looking at Earth as a whole. The following lists the levels of detail in this hierarchy:

Metabolism	All of the chemical reactions within an organism that sustain life.
Organelle	Subcellular structures within cells that carry out specialized functions.
Cell	The basic unit of life, a structure completely surrounded by a membrane, containing a nuclear region and cytoplasm; the smallest structure capable of having all of the characteristics of life.
Tissue	A group of similar cells having the same function in a multicellular organism.
Organ	A single structure of two or more tissues that performs one or more functions in an organism.
Organ system	A group of organs that carry out related functions.

Organism	An individual entity that has all of the characteristics of life described above and possessing the same hereditary information in all its cells.
Population	A group of individuals of the same species living in the same environment and actively interbreeding.
Community	A group of interacting populations occupying the same environment.
Ecosystem	The combination of a community and its environment.

To understand the last several items, it is necessary in addition to define **environment**: the physical and chemical surroundings in which individuals live. Strictly speaking, the environment does not have boundaries. In practice, of course, it is common to restrict the discussion to a particular region, such as a single forest, a particular glen within that forest, or just the soil in a glen in a forest.

The first half of this book is organized roughly along the lines of the hierarchy. A more detailed description of the items in the hierarchy follows.

Metabolism This is the view of life at the chemical level. The study of chemical reactions in organisms is called **biochemistry**. The reactions can be classified into (1) energy conversion reactions, (2) synthesis and breakdown of cell material, and (3) reactions associated with specific functions such as reproduction or motility.

The energy conversion reactions include those that capture energy from sunlight (photosynthesis) and convert it into food or that convert food energy into a simple form that is available for other reactions (respiration, fermentation). The synthesis reactions include production of the components of the major constituents of cells, such as proteins, carbohydrates, and lipids (which include fats), or minor ones (in terms of mass), such as nucleic acids, hormones, and vitamins. Reactions that break molecules down into simpler forms may facilitate the removal of waste products.

All of the metabolic reactions are connected to each other by a web of **metabolic pathways**, which consists of sequences of biochemical reactions. A particular compound can often participate in several reactions, thus becoming a link between those pathways.

Organelles Some of the specialized functions carried out by these substructures include protein synthesis, photosynthesis (the conversion of light energy to chemical energy), and respiration (the release of chemical energy into a form usable by cells). The organelles that perform these functions are the **ribosomes**, the **chloroplasts**, and the **mitochondria**, respectively. There are many other organelles, especially in higher organisms. Not all cells have all types of organelles.

Cells All living things are made of cells. Some are composed of a single cell and are called **unicellular**. Organisms made of more than one cell are called **multicellular**. A key structure of all cells is the **plasma membrane**. This separates the cell contents from its environment and forms the boundary of many of the cell's organelles. There are two primary types of cells. The **prokaryote** is the simpler of the two. It has no internal membrane structures, and the only organelle is the ribosome. Bacteria are typical prokaryotes. The other type is the **eukaryote**, which has internal membrane-bound structures such as mitochondria and chloroplasts. All the plants and animals are eukaryotic organisms, as are some single-celled organisms such as protozoans and algae.

Tissues These are present only in multicellular organisms, of course. Examples include muscle tissue, bone tissue, or nerve tissue. Tissues should not be confused with organs. Although they may be composed predominantly of one type of tissue, organs may also be formed from a variety of tissues.

Organs This is a complete unit such as an entire muscle, a bone, or the brain. Many organs serve a single function. Others organs have multiple functions, such as the pancreas and the adrenal gland. Both of these glands produce more than one hormone, which have unrelated functions.

Organ Systems Some organs work in concert with each other and form a system. Examples are the nervous system, the circulatory system, the respiratory system, the skeletal system, and the endocrine system.

Organism An organism is a living thing with a single **genome** (the set of hereditary information contained in all its cells' nuclear regions), which exists, for at least part of its life cycle, in the environment and separately from others of its kind. Some organisms, such as the algae and the fungi in lichens, must live together, but they have different genomes. Others live in colonies but exist separately at an earlier stage of their lives. An example of the latter is the jellyfish, which is really a colony of organisms that started out as free-swimming larvae. The individual cells of a jellyfish may come from different parents, yet it is difficult not to think of a jellyfish as a single organism. This is another example of the difficulty in making distinctions in biology.

Population Examples of populations include all of the striped bass that breed in the Hudson River (although they spend most of their lives in the Atlantic Ocean), and the *Nitrosomonas europaea* bacteria in a biological wastewater treatment plant.

Sometimes the definition of population is extended to any group of organisms sharing a characteristic, such as the population of invertebrates (animals lacking an internal skeleton) in the soil, or the population of deer ticks that carry the Lyme disease bacteria. Thus, in this usage, a population may either incorporate more than one species or may be a subset of a species. Although such usage is common, it should be avoided. It would be more proper to label multiple-species groups as *populations* (note the plural) and to call the subset of a species a *subpopulation*.

Community Strictly speaking, a community comprises all of the organisms in a region. Thus, an earthworm may be considered a member of a number of communities, depending on the region defined: It may be a member of the soil community, the forest community, or the community of organisms on a particular island in a lake.

The word *community* is sometimes used in a looser sense, similar to the second usage of the word *population* described above. For example, some may speak of the community of soil bacteria when they are concerned about the interactions among those members, even though there are other species in the same environment. Again, it would be more precise to use the term *populations*.

Ecosystem The ecosystem is the most inclusive unit studied in biology. Again, the term may be restricted to local systems, such as a particular lake, or an island and nearby waters. Strictly speaking, since all of these systems are interconnected, there is really

only one known ecosystem—the Earth's. This all-inclusive ecosystem is also known as the **biosphere**.

2.3 EVOLUTION

Evolution is the process of genetic change by which species adapt to their environment or develop new ways of coping with environmental stress. The theory of evolution is the most fundamental organizing principle in biology. It can be invoked to explain the origin of almost any feature of living things. By the early nineteenth century enough geological and fossil evidence had accumulated to challenge the prevailing idea that Earth and the life on it were unchanging. Jean-Baptiste Lamarck then proposed the ultimately rejected theory that species evolved by passing on new characteristics that were acquired by changes during their lifetime. For example, it was suggested incorrectly that early giraffes stretched their necks by reaching for leaves from high branches and that their offspring retained this change.

Two English naturalists then developed a better explanation for evolution. From 1831 to 1836, Charles Darwin served on the round-the-world voyage of HMS *Beagle*. His observations in South America, especially in the Galápagos Islands off Ecuador, led him to form the modern theory of evolution. Darwin wrote a summary of the theory in 1842 but did not publish it immediately. Independently, and several years later, Alfred Russell Wallace developed the same ideas, even using the same term, *natural selection*. After Wallace published several papers he sent one to Darwin, asking him to forward it to the Linnean Society for publication, which Darwin did. Darwin then rushed his own life's work into print in 1859 (giving proper credit to Wallace) in the form of the book *The Origin of Species*.

Our modern understanding of evolution is based on genetic theory. However, its original development preceded that knowledge. Here a detailed discussion of heredity and genetics is deferred to Chapter 6. Evolution can be described based on the understanding that individuals in a population vary in numerous traits (observable characteristics) that can be inherited by their offspring. The traits may be of various types, such as **morphological** (related to structure, such as height or shape of the eyes), biochemical (such as the ability to produce their own vitamin C), or even behavioral (e.g., aggressiveness in dogs).

The theory of evolution can be reduced to two mechanisms that act in combination:

1. **Random variation.** The sources of the variation in traits within a population are random mutations in the genetic code, and sorting and recombination of genetic material that occurs during *meiosis*, a type of cell reproduction. Only a minority of genetic changes may confer an advantage on an individual. In fact, most changes are probably fatal and are not passed on to future generations. Mutations are caused by errors in the biochemical processes of reproduction in which the genetic material is copied for progeny, or by damage from chemical or physical agents such as ionizing radiation.
2. **Natural selection.** Because organisms have an inherent reproductive growth rate that would cause the population to exceed the ability of the environment to support it, not all individuals survive to reproduce. Individuals with heritable traits that do confer an advantage tend to leave more offspring than those without such traits. Consequently, those traits become more common in succeeding generations.

These cause the traits held by a population to tend to change with time either because novel traits are developed randomly that confer an advantage in the current environment, or because different traits are selected for when the environment changes, such as by climate change, introduction of new competing species to the area, or various forms of human intervention. Favorable traits, which increase the fitness of a population to an environment, are called **adaptations**. The Galápagos Islands, which have become a field laboratory for evolution, furnish an example. In 1977 a drought wiped out 85% of a species of finch. Studies showed that the survivors were mostly birds with larger beaks. It was found that this was because during the drought there were fewer herbs and grasses that produced small seeds. The birds with small beaks were unable to eat the larger seeds that remained, and they did not survive to pass on their characteristics.

Prior to our modern understanding of genetic theory and molecular biology, the theory of evolution could be supported by three types of evidence: the fossil record, comparisons between the structure and function of different species, and by an analysis of the geographic distribution of existing species. The fossil record shows that (1) different organisms lived at different times, (2) different organisms lived in the past than are in existence today, (3) fossils found in adjacent sedimentary layers (and therefore relatively close to each other on a geological time scale) are similar, (4) intermediate forms of species are sometimes found, and (5) older rocks tend to have simpler forms.

Comparison of species falls into three categories: comparative anatomy, comparative embryology, and comparative biochemistry. **Comparative anatomy** shows that similar organisms have similar structures, but structures that serve different functions. For example, the same bones that a human has in the forearm are found in the flipper of a whale and the wing of a bat. It was easier for nature to modify existing structures of these mammals than to develop completely new, specialized structures. Sometimes a structure loses its function altogether, forming a **vestigial organ**. For example, whales and snakes retain the pelvis (hipbone) and femur (thighbone). **Comparative embryology** finds that similar organisms have similar **embryos** (the earliest multicellular form of an individual). For example, all vertebrate embryos, including humans, have gill slits, even if the adult does not. Evolution accounts for this by explaining that those features are retained from ancestral forms. In an example of **comparative biochemistry**, techniques of molecular biology have shown that similar species have similar genetic material. It is possible to compare species based on the degree of similarity between their DNA (the chemical in the nuclei of cells that stores the hereditary information). This has shown definitively that species that are similar on an evolutionary scale (based on other evidence) are also similar genetically. Furthermore, the code that converts DNA into proteins is the same in all living things from bacteria to humans (see Table 6.2). There is no fundamental reason that this should be so unless all these organisms developed from a common ancestor.

The third line of evidence is from **biogeography**, the study of geographic distribution of living things. This type of evidence was particularly striking to Darwin. He observed many unique species in the Galápagos, off South America, and in the Cape Verde Islands, off Africa. Although the two island groups have similar geology and climate, their species are more similar, although not identical, to those on the nearby mainland than to each other. This suggested that the islands were colonized from the nearby mainland by organisms swimming, flying, or rafting on floating vegetation, and that evolution continued through their subsequent isolation. At the same time, unrelated organisms of the two island chains had similar characteristics, suggesting that evolution formed similar structures in response to similar requirements.

The study of evolution has helped to understand changes in populations other than the formation of new species. Random changes in traits can occur in a population, resulting in what is called **genetic drift**. This is seen when a population becomes divided by some circumstance, such as the formation of an island from a peninsula by rising water levels. If two populations are isolated from each other long enough, they can diverge to form distinct species, even if both are in similar environments. This is called **divergent evolution**. The differences between Galápagos species and the mainland species with which they share ancestry is an example.

Another form of genetic drift is called the **bottleneck effect**. This occurs if some catastrophe destroys a large portion of a population. As a result, only those traits carried by the survivors are found in future generations. Many of the less common traits will disappear, and some rare ones may become common (see Figure 2.1). The bottleneck effect is also seen when a small number of a species are introduced to a new ecosystem and flourish there. The descendants share a few recent ancestors and limited genotypes.

Environmental stresses can cause changes in the genetic makeup of a population by favoring organisms with certain alleles more than others. This is, in fact, the normal way that populations can adapt rapidly to changes in their environment without mutations being required to produce new adaptations. It is also the reason why populations with genetic diversity are more likely to survive in the face of change. However, there is another side of this phenomenon related to human impacts on populations. Toxins added to the environment exert selection pressure for individuals that are more tolerant of the toxins. One negative impact of this is that it can reduce the genetic diversity of a population, making it vulnerable to further stresses. Another problem occurs if the organism is a pest and the toxicant is an agent such as a pesticide or antibiotic. As a result of the selection pressure, the population seems to develop tolerance or resistance to the agent, which then becomes less effective.

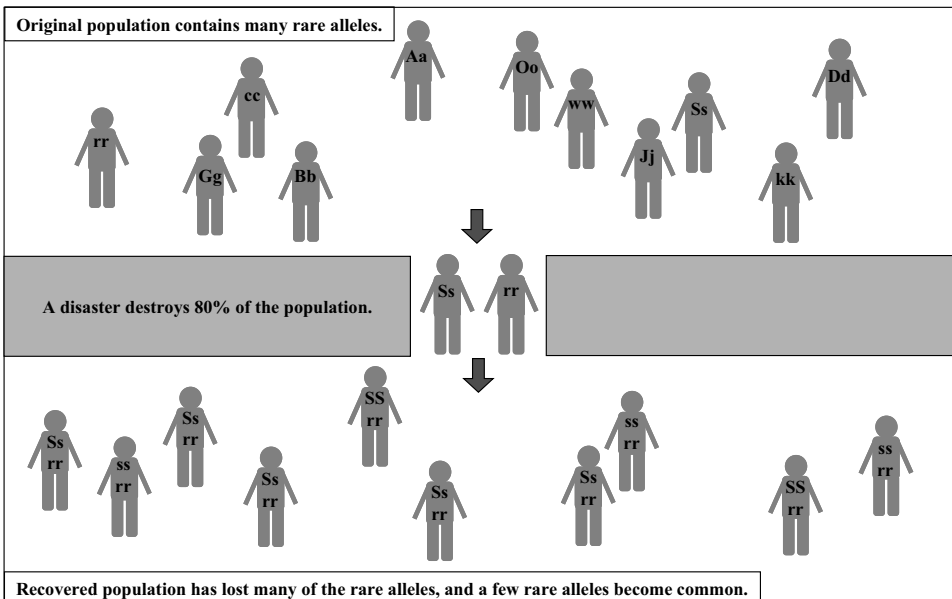


Figure 2.1 Bottleneck effect. (Based on Wallace et al., 1986.)

Sometimes very different species develop similar characteristics in response to similar environmental conditions. This is called **convergent evolution**. Because of this it is not always possible to consider species to be related evolutionarily because of superficial similarities. For example, most of Australia's original mammals are **marsupials**, which nurture their fetuses in pouches; whereas North America is dominated by **placental mammals**, whose fetuses grow internally in the uterus until ready to live independently. Despite their being very different groups, similar species have arisen on both continents, such as marsupial analogs to the wolf, mouse, and even the flying squirrel.

The Pace of Evolution The traditional view of evolution has been that it proceeds by the accumulation of small increments of change. This view is called **gradualism**. Some fossil evidence supports this. For example, fossils have shown a series of species leading from a small, dog-sized animal, to the modern horse. However, the fossil record is more compatible with the view that species remained stable for millions of years before suddenly disappearing and being replaced by new ones. An alternative view, called **punctuated equilibrium**, was proposed in 1972 by Niles Eldredge and Stephen Jay Gould. This predicts that evolutionary changes occur rapidly over short periods, forming new species in small populations. These stay relatively unchanged for millions of years until they become extinct. Gould suggests that the rapid changes could be caused by small, yet influential genetic modifications. For example, radical changes in the body plan of an organism could be mediated by a small number of mutations.

The theory of punctuated equilibrium answers the criticisms directed at evolution theory for the absence of "missing links" in the fossil record. However, gradualism also explains some of the features observed in the living world. The structure of the eye has been cited as being so complex as to defy explanation in terms of development from simpler forms. However, four different species of mollusk illustrate stages of a continuum in eye development (see Figure 2.2).

Extinction Extinction is the elimination of a species from Earth. The term is also used to describe elimination of a species from a particular area or ecosystem. Today, there is serious concern because human activities are causing the extinction of numerous species each year. Activities that destroy ecosystems or even just reduce their size cause loss of species. Some biologists estimate that human population pressure on natural ecosystems could eliminate 20% of Earth's species over the next 25 or 30 years. The term **biodiversity** describes the taxonomic variation on Earth or in an ecosystem. The loss of species due to human activities eliminates adaptive information created by nature over eons. Many hope to protect against loss of biodiversity. Besides the moral motivation, there is also the utilitarian concern that lost species might have been useful, such as for drug development or to help control biological pests.

Extinctions also occur naturally, of course. A species may become extinct because of competition or increased predation from another species. This could occur if the other species is one that is newly evolved or that has invaded the ecosystem from other locations. Such invasions are caused by geological and/or climatic changes such as land bridges that form between major islands and continents due to fluctuation sea levels, or elimination of a climatic barrier between, say, ecosystems separated by mountains or desert. Human importation of exotic species, intentional or not, produces a similar effect.

The fossil record shows that a number of mass extinctions have occurred in the past. At the end of the Permian Period, some 250 million years ago, 96% of species, such as

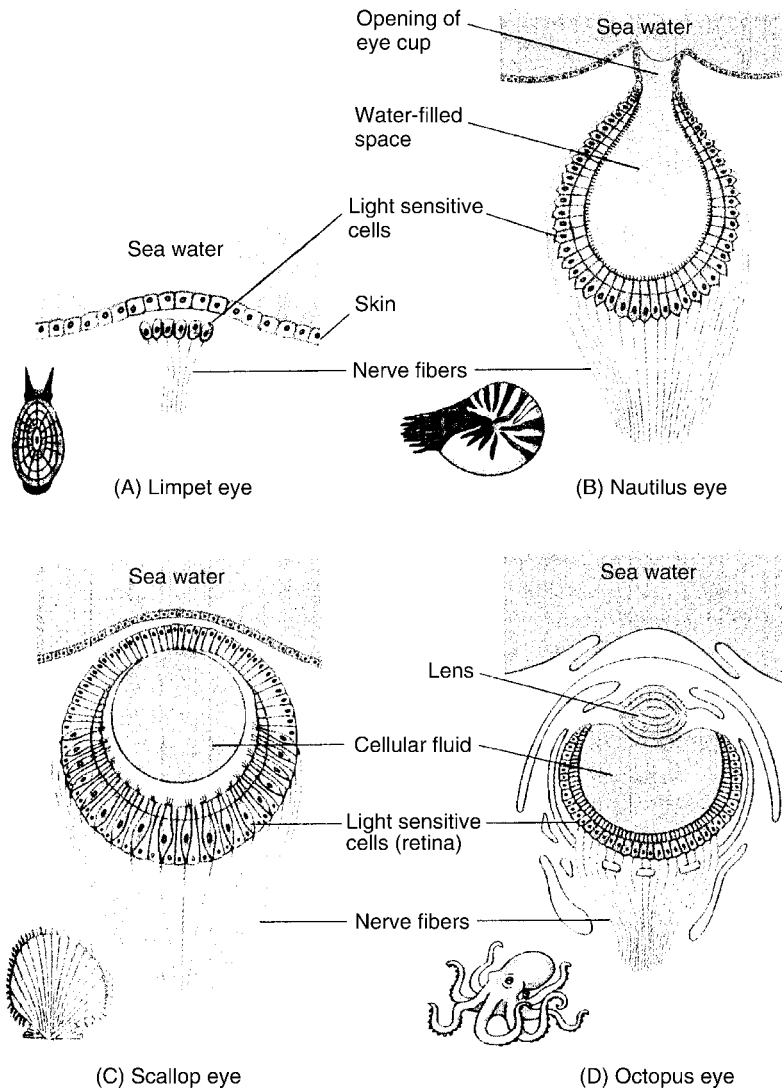


Figure 2.2 Development of the eye in mollusks: limpet, nautilus, scallop, octopus. (From Postlethwait and Hopson, 1995.)

the trilobite, disappeared from the fossil record. Some 65 million years ago, at the end of the Cretaceous Period, known as the **K-T boundary**, as much as 76% of species disappear, including the dinosaurs. Recently, geologic evidence has established that this mass extinction was caused by a large meteorite or comet striking Earth at the Yucatan Peninsula in what today is Mexico. Shock waves traveling through Earth's crust seem to have focused on the opposite point of the globe, southwest of India, causing massive volcanic outpourings. The impact plus the volcanism are thought to have sent dust and smoke into the atmosphere, darkening the sun, directly wiping out many ecosystems and reducing the primary productivity of the Earth (Chapter 14), starving many species into extinction.

Mass extinctions seem to be followed by a period of accelerated evolution of new species. The elimination of dinosaurs, for example, paved the way for the further development of mammals. Human activities are currently being blamed for causing the extinction of great numbers of species, mostly by encroaching on their habitats.

2.4 TAXONOMY

There are an estimated 50 million species on Earth. Of the 1.5 million species that have been named, about 5% are single-celled organisms (prokaryotes and eukaryotes), and plants and fungi make up about 22%. About 70% of the known species are animals. Most of these are invertebrates, especially insects, of which there are about 1 million known species. The earliest and, until this century, the most dominant activity in biology has been the classification of species. Aristotle was concerned with it. Even Charles Darwin, who started developing his theory of evolution while on the famous round-the-world voyage of the *Beagle*, was occupied primarily with collecting and categorizing new species of organisms.

Why should environmental engineers and scientists study taxonomy? One reason is so they won't be at a loss to see how any particular organism fits in with others. Does that worm always live where it is, or will it someday metamorphose into an insect and fly away, perhaps carrying biological or chemical contamination with it? At a more fundamental level, classification is a prerequisite to the identification of patterns, which leads to generalizations or hypotheses, and ultimately to tests of hypotheses by experiment or further observations. Thus, classification can be seen as a basis for the scientific method. The generalizations came later to biology than they did to physics and chemistry, perhaps owing to the dazzling variety of life and the inherent complexity of the underlying mechanisms.

Taxonomy is the science of classification of organisms. Taxonomy (except for microorganisms) was a fairly settled area until recently. Now, genetic techniques are reopening old questions and revealing new things. The possibility that humans are causing a new mass extinction lends a new urgency to knowing the organisms that now exist on Earth. This loss in the diversity of life would have several potential consequences. From a utilitarian point of view, destruction of species results in a loss of genetic material that may include useful traits, such as production of chemicals that may have medical uses, or traits that may be useful for invigorating agricultural plants or animals. Ecological relationships may link the survival of one species to many others. Finally, it may be argued from several ethical viewpoints that we have a moral imperative to preserve Earth's biological heritage regardless of actual or potential utility.

Two ways to classify organisms are to group them (1) by structure and function or (2) by closeness of evolutionary descent. The two approaches often produce similar results, but not always. Convergent evolution can make dissimilar evolutionary branches form similar characteristics, whereas divergent evolution does the opposite. Barnacles and limpets both live in shells glued to rocks in the sea, but barnacles are arthropods, like crabs, whereas limpets are mollusks, like clams. The use of evolutionary descent was constrained in the past due to the incompleteness of the fossil record, resulting in ambiguity in classifying existing organisms. Recently, however, the development of genetic engineering techniques has led to quantitative measures of genetic similarity. These have settled old classification questions and even led to increased detail in classification by

dividing old groups, forming new ones, and producing new species, phyla, and even kingdoms (see below).

Biologists use the **Linnaean system** to classify organisms, which consists of a hierarchy of groupings and a naming convention. The lowest level of the hierarchy is the *species*. Similar species are grouped into a **genus**. The naming convention, called **binomial nomenclature**, assigns to each species a two-word name. The first word, which must be capitalized, is the name of the genus, and the second, which is uncapitalized, is the name of the species. For example, modern humans are in the genus *Homo* and the species *sapiens*; thus, they're called *Homo sapiens*. Other species in our genus are extinct, such as *Homo habilis*. Genus and species names are either italicized or underlined when written, and the genus name may be abbreviated by a capitalized first initial once it has already been written out in full: *H. sapiens*.

In increasing degrees of generality, the other classifications are **family**, **order**, **class**, **phylum** or **division** (in plants and fungi), **kingdom**, and **domain**. Each of these may sometimes be subdivided: for example, subkingdom, subphylum, or subspecies. The following phrase is a memory trick for the sequence from kingdom to species:

King Phillip came over from Greece Saturday.
Kingdom Phylum Class Order Family Genus Species

The highest-level category is the **domain**. It is based on the type of cell comprising the organism, of which there are three: the bacteria, the archaeans, and the eukarya. Each domain is subdivided into kingdoms. Some biologists consider the archeans and the bacteria each to consist of only one kingdom. However, microbiologists note that molecular biology methods have shown that different groups of bacteria, for example, are more distinct from each other genetically than plants are from animals. Therefore, archaea have been divided into three kingdoms, bacteria into 15, and eukarya into four. Although this method of classification has not yet become universal among biologists, in this book we adopt this approach.

One domain is that of the **bacteria**, also sometimes called **eubacteria**. Their cell type is the **prokaryote**, which is a simple type lacking any internal membrane structures. Their size is typically 0.2 to 2.0 micrometers (μm). Based on **morphology** (physical structure) and biochemical characteristics, the bacteria have classically been organized into 19 groups. Examples are *Pseudomonas*, a common soil bacterium that is also exploited in wastewater treatment processes; and the *Cyanobacteria*, or blue-green bacteria, important in the environment because they convert atmospheric nitrogen into a useful nutrient. Based on genetic techniques, new groups have been found and some of the older ones combined; one current classification system now has 15 high-level groupings.

Another prokaryotic domain is that of the **archaea**, which includes three kingdoms. Archaea includes the methanogenic bacteria that produce methane gas in a wastewater treatment plant's anaerobic digester. Archaeons were once considered to be bacteria. However, unsuccessful attempts to transfer genes from eubacteria to archaeobacteria led to the discovery that their membranes, although structurally similar to the other domains, are chemically distinct. Many of the archaea are notable for the harsh chemical and physical environments in which they thrive. Because of this it is thought that archeons may be relics of the earliest forms of life that still exist today.

The third domain is that of the **eukarya**, which comprises four kingdoms, including the familiar plants and animals. The cells of this domain are called **eukaryotic**. This is a more

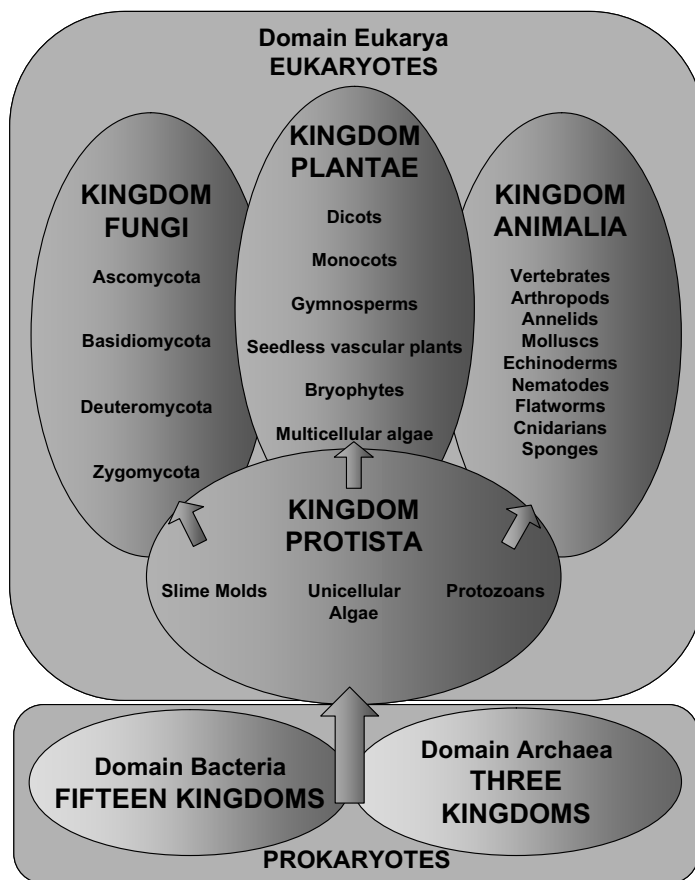


Figure 2.3 The six kingdoms, according to one taxonomic approach.

complex cell type that is characterized by internal membrane structures and membrane-based organelles. Eukaryotic cells are much larger than prokaryotes; animal cells are typically about 20 μm across, and plant cells are about 35 μm .

The next level of classification below kingdom is **phylum** (in animals) or **division** (in plants and fungi). Figure 2.3 summarizes the variety of life at the domain and kingdom level and shows some of the major phyla and divisions. Table 2.1 shows how several

TABLE 2.1 Classification of Several Familiar Eukaryotes

Kingdom	Animalia	Animalia	Animalia	Kingdom	Plantae
Phylum	Chordata	Chordata	Arthropoda	Division	Anthophyta
Subphylum	Vertebrata	Vertebrata	Uniramia	Subdivision	
Class	Mammalia	Mammalia	Insecta	Class	Dicotyledones
Order	Primates	Cetacea	Orthoptera	Order	Sapindales
Family	Pongidae	Mysticeti	Tettigoniidae	Family	Aceraceae
Genus	<i>Homo</i>	<i>Balenoptera</i>	<i>Scudderia</i>	Genus	<i>Acer</i>
Species	<i>H. sapiens</i>	<i>B. musculus</i>	<i>S. furcata</i>	Species	<i>A. rubrum</i>
Common name	Human	Blue whale	Katydid	Common name	Red maple

familiar organisms are classified according to this system. Biology does not have a central authority for determining how to organize animals into phyla. The classifications gain currency by general usage and adoption in textbooks.

Species may be further subdivided into **subspecies**, **strain** (especially in prokaryotes), or **cultivar** (in crop plants).

Formerly, the eukaryotic domain was considered to consist of only two kingdoms, plants and animals. Now it has been further subdivided to include fungi and protists. Several of these kingdoms are characterized based on their source of carbon. Autotrophs obtain their carbon from the inorganic form, in particular carbon dioxide. Heterotrophs are organisms that must obtain their carbon in the form of organic chemicals such as sugars, fats, or proteins.

The **fungi** kingdom is defined to include the plantlike, mostly multicellular heterotrophic organisms lacking the green pigment chlorophyll. Fungal cells are surrounded by a rigid capsule called a **cell wall**. Fungal cell walls are made of a polymer called chitin. Fungi have a major ecological role in breaking down dead organisms and making their nutrients available to other organisms. Four divisions have been recognized: the ascomycetes include yeast, mildew, and the prized edibles morels and truffles; basidiomycetes include most of the common mushrooms; deuteromycetes include the mold that produces penicillin; zygomycetes include common black bread mold.

Plants are multicellular photoautotrophs that reproduce sexually to form **embryos** (an early stage of multicellular development). Photoautotrophs are autotrophs that get their energy from light (as opposed to chemical sources of energy). Plant cells usually contain chloroplasts, which are organelles containing the chlorophyll. The cells of plants are surrounded by a cell wall composed largely of cellulose fibers. The major ecological role is the capture of light energy from the sun to fix atmospheric carbon dioxide and produce oxygen in the process called photosynthesis. This provides food for other organisms and oxygen for their respiration, the biochemical oxidation of organic matter to produce energy that is the opposite reaction to photosynthesis. The plant kingdom consists of 12 divisions: the *bryophytes* (mosses and relatives), four *seedless vascular plants* divisions (e.g., ferns), *gymnosperms* (including conifers), and *anthophyta* (also referred to as angiosperms, the flowering plants).

Like the fungi, animals, are multicellular heterotrophic eukaryotes. In addition, they reproduce primarily by sexual reproduction, are motile in some part of their life cycle, and their cells lack a cell wall. There are 33 animal phyla, including several marine organisms, such as sponges, corals, and jellyfish; several phyla containing wormlike organisms; mollusks; arthropods (which include crustaceans and insects); and the chordates. The latter include the vertebrates, which are the organisms with an internal skeleton. Thus, we humans are chordates. All of the other animal phyla, plus a small group within the chordates, are called invertebrates.

The remaining kingdom in domain eukarya is that of the protists. This kingdom somewhat arbitrarily combines single-celled eukaryotes that would otherwise be part of either the fungi, plant, or animal kingdoms. Thus, they are classified into three groups: animal-like protists, or protozoans, which have four phyla, including those with *paramecium* and the *amoeba*; plantlike protists, with six divisions, *euglena*, *dinoflagellates*, *diatoms*, *red algae*, *brown algae*, and *green algae*; and funguslike protists, with three divisions, including *slime molds*. Each of these groups function ecologically in ways that are similar to their analogous multicellular kingdom.

The six divisions of the plantlike protists are also called algae. Three of these divisions, the red algae, brown algae, and green algae, are dominated by multicellular forms. For example, kelp is a brown algae and sea lettuce is a green algae. For this reason, some textbooks place them in the plant kingdom. However, these divisions also include many unicellular forms. Many phytoplankton are green algae, including *Chlamydomonas* and a family called the desmids. In this book we adopt the convention of keeping them with the other algae in kingdom Protista, although in Chapter 10 their modern taxonomy is examined more closely. Plankton are very small aquatic or marine plants, animals or algae. Plant and algal plankton are referred to as phytoplankton, and animal plankton or animal-like protists are called zooplankton.

Viruses, viroids, and prions are infectious agents not considered to be members of a living kingdom. They do not have a cytoplasm or cell membrane and are not capable of any metabolic reactions within their own structure. They reproduce by infecting living cells and causing them to produce more of the infectious particles. The resulting damage is responsible for many diseases. They may be more properly considered to be chemical agents. Viruses are the largest and most complex, being a geometrical particle of DNA or RNA (the chemical agents of heredity), and surrounded by protein. They may be 1/1000 to 1/10,000 the size of prokaryotic cells. An important medical distinction between viruses and bacteria, which also cause disease in humans, is that since viruses do not metabolize, virus diseases cannot be treated by antibiotics, which act by killing or otherwise preventing the reproduction of microbes. However, viruses can often be prevented by vaccines, which stimulate the human immune system to destroy the virus particles within the body.

Viroids are even simpler than viruses, consisting of a single RNA molecule. They have been found to cause some crop diseases. **Prions** are similar in that they consist of a single molecule; however, in this case the molecule is a protein. They are poorly understood. Prions are suspected causes of several serious neurological diseases in humans and animals, including scrapie in sheep, bovine spongiform encephalopathy in cows (mad cow disease), and Creutzfeldt–Jakob disease and kuru in humans. They are remarkable in that they may be the only biological agent that reproduces yet does not have DNA or RNA, the chemical basis of heredity.

2.5 INTERACTION OF LIVING THINGS WITH THE ENVIRONMENT

Living things don't just live *in* the environment: To a great extent they create it. Photosynthetic plants and microorganisms are responsible for our atmosphere consisting of 21% oxygen and having only trace levels of carbon dioxide. Without them the atmosphere would more closely resemble that of the primitive Earth, which was composed of carbon dioxide, nitrogen, water vapor, hydrogen sulfide, and traces of methane and ammonia.

It is not only chemical changes that are wrought, but also physical ones, from the temperature of Earth to the form of our landscape. The temperature of Earth's surface is strongly affected by plants' ability to remove carbon dioxide, a *greenhouse gas* that prevents radiation of heat energy from Earth into space. Bacteria in the gut of termites have been found to be responsible for the release of methane gas, another greenhouse gas, into our atmosphere. Trees, grasses, and other plants reduce soil erosion, affecting the shape of the landscape.

The two-way relationship between the all the living things on Earth and the physical environment has been recognized in the **Gaia hypothesis**, put forward by the English scientist James Lovelock (1987). His statement of the hypothesis is: “The biosphere is a self-regulating entity with the capacity to keep our planet healthy by controlling the chemical and physical environment.” Lovelock is also known for another important contribution to environmental protection. He is the inventor of the electron capture detector, used in gas chromatographs to analyze for organics containing halogens or oxygen with exceptional sensitivity. By revealing the fate and transport of minute chemical quantities such as pesticides, this device can take some credit for stimulating the environmental revolution.

Lovelock illustrated the Gaia hypothesis with a computer model that demonstrated how organisms could control the environment to their advantage. In a model he called Daisyworld, he postulates a planet like Earth receiving energy from the sun and covered with two species of daisy, one light-colored and the other dark (see Figure 2.4). Both species had an optimum temperature for growth, with the light daisy’s optimum higher than that of the dark daisies. He then simulated the system and varied the amount of energy radiated by the sun. The simulation showed that when the energy input increased, raising the temperature, the population of light daisies would increase and the dark would decrease. This increases the planet’s **albedo**, the fraction of incident energy that is reflected back into space. By reflecting more energy, the temperature of the surface is prevented from increasing as much as it would otherwise. At lower incident radiation, the cooler temperatures would favor dark daisies that decrease the albedo. Without the organisms, the surface temperature increases smoothly as radiation increases. With the daisies present, as radiation is increased, the temperature first increases, then forms a plateau within which the organisms stabilize the system.

As evidence for the Gaia hypothesis, Lovelock cites the fact that Earth’s atmosphere is far from equilibrium. Without organisms to maintain it, he says that the nitrogen and oxygen would eventually combine to form nitrates, which would dissolve in the oceans, leaving an atmosphere consisting mostly of CO_2 , like that of Mars.

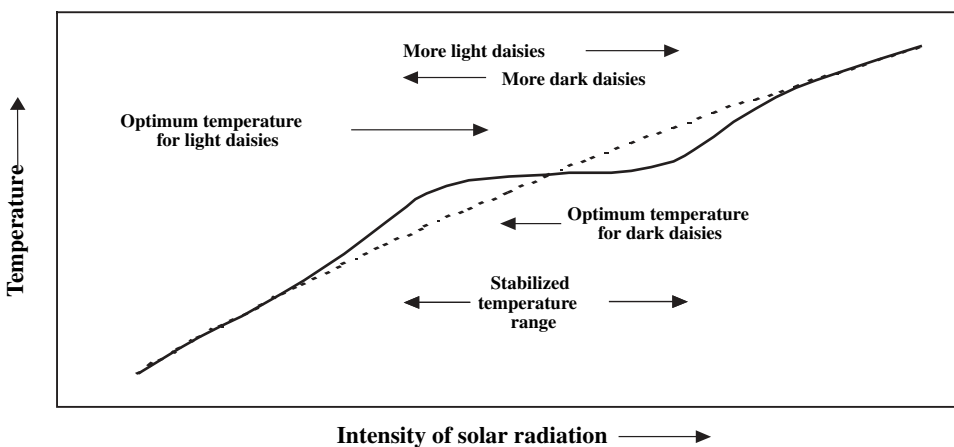


Figure 2.4 Temperature vs. radiation intensity for Daisyworld. The dashed line shows the global temperature in the absence of the two daisy populations. The solid line shows how temperature would vary with their influence included.

Individual organisms employ control mechanisms to regulate their internal environments, such as body temperature or blood chemistry in mammals. Because of this similarity, some have extended the Gaia concept to mean that Earth itself *is* a living organism, rather than saying that it *is like* one. This has created controversy for the hypothesis, but it is not part of Lovelock's conception. Although suggestive, Daisyworld is not proof of the Gaia hypothesis. Proof awaits stronger evidence that such feedback mechanisms actually operate on Earth.

Although the self-regulating nature of Earth's ecosystem as a whole remains to be proven, there are many examples of environmental conditions that are caused by biological activity, some of which involve self-regulation. Some examples include the cycling of minerals and elements in the environment, the formation of soil, and the control of pH in anaerobic digestion.

Biogeochemical cycles describe the various reservoirs for an element, and the reactions and transformations that convert the matter from one reservoir to another. For example, the major reservoirs for carbon are atmospheric CO₂, aquatic or marine CO₂, the biosphere (in the form of living or dead biological material), and the **lithosphere** (solid minerals, i.e., rocks or soil) as carbonate rocks or as fossil carbon (coal, oil, or natural gas). The cycles can be described quantitatively in terms of the amount in each reservoir and the rate of each reaction. Look ahead to Figure 14.5 to see that most of Earth's carbon is stored in carbonate rocks such as those that form the Rocky Mountains. It is interesting to realize that the Rockies and similar mountain chains worldwide are formed entirely from biological activity, by the gradual accumulation of the skeletons of microscopic plants in sediments on the ocean floor, followed by geological upheavals.

Biogeochemical cycles are a starting point for the analysis of the effect of humans on the environment. Since the heat-trapping effect of atmospheric CO₂ and methane are a serious concern, it is important to understand the rate of **anthropogenic** (human-caused) emissions of these gases and the rates at which they are naturally removed. Such an analysis has led to the conclusion that half of the CO₂ released by combustion of fossil fuel since the beginning of the Industrial Revolution remains in the atmosphere. It is thought that the ocean has absorbed the remainder. The details of biogeochemical cycles are discussed in Chapter 13 and Section 14.2.

Soils may be formed abiotically, but the result is very different when mediated by living things. First, the rate at which rocks are broken down into soil can be accelerated by the action of acids produced by **lichens** (an association of fungus and algae) and by mechanical effects of the roots of plants, which can widen cracks in rocks, exposing more surface area to weathering. Plants prevent the soil from eroding by absorbing moisture and by the action of their root structure. Dead plant matter is degraded by fungi and bacteria to form **humic substances**. These are complex polymeric phenolic compounds that resist further biodegradation. Their presence enhances soil water-holding capability and makes it more **friable** (easy to crumble), which makes it easier for roots to penetrate. Humic substances also enhance the ability of soils to adsorb organic pollutants. Insects and other invertebrates, especially earthworms, aerate and mix the upper soil. Charles Darwin's major preoccupation in the years after he published *The Origin of Species* was a detailed study of how earthworms affect the soil, especially by moving soil continually from the depths to the surface. Microorganisms in the soil and associated with the roots of plants convert atmospheric nitrogen to a form available to plants, effectively producing a fertilizer in place. These changes are both caused by organisms and benefit them.

Anaerobic digestion, an environmental engineering process used to biodegrade concentrated slurries of biomass, provides another good example of organism–environment interaction. Here, the pH is controlled by a delicate balance between two populations of microorganisms. The acidogens break down organics into simple volatile fatty acids such as acetic and propionic acids. This consumes alkalinity. The methanogens use the acids to make methane, restoring the alkalinity. The methanogens are more sensitive to environmental changes, including pH, than the eubacterial acidogens. Should some disturbance affect the methanogens adversely, the acid generation can cause a pH drop, further slowing acid destruction and causing a cessation of methane formation from which it is difficult for the system to recover. This is similar to Daisyworld, where the organisms control their environment until conditions are forced outside the range in which control can occur, and the system becomes unstable.

2.6 BRIEF HISTORY OF LIFE

With the overview of the types of living things and the mechanisms by which they evolve, as given above, let us take a brief look at the changes that have occurred in the biology of Earth. One of the biggest questions is: How did life originate from prebiotic conditions? After the formation of Earth and the cooling of its crust, the atmosphere consisted mostly of water vapor, carbon dioxide, carbon monoxide, and N_2 . The dominant theory derives from the ideas of Haldane and Oparin, early twentieth-century biochemists. It holds that energy from sunlight, lightning, and volcanic action gradually formed simple organic molecules from these precursors. In the 1950s, Urey and Miller conducted famous experiments that proved that this could occur. They passed spark discharges through similar

TABLE 2.2 Timeline for Life on Earth

Million Years Ago	Event
4,600	Earth forms.
3,800	Life begins.
3,000	Prokaryotes appear.
1,000	Eukaryotes appear.
570	Algae and marine invertebrates (e.g., trilobites) dominate.
405	Terrestrial plants and vertebrates appear.
225	Dinosaurs appear.
135	Flowering plants appear.
65	Mass extinction, including dinosaurs and up to 70% of all animal species.
	Mammals begin to dominate.
40	Primates appear.
4	Hominids appear.
2	Genus <i>Homo</i> appears.
Years Ago	
30,000	<i>Homo sapiens neanderthalis</i> disappears. <i>H. sapiens sapiens</i> appears.
5,000	Development of agriculture.
146	Publication of <i>The Origin of Species</i> (1859).
52	Discovery of DNA structure (1953).
8	Cloning of mammals (1997).

primitive atmospheres in a sealed glass apparatus and produced aldehydes, carboxylic acids, and most important, amino acids, the building blocks of proteins. In the absence of life on early Earth, these compounds could accumulate until the seas consisted of **primordial soup**. These compounds could be further concentrated in drying coastal ponds or at hot springs. Experiments have shown that under realistic conditions, polymeric macromolecules could be formed. Other steps along the way to a viable self-replicating cell have been reproduced, but many critical steps have not. Overall, the process is still a mystery.

However the origin occurred, the fossil record shows that life developed in complexity continuously (Table 2.2). Humans are a very recent addition. Notice how long the dinosaurs were on Earth relative to our tenure here.

PROBLEMS

- 2.1. Consider a toxic pollutant such as gasoline, the dry-cleaning solvent perchloroethylene, the heavy metal mercury, or the pesticide DDT. Can you think of ways in which the pollutant might have some effect at each level of the biological hierarchy from metabolism to ecosystem?
- 2.2. How are ecosystem and environment distinguished from each other? Note that these two terms are often confused by the public.
- 2.3. How could anthropogenic effects change the course of evolution?
- 2.4. Can you think of some pollutants that have different effects on different biological kingdoms? How will these effects differ from each other?
- 2.5. All of the following have been used for biological waste treatment: bacteria, cyanobacter, green algae, fungi, green aquatic plants, earthworms. Try to think of how each could be used, and for what type of waste each would be applicable.
- 2.6. Think about how you would create a model like Daisyworld. What laws and relationships would you use?
- 2.7. Assuming that the Gaia hypothesis were true, which of the criteria for life does Earth's ecosystem as a whole satisfy, and which does it not satisfy?

REFERENCES

- Doolittle, W. F., 2000. Uprooting the tree of life, *Scientific American*, Vol. 282, No. 2.
- Lovelock, James, 1987. *Gaia: A New Look at Life on Earth*, Oxford University Press, New York.
- Odum, Eugene, 1993. *Ecology and Our Endangered Life Support Systems*, Sinauer Associates, Sunderland, MA.
- Postlethwait, J. H., and J. L. Hopson, 1995. *The Nature of Life*, McGraw-Hill, New York.
- Schrödinger, Erwin, 1956. *What Is Life?*, Doubleday Anchor Books, Garden City, NY.
- Wallace, R. A., J. L. King, and G. P. Sanders, 1986. *Biology: The Science of Life*, Scott, Foresman, Glenview, IL.

3

THE SUBSTANCES OF LIFE

A useful simplification of biological organisms sometimes made by environmental engineers and scientists is to view them as catalysts for chemical reactions, such as the oxidation of ammonia or ferrous iron, or production of methane and carbon dioxide from acetic acid. Such a view hides the detailed mechanisms, including the sequence of chemical intermediates and the specific chemical nature of the catalyst. Examining these details will help us to understand more complex chemical interactions between organisms and their environment, such as biodegradation of toxic organic chemicals or the effect of chemicals on the health of organisms and ecosystems. The details of biochemistry begin with knowledge of the four most important types of chemical substances comprising living things: carbohydrates, lipids, proteins, and nucleic acids. Later, in the chapters on toxicology, we consider the biochemical reactions involving **xenobiotic** compounds (those that are, literally, “foreign to life,” that is, substances not normally found in living things).

3.1 BASIC ORGANIC CHEMICAL STRUCTURE

A fairly simple summary of organic chemistry is sufficient for understanding much of the structure and reactions of biochemicals. There are only two types of **chemical bonds** that need to be considered at this point: ionic bonds and covalent bonds. The great majority of biochemicals are composed of only six elements connected by those bonds: carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus. In addition, the attractions of dipole forces such as hydrogen bonds and van der Waals forces act between molecules or between different parts of the same molecule. The structure of most organic chemicals can be described by combining the six elements with ionic and covalent chemical bonds.

Physicochemical interactions are attractions or repulsions between molecules, or between different parts of the same molecule, which do not result in formation or breaking of ionic or covalent bonds. They are much weaker than chemical bonds and are much more sensitive to changes in temperature. These forces change the shape of molecules, causing them to bend, fold, or form liquids or crystals. This affects physical properties such as solubility or boiling point as well as the ability of molecules to enter into chemical reactions. Much of this physicochemical behavior can be related to a few types of atomic groups on the molecule that are called *functional groups*.

The main importance of this section is to arrive at an understanding of what controls the shape of biochemical compounds. Biochemicals are often large, polymeric molecules, whose function is intimately related to their shape. Thus, their behavior is not determined completely by their chemical formula, but also depends on how they are folded or coiled or by how they are arranged relative to neighboring molecules.

3.2 CHEMICAL BONDING

Atoms in a molecule are held together by covalent or ionic bonds. These bonds involve a sharing of electrons between pairs of atoms. Bonds can be classified in terms of how equally the electrons are shared or by the amount of energy required to break the bond. The electrons in **covalent bonds** are equally or almost equally shared, whereas those in **ionic bonds** are associated almost completely with one of the atoms in the bonded pair.

Electrons in bonds between identical atoms tend to be shared equally between the two. But if the two atoms are different, the electron cloud making up the bond may be displaced toward one of them. As a result, the center of charge of the electrons is different from the center of charge of the nuclei of the atoms, and the bond will produce an electrostatic field in its vicinity. A bond that produces an electrostatic field is said to be **polar**. Polarity produces attractions between molecules.

For example, Figure 3.1 shows an ethylene molecule. The bond between the two carbons will be nonpolar. A molecule of ethanol is also shown. The carbon and oxygen atoms

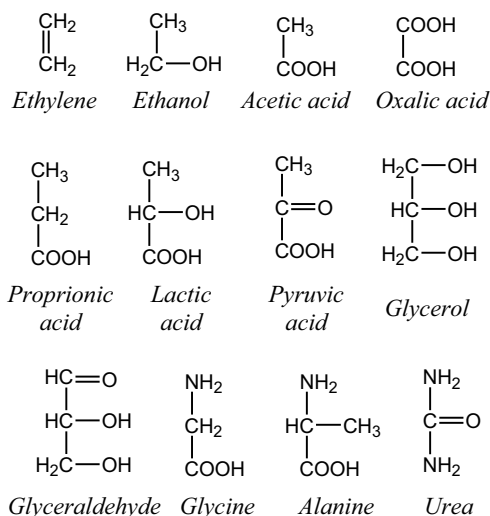
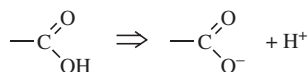


Figure 3.1 Structures of several small, biologically important organic molecules.

are very different in their tendency to attract electrons; thus, this molecule is polar. The tendency of atoms to attract electrons is called its **electronegativity**. Oxygen is more electronegative than carbon; therefore, the ethanol molecule will be polarized with a positive charge toward the carbon and negative charge toward the oxygen. Sometimes oxygen can attract electrons away from a neighboring hydrogen so completely that it leaves the hydrogen fairly free to dissociate from the molecule as a proton, producing an acid. This is seen most commonly in organic chemicals in the case of the carboxylic acid group:



also written ---COOH . The two oxygen atoms act together to strip the electron from the hydrogen.

Fluorine is the most electronegative of all the elements. Figure 3.2 shows the electronegativity of all the elements that have been shown to be essential in at least some living things. The electronegativity of the other elements (except the noble elements) tends to decrease with distance from fluorine in the periodic table. Thus, chlorine is somewhat less electronegative than fluorine. The scale decreases more rapidly by moving to the left; thus, oxygen, nitrogen, and carbon represent a sequence of decreasing affinities for electrons. The leftmost column contains the alkali elements that are so low in electron affinity that they tend to give up their electrons entirely in bonds formed with the halogens on the right. These form the most polar of the bonds, the ionic bond.

The symbol-and-stick diagram for atoms and bonds in Figure 3.1 shows features that can be used to recognize the covalent and ionic bonding arrangement for the vast majority of organic compounds. Atoms form bonds in order to give themselves enough electrons to fill an orbital shell, such as the noble elements have. In simpler terms, each element generally shares as many electrons (i.e., forms as many bonds) as corresponds to the number of columns that element is away from a noble element in the periodic table. For example, oxygen is two columns away from argon, so it forms two bonds and should be drawn as ---O--- or =O , the latter showing that two single bonds can be combined into a double bond. Carbon, nitrogen, and phosphorus can also form triple bonds, although the amount

H 2.1																			
Li 1.0	Be 1.5											B 2.0	C 2.5	N 3.0	O 3.5	F 4.0			
Na 0.9	Mg 1.2											Al 1.5	Si 1.8	P 2.1	S 2.5	Cl 3.0			
K 0.8	Ca 1.0	Sc 1.3	Ti 1.5	V 1.6	Cr 1.6	Mn 1.5	Fe 1.8	Co 1.8	Ni 1.8	Cu 1.9	Zn 1.6	Ga 1.6	Ge 1.8	As 1.9	Se 2.4	Br 2.8			
					Mo 1.8								Sn 1.8			I 2.5			
					W 1.7														

Figure 3.2 Electronegativity of biologically important elements. This shows the portion of the periodic table containing many of the elements that are important to life. The numbers indicate the electronegativity of the corresponding elements. (From Pauling, 1970.)

TABLE 3.1 Number of Bonds Commonly Formed by the Six Principal Elements of Biochemical Compounds

Element	C	N	O	S	P	H
Number of bonds	4	3	2	2	5	1

of energy required makes these uncommon. Table 3.1 shows the number of covalent or ionic bonds formed by the six principal elements.

There are several important exceptions to this simple scenario for an element that forms the number of bonds corresponding to its valence state (see Table 13.1). One of these exceptions is the metals. For example, iron forms two bonds in the ferrous (II) state and three in the ferric (III) state. Sulfur typically forms two bonds in organic compounds but can have other numbers in inorganics. Even carbon has exceptions to the rule, as in the case of carbon monoxide. Also, phosphorus is almost always bound in the phosphate group (PO_4^{3-}), which is usually considered as a unit.

Ionic bonds are much weaker than covalent bonds. As a result, the atoms in ionic bonds can be separated by the relatively low-energy physicochemical forces. Although ionic and covalent bonds seem quite distinct, there is actually a continuum of bonds of varying polarity from ionic to covalent.

3.3 ACID–BASE REACTIONS

A special type of ionic bond is when one of the ions is either H^+ or OH^- , resulting in an acid or a base, respectively. Water serves as a source and sink for hydrogen ions that are generated or consumed by the dissociation of acids and bases. In fact, the very ability of other acids in solution to act as acids may depend on their being dissolved in water. Put another way, the presence of water shifts the acid dissociation equilibrium. The prototypical acid–base reaction is



where HA is the undissociated acid and A^- is its conjugate base. The equilibrium constant is called the *acid dissociation constant*, K_a (square brackets denote molar concentration):

$$K_a = \frac{[\text{H}^+][\text{A}^-]}{[\text{HA}]} \quad (3.2)$$

Taking the logarithm of equation (3.2), substituting the relations $\text{pH} = -\log[\text{H}^+]$ and $\text{p}K_a = -\log[K_a]$, and rearranging, we obtain an expression for the fraction of undissociated acid:

$$\frac{[\text{HA}]}{[\text{HA}] + [\text{A}^-]} = \frac{1}{1 + 10^{\text{pH} - \text{p}K_a}} \quad (3.3)$$

Thus, the relative proportion of HA and A^- depends on the pH. At low pH most of the acid is undissociated. At high pH most is dissociated. The $\text{p}K_a$ is the pH at which the

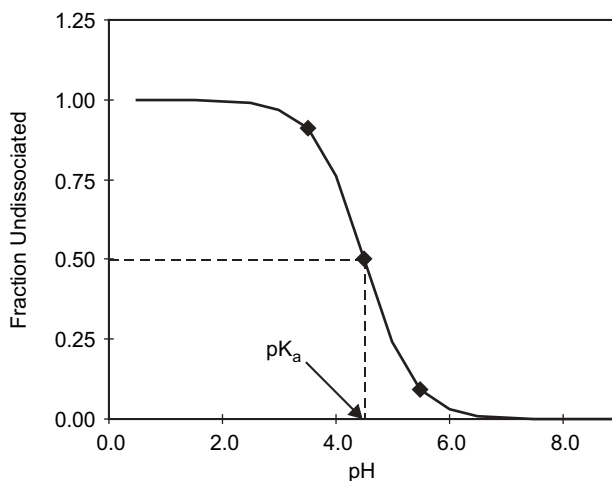


Figure 3.3 Fraction of undissociated acid for acetic acid ($pK_a = 4.7$). Points shown are for pH 3.7, 4.7, and 5.7.

equilibrium is positioned at the 50:50 point: half as HA and half as A^- . Figure 3.3 shows a plot of the fraction $[HA]/C_T$ for acetic acid, where $C_T = [HA] + [A^-]$ is the total acid concentration. Table 3.2 shows pK_a values for some important chemicals. Note that at 1 or 2 pH units below pK_a , the acid is almost completely undissociated, whereas at 1 or 2 units above pK_a , it is almost completely dissociated.

Example 3.1 What fraction, f , of acetic acid is undissociated at pH 7.0? The pK_a is 4.7; thus, the fraction undissociated is

$$f = \frac{1}{1 + 10^{7.0-4.7}} = \frac{1}{1 + 200} = 0.50\%$$

The pH strongly influences the shape of biochemicals by altering the proportion of dissociation of acidic groups on the molecule. Large biomolecules may have numerous acidic groups with various pK_a values. Varying the pH adds or removes hydrogen ions. This affects which portion of the molecule can form hydrogen bonds, or changes the polarity of a molecule, thereby significantly changing its shape and function.

TABLE 3.2 pK_a Values for Some Biologically Important Chemicals

Compound	pK_a	Compound	pK_a
Phosphoric acid (pK_1)	2.0	Carbonic acid (pK_1)	6.3
Citric acid (pK_1)	3.1	Citric acid (pK_3)	6.4
Formic acid	3.8	Phosphoric acid (pK_2)	6.7
Lactic acid	3.9	Boric acid	9.2
Benzoic acid	4.2	Ammonium	9.3
Acetic acid	4.7	Carbonic acid (pK_2)	10.4
Citric acid (pK_2)	4.7	Phosphoric acid (pK_3)	12.4

3.4 PHYSICOCHEMICAL INTERACTIONS

Atoms on a molecule can also be attracted to atoms on another molecule, producing **intermolecular forces**. These forces are primarily electrostatic. The strength of these forces range from that of hydrogen bonds, the strongest, to the van der Waals forces, the weakest. However, all of them are weaker than the forces involved in chemical bonding.

Hydrogen bonds are intermolecular attractions that occur between electronegative atoms on one molecule (e.g., O, N, or Cl) and with hydrogen atoms in another molecule. They will occur only if the hydrogen is bonded to other atoms more electronegative than carbon (e.g., O or N). The latter atoms pull the electrons away from the hydrogen, creating a strong local positive charge. This charge consequently has a strong attraction to electronegative atoms on the other molecules.

Even in the absence of polarity-producing asymmetry, a molecule can exhibit a temporary polarity as electrons shift from one side to another, or shift in response to the presence of the electron cloud of another molecule nearby. This produces a weaker electrostatic attraction, the **van der Waals force**.

Attractions due to hydrogen bonds, van der Waals forces, or polarity produce several important effects:

- The strength of these attractions allow chemicals to form liquids and solids. In more precise terms: They tend to raise the boiling point and melting point, increase the heat capacity and heat of vaporization, and decrease the vapor pressure.
- Dissimilar molecules that have sufficient attraction to each other can dissolve or mix, whereas those that do not attract tend to form separate phases.
- They contribute to the shape of large molecules because of attractions between different parts of the same molecule, modified by competition with other attractions, such as with solvent molecules or other dissolved species.
- They affect the rate of chemical reactions between like and unlike molecules by affecting the proximity and orientation of molecules to each other.

Water illustrates several physicochemical interactions and also plays a key role in biochemistry. Water is the most abundant chemical in living things. Living things are composed of between 50 and 90% water by weight. In humans, 99 of 100 molecules are water. The water molecule is bent; that is, rather than being directly on opposite sides of the oxygen, the two H—O bonds form a 104.5° angle with each other. The electronegativity of the oxygen pulls the electrons from the hydrogen. This leaves the molecule with a strong dipole, and each atom can form hydrogen bonds with other water molecules. These properties give it strong self-attraction. This results in the highest boiling point and heat of vaporization of any chemical of similar size or molar mass (i.e., molecular weight). Water's heat capacity and latent heat helps it regulate the temperature of living things, especially animals, which can generate heat at a rapid rate. Evaporation of water carries away a large amount of heat. If a human consuming 2000 Calories per day (note that 1 dietary Calorie = 1000 calories, distinguished in writing by their capitalization) were to release all that energy as heat, it could be consumed by evaporation of 3418 grams of water, less than 1 gallon. The actual evaporation is less because not all dietary calories are released as heat, and some heat is lost by convection.

Water's polarity also enables it to reduce the repulsive forces between charged particles such as ions, because it can align itself with the ion's electric field. The reduction in

TABLE 3.3 Properties of Various Chemicals Compared to Water

Substance	Molar Mass (g/mol)	Boiling Point (°C)	Specific Heat	Heat of Vaporization (cal/g)	Dielectric Strength
Water	18	100	1.0	585 (20°C)	80
Methanol	32	65	0.6	289 (0°C)	33
Acetone	58.1	56.2	0.51	125 (56°C)	21.4
Chloroform	119.5	61.7	0.24	59 (61°C)	5.1
Benzene	78	80.1	0.5	94 (80°C)	2.3

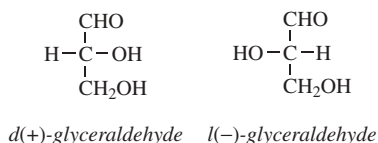
Source: Smith et al. (1983), Table 2.2.

electrostatic force relative to a vacuum is called the **dielectric strength**. This property is what makes water an excellent solvent for ions, since less work is required to place the ion into the water matrix. In addition, the polarity and hydrogen-bonding capability of water facilitates direct attraction to ions and other molecules that are polar or form hydrogen bonds. Polar or hydrogen-bonding compounds with appreciable solubility in water are termed **hydrophilic** (water-loving). Nonpolar compounds with negligible aqueous solubility are called **hydrophobic**, or **lipophilic**. Hydrophobic compounds are important for forming separate phases within cells. The resulting interfaces are an important location for many biochemical reactions and control the movement of hydrophobic toxicants into and out of cells. Table 3.3 summarizes some of the interesting physicochemical properties of water and compares them to other solvents.

The physicochemical forces associated with large biological molecules depend in a very complex way on the complete chemical structure of the molecule and on its chemical environment. However, much of their behavior can be described in terms of local chemical structures, called **functional groups**, some of the most important of which are listed in Table 3.4. Consider any hydrocarbon molecule, consisting only of a carbon backbone and hydrogens. Replace any of the hydrogens with one of the functional groups from Table 3.4 and you produce a compound with very different properties. A simple example is methane, CH₄. Replace a hydrogen with a hydroxyl group, and methanol results, which has a much higher boiling point and forms a liquid that is completely miscible with water. Replacing with carboxyl forms acetic acid. Taking the three-carbon hydrocarbon propane and replace one hydrogen from each carbon with a hydroxyl produces glycerol, a basic component of biological fats.

3.5 OPTICAL ISOMERS

One of the simplest of the sugars is *glyceraldehyde*, which has two isomeric forms:



These structures may seem practically identical, and in fact they have the same physicochemical properties, such as melting point and aqueous solubility. However, the difference between them is biochemically critical. One is an **optical isomer** of the other; that

TABLE 3.4 Functional Groups and Their Properties^a

Hydroxyl (OH)	$R-OH$	Polar; increases solubility in water; forms hydrogen bonds; characteristic of alcohols
Carboxyl (COOH)	$R-\overset{\text{O}}{\parallel}{C}-OH$	Polar; most important acidic group in biochemicals; pK_a depends on R (the more electronegative, the lower the pK_a)
Amine (NH ₂)	$R-NH_2$	Weak base; electronegative nitrogen attracts an additional H^+ from solution to become positively charged; common in proteins
Aldehyde (CHO)	$R-\overset{\text{O}}{\parallel}{C}-H$	Polar and water soluble; common in sugars and as fermentation products
Keto (CO)	$R_1-\overset{\text{O}}{\parallel}{C}-R_2$	Polar and water soluble; common in sugars and as fermentation products
Methyl (CH ₃)	$R-\overset{\text{H}}{\underset{\text{H}}{\mid}{C}}-H$	Nonpolar; reduces water solubility
Phosphate (PO ₄)	$R-\overset{\text{OH}}{\underset{\text{OH}}{\mid}{P}}-O$	Polar acidic group; important in energy metabolism; found in DNA, sugars; additional organic side chains can replace the two hydrogens; phosphorus is usually present only in the form of phosphate
Sulfhydryl	$R-S-H$	Polar; forms disulfide bonds to link molecules
Disulfide	$R_1-S-S-R_2$	Formed from two sulfhydryl bonds; important in protein folding

^aR stands for the rest of the molecule.

is, they rotate polarized light in opposite directions due to their mirror-image asymmetry. To understand this, it is necessary first to recognize that the four bonds that a carbon atom can participate in are arranged to point to the vertices of a tetrahedron if each bond connects to identical structures. This can be seen in Figure 3.4, which shows the tetrahedral

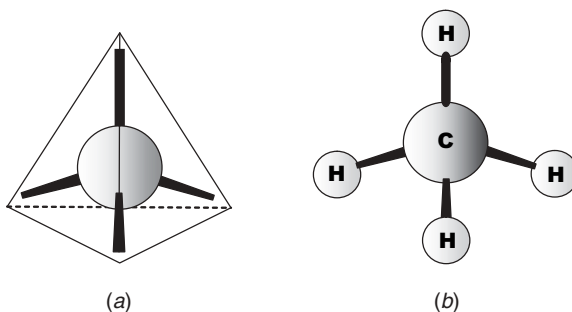


Figure 3.4 (a) Tetrahedral structure of carbon bonding and (b) a methane molecule. (Based on Gaudy and Gaudy, 1988.)

structure and a methane molecule having that form. If the functional groups on all four bonds are identical, the angle between any two bonds will be 109° .

The difference between the two types of glyceraldehyde is not obvious in the two-dimensional representation above. It seems that it should be possible to rotate the molecule around two of the bonds to change one form to the other. That it is not possible will be clearer if the molecule is viewed in its true three-dimensional form. The central carbon atom could be viewed as being at the center of a tetrahedron, with each of its four bonds pointing to a vertex. However, each of these bonds connects to a different group: an H, an OH, a CHO, and a CH_2OH . Such asymmetrical carbons are called **chiral centers**. Molecules with chiral centers can rotate polarized light either to the right, designated (+), or the left, designated (-). Biochemical compounds are often designated *d*- for *dextro*, meaning “right” or *l*- for *levo*, meaning “left,” based on a relationship to the structure of (+)glyceraldehydes or (-)glyceraldehydes, respectively. More complex molecules may have multiple carbon atoms that can form centers for optical rotation. In such cases, the *d*- or *l*- notation indicates a relationship to the structure of glyceraldehydes, not whether the molecule actually rotates light to the right or left. Whether the molecule actually rotates polarized light to the right or left is designated by including (+) or (-) in the name, respectively.

Figure 3.5 shows three-dimensional views of *d*- and *l*-glyceraldehyde. In part (a) the two forms seem identical, but a close examination will show that bonds that point out of the plane of the page in one form point inward in the other. The difference between the two becomes more clear in part (b), which could be formed by taking hold of the hydrogen bonded to the central carbon of each compound and pointing it toward the viewer. The CH_2OH group is pointed to the left (the oxygen is hidden behind the carbon). Then it can clearly be seen that the two compounds cannot be superimposed on each other

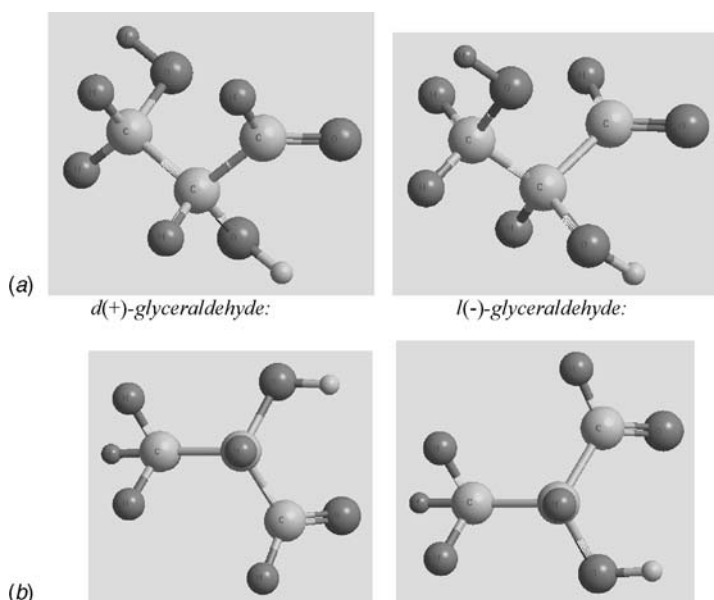


Figure 3.5 Three-dimensional views of the glyceraldehyde structure: (a) mirror-image views; (b) views showing the orientation with hydrogen of the central carbon pointed toward the viewer.

because the three groups attached to the central carbon atom are arranged in opposite directions around the carbon.

The importance of chirality is that these isomers are biochemically different and will react differently from each other. Fundamentally, optical isomers have different shapes from each other. The shape of a molecule determines how it can form complexes with other molecules. As described below, the formation of complexes, especially with enzyme molecules, is a key step in a biochemical reaction. For example, *d*-glucose can be used for energy by the brain, but *l*-glucose cannot. Similar differences are true for many other stereoisomeric biochemical compounds. Another name for *d*-glucose is *dextrose*, the familiar ingredient in manufactured food items.

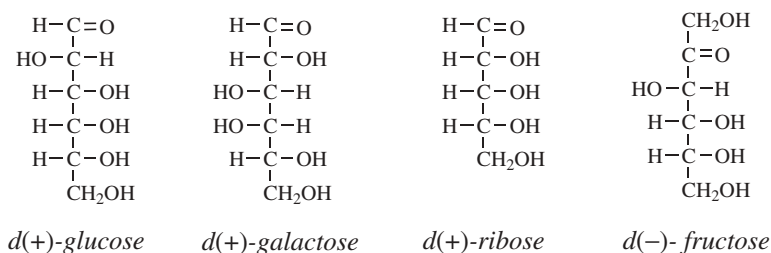
3.6 THE COMPOSITION OF LIVING THINGS

Four groups of compounds are of primary importance in living things: carbohydrates (including sugars, starches, cellulose, and glycogen), lipids (fats and oils), proteins, and nucleic acids (which form DNA and RNA). The first three of these form the majority of cell dry weight and are important for structural material, energy metabolism, and other metabolic functions. Nucleic acids are significant in reproduction and in energy metabolism. Finally, there are many compounds that do not fit neatly into these categories or may be hybrids of two or more.

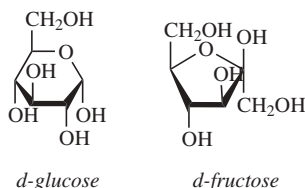
3.6.1 Carbohydrates

Carbohydrates include sugars, starches, and structural materials such as cellulose. All have the empirical chemical formula $(\text{CH}_2\text{O})_n$. For example, *glucose* is $\text{C}_6\text{H}_{12}\text{O}_6$, so *n* is 6. Glyceraldehyde is one of the simplest carbohydrates, with an *n* of 3. The large number of hydroxide groups on carbohydrates renders them hydrophilic. Carbohydrates are classified into several groups: **Monosaccharides** are the simplest and are building blocks for the others. They have relatively low molar masses, and *n* in the formula can range from 3 to 9. Monosaccharides can form chains, called **polymers**, producing **disaccharides**, which are formed from pairs of monosaccharides, or the long-chain **polysaccharides**, which can have molar masses as high as 1 million. Large molecules such as polysaccharides, proteins, or DNA are called **macromolecules**.

The structures of several monosaccharides that are commonly found in nature are shown below. *Ribose* is a five-carbon sugar; the others are six-carbon sugars. Glucose is a particularly important six-carbon sugar. It is the principal sugar formed by photosynthesis and is the main immediate source of energy for all cells. Nervous tissue in animals can only use glucose for energy.



One end of monosaccharides such as glucose reacts spontaneously with either the other end or the adjacent carbon to form ring structures. For example, glucose can form a six-membered ring, and fructose, a five-membered ring.

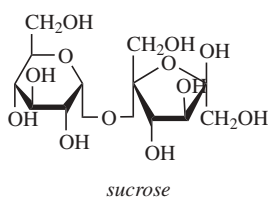


The rings are closed by an oxygen atom. The ring form and the open-chain form freely interconvert. However, for glucose, for example, the equilibrium highly favors the ring form.

A number of monosaccharide derivatives are important. Conversion of ends to $-\text{COOH}$ groups produces the **sugar acids**, such as glucuronic acid. Fermentation may result in the production of sugar acids as intermediates. **Amino sugars** are formed by replacing one of the hydroxyl groups on certain monosaccharides with a nitrogen-containing amino group (see below under proteins). Another derivative is the **deoxy sugar**, formed by replacing one of the hydroxy groups with a hydrogen; thus, one of the carbons will have two hydrogens. A very important deoxy sugar is deoxyribose, an important component of DNA.

Monosaccharides can also form a special type of bond with each other or with other molecules. This **glycosidic bond** forms between a hydroxide on the monosaccharide and a hydroxide on another molecule, which may be another monosaccharide, with the elimination of one molecule of water. Again, the link will be through an oxygen atom.

If the other molecule is another monosaccharide, the result is a disaccharide. Familiar table sugar is sucrose, a disaccharide formed from the monosaccharides glucose and fructose. Lactose, the sugar in milk, is formed from glucose and galactose. The same two monosaccharides can form disaccharides in several ways, depending on orientation and location of the connection. For example, *maltose* and *cellobiose* are both made from two glucose residues.



Glycosidic bonds can form longer-chain carbohydrates called **oligosaccharides**, those with only a few monosaccharides, which include the disaccharides, and the much longer-chain polysaccharides. **Starch** is a type of polysaccharide produced by plants for energy storage. Humans obtain most of their dietary carbohydrate in the form of starch from grain. Starch is a chain of glucose residues bonded as in maltose. The chain may be straight, as in *amylose*, which makes up about 20% of potato starch; or it may be branched, as in *amylopectin*, which forms the other 80% of potato starch.

Animals store carbohydrates in a polysaccharide called **glycogen**. Glycogen is similar to starch except that the chain is much more highly branched. It is thought that by having more “ends” to the glycogen molecule, it is more available for rapid conversion to

glucose for the sudden energy demands of animals. Depletion of glycogen in the muscle may cause the “wall” experienced by marathoners after several hours of running, which prevents them from continuing the race. With glycogen gone, the body switches to fat, which does not provide energy fast enough and produces other physiological stresses. In mammals, skeletal muscle contains about two-thirds of the body’s glycogen, and the liver holds most of the rest. The liver uses the glycogen to control glucose levels in the blood. Figure 3.6a shows the basic structure common to both starch and glycogen.

Cellulose is an unbranched polysaccharide also composed exclusively of glucose residues, but with an important difference from starch. The glycosidic bond is reversed, as in the cellobiose disaccharide (see Figure 3.6b). This prevents the molecule from twisting, making it stiffer. As a result, it finds use as a structural material located in the cell walls of plants and forming the major component of wood. (It should be noted that the hardness of wood comes not from cellulose but from *lignin*, described below.) Another important fact about cellulose is that only a very few animals (such as garden snails) can digest it. Most cannot break it down to glucose to make the stored energy available. However, several animals, such as termites and cows, have developed associations with microorganisms that live in their digestive systems. The microorganisms accomplish the digestion for the animals.

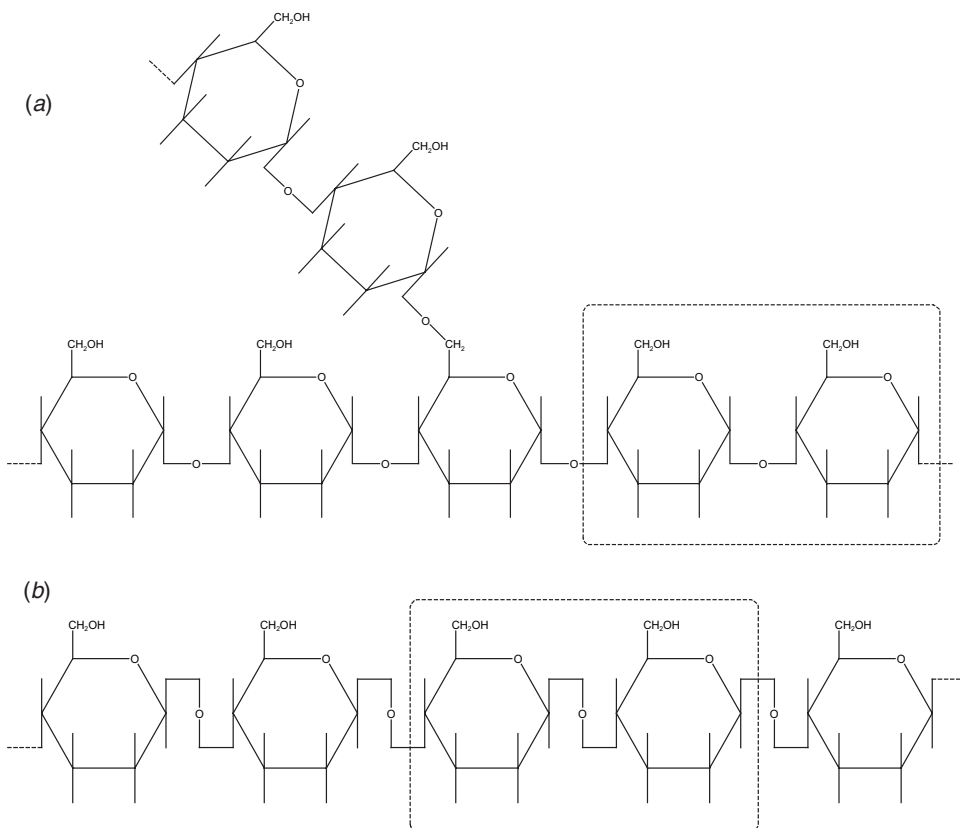


Figure 3.6 Polymers of glucose: (a) starch or glycogen showing a maltose repeating disaccharide unit; (b) cellulose with a cellobiose repeating unit.

Another structural polysaccharide is *chitin*, which forms the hard shell of arthropods such as insects and crabs, as well as the cell walls of most fungi. Chitin is a polymer of a sugar amine, *N*-acetyl glucosamine; crustaceans also include calcium carbonate in their shells. Chitin has been studied for use as an adsorption media for removing heavy metals from water. Other important structural polysaccharides include *agar* and *carrageenan*, which are extracted from seaweed. The former is used as a substrate for culturing bacteria, and the latter is used as a food thickener.

3.6.2 Lipids

Lipids refer to a loose category of compounds with the common property that they have fairly low solubility in water or are extracted from biological materials by solvents having polarity much less than water, such as ethanol or chloroform. There are five major types, of which the first four are described here and the fifth in a later section.

- Fatty acids, long-chain aliphatic carboxylic acids
- Fats, esters of fatty acids with glycerol
- Phospholipids, esters of phosphate and fatty acids with glycerol
- Lipids not containing glycerol, including waxes and steroids
- Hybrid lipids, such as those combined with carbohydrates or proteins

Fatty acids are simply straight-chain hydrocarbons with a carboxylic acid functional group at one end (Figure 3.7). They usually, but not always, have an even number of carbon atoms. It is the hydrocarbon chain that imparts hydrophobicity, since the carboxylic acid group is water soluble. The larger the chain is, the more hydrophobic the molecule. The simplest fatty acid is *formic acid*, where a simple hydrogen makes up the variable R-group. The most familiar is *acetic acid*, formed with a methyl group. Vinegar is about 5% acetic acid. Both of these are quite water soluble. The melting point of fatty acids tends to increase with chain length.

Fatty acids usually do not accumulate in nature. Systems may be engineered to produce them, as is done in fermentation processes. An important environmental application is anaerobic digestion, in which fatty acids consisting mainly of acetic acid, but also

Basic structure:



Saturated fatty acids:

Formic	HCOOH
Acetic	CH ₃ COOH
Propionic	CH ₃ CH ₂ COOH
<i>n</i> -Butyric	CH ₃ (CH ₂) ₂ COOH
Caproic	CH ₃ (CH ₂) ₄ COOH
Palmitic	CH ₃ (CH ₂) ₁₄ COOH
Stearic	CH ₃ (CH ₂) ₁₆ COOH

Unsaturated fatty acids

Oleic	CH ₃ (CH ₂) ₇ CH=CH(CH ₂) ₇ COOH
Linoleic	CH ₃ (CH ₂) ₄ CH=CHCH ₂ CH=CH(CH ₂) ₇ COOH
Arachidonic	CH ₃ (CH ₂) ₄ -(CH=CH-CH ₂) ₄ -(CH ₂) ₂ -COOH

Figure 3.7 Structures of some of the more common fatty acids found in nature.

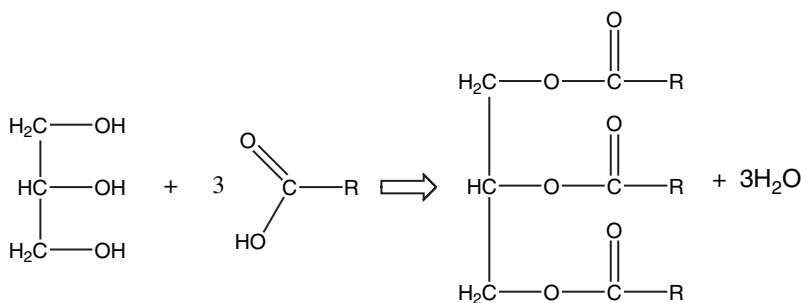


Figure 3.8 Formation of triglyceride from glycerol and fatty acids.

propionic, butyric, and others, can accumulate to levels typically below 1%, as an intermediate in methane production.

Saturated fatty acids are those in which the maximum number of hydrogens have been bonded with the carbons in the hydrocarbon chain. If a hydrogen is removed at a point in the chain, the corresponding carbon has an extra bond to form, to fill its complement of four. It satisfies this requirement by forming a double-bond with its neighbor (which also loses a hydrogen). Fatty acids containing one or more double-bonded carbons are called **unsaturated fatty acids**. Unsaturation puts a kink in the chain, reducing the ability of the molecules to pack together. As a result, they are less likely to form solids (i.e., their melting points are lowered).

Except for formic acid ($\text{p}K_a = 3.75$), all of the saturated fatty acids have acid dissociation constants averaging around 4.85, similar to that of acetic acid ($\text{p}K_a = 4.76$).

Fats are formed from the covalent bonding of three fatty acids with the three hydroxides of a glycerol (Figure 3.8). For this reason they are often called **triglycerides**. The bonding of a hydroxyl of an alcohol with the hydroxyl of a carboxylic acid, with elimination of a water molecule, results in an **ester linkage**. This eliminates the hydroxide from the alcohol and the ionizable portion of the acid. With the loss of these functional groups, polarity is greatly reduced, ionization is eliminated, and water solubility is therefore decreased. Because the ester linkage is only slightly polar, the properties of fats are dominated by the properties of the hydrocarbon chains of the fatty acids that form them.

The reverse of the esterification reaction is **hydrolysis**, which means “splitting with water.” Hydrolysis of ester bonds is catalyzed by H^+ or by enzymes called **lipases**. The ester bond can also be hydrolyzed in a strong basic solution, in a reaction called **saponification**. The salts of the fatty acids thus formed are soaps. In fact, soap was made in preindustrial households by reacting fats collected from meat with lye (sodium hydroxide) leached from ashes.

Oils are fats that are liquids at room temperature. Fats made from unsaturated fatty acids are **unsaturated fats**. As with the fatty acids, they will have lower melting points. This is why you may read that margarine or shortening contains “partially hydrogenated fats.” Fats are hydrogenated by reacting unsaturated vegetable oils with hydrogen, reducing the number of double bonds, in order to decrease the melting point, allowing the oil to form a solid. In a similar way, living things select for the saturation of fats to obtain properties that are useful.

The major functions of fats in organisms are for energy storage and structural use. Fats yield twice as much chemical energy as carbohydrates or proteins; fats average about 9.3 Calories per gram vs. 4.1 Calories per gram for both proteins and carbohydrates. (Note that the dietary *Calorie*, which must be capitalized, is equivalent to the kilocalorie

TABLE 3.5 Percentage of Types of Fats in Some Dietary Fats and Oils

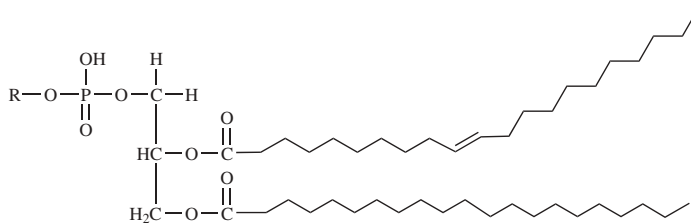
	Saturated	Mono-unsaturated	Poly-unsaturated	Other	Cholesterol (mg/tB)
Canola oil	6	62	31	1	0
Safflower oil	9	12	78	1	0
Olive oil	14	77	9	0	0
Beef fat	51	44	4	1	14
Butter	54	30	4	12	33
Coconut oil	77	6	2	15	0

commonly used in thermodynamics.) However, fat storage is long term. The energy contained in fats is not released as rapidly as with the polysaccharides starch or glycogen. Other functions of fats are for insulation for animals exposed to cold, and for flotation in marine animals. The blubber of sea mammals is an example of both of these functions.

The degree of fat saturation in the human diet is linked to human health. A small amount of unsaturated fat is required in the diet, because humans cannot form fatty acids with double bonds. One of these in particular, linoleic acid, can be converted into all the other fatty acids needed by humans. For this reason, it and several others are placed in a dietary group called the **essential fatty acids**.

A mammalian diet containing a high proportion of saturated fats is associated with cardiovascular disease, via its connection with cholesterol and blood lipoproteins. (Cholesterol is another type of lipid, described below. Lipoproteins are hybrid compounds, also described below.) Among the unsaturated fats, **monounsaturated fats**, those with only one double bond, seem to be even more healthful than **polyunsaturated fats**, those with more than one double bond. Table 3.5 shows how various fats compare in these dietary constituents. Olive oil has the highest monounsaturated fat content of all. This has lent support to the “Mediterranean diet,” in which olive oil replaces butter and other animal fats in recipes, to the extent of placing a plate of oil on the table for dipping bread instead of a butter dish. Lest one should think that only animal fats are suspect, notice the high saturated fat content of coconut oil. High polyunsaturated fat content also seems to be beneficially lower blood lipid concentration. Safflower oil is best in this regard, followed by corn, peanut, and cottonseed oils.

Phospholipids are particularly critical to life, as they form the basic structure of cell membranes. Glycerol can form ester linkages with inorganic as well as organic acids. Phospholipids consist of ester linkages of glycerol with two fatty acids and with phosphoric acid in the third position. Usually, another of the phosphate hydroxyl groups form, in turn, another ester bond with still another organic molecule, called a *variable group*. The variable group often contains nitrogen, adding to the polar character of the lipid.



phospholipid structure

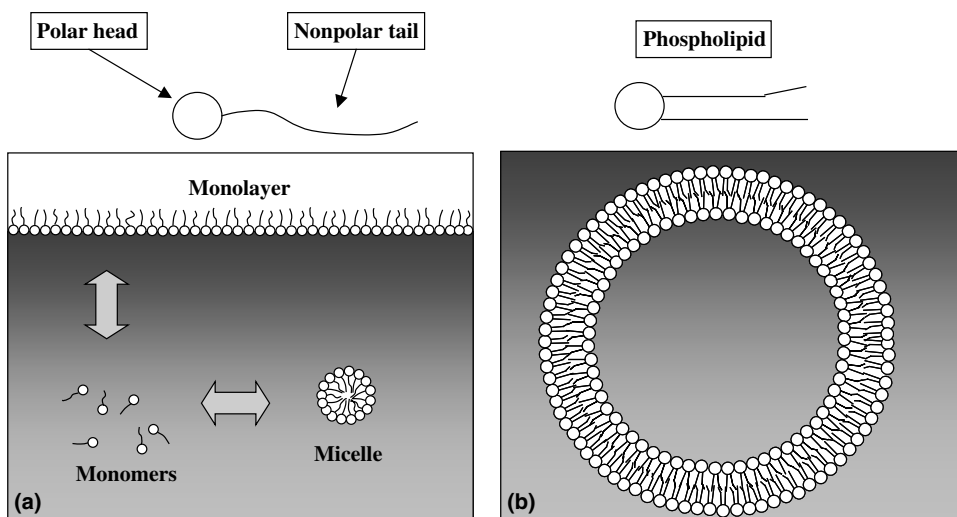


Figure 3.9 Surfactant structures formed in solution: (a) behavior of surfactants in solution; (b) phospholipid bilayer structure.

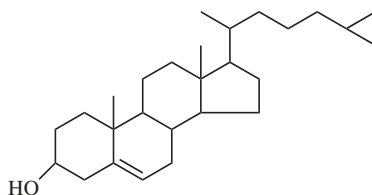
This structure results in a **surfactant**, a molecule that has a hydrophilic part and a hydrophobic part. Similar to soaps and detergents, if there are enough molecules in solution, they will form aggregates called **micelles**, a sort of “circling the wagons” in which the polar ends face the water and the hydrophobic ends form a separate phase in the interior of the micelle (Figure 3.9). One of the phospholipids is *lecithin*, which is important in metabolism of fats by the liver. Egg yolks are rich in lecithin, and its detergent nature helps maintain the emulsion between oil and vinegar in mayonnaise.

Biological lipids show an important difference in behavior from other surfactants. Under the right conditions, they form micelles with multilayered structures that can become **vesicles** (water-filled cavities) bounded by a **lipid bilayer**, as also shown in Figure 3.9. This important structure is the basis for the cell membrane, and therefore for the cell itself. The bilayer membrane forms a barrier to the uncontrolled passage of water-soluble constituents into and out of the cell. However, its lipophilicity makes it the site of action of many lipophilic pollutants, such as some industrial organic solvents.

Other lipids: Since the definition of lipids is based on physicochemical properties and not chemical structure, it is not surprising that the group is very diverse. A variety of other biological compounds fit the category. **Waxes** are long-chain fatty acids combined with long-chain alcohols other than glycerol. They are formed by plants to produce protective and water-conserving layers on their surfaces and by animals such as the honeybee, or for ear canal protection. **Terpenes** are long-chain hydrocarbons based on units similar to the compound isoprene. They include essential oils from plants, among other compounds.

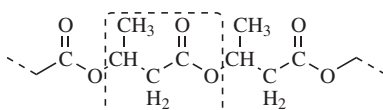
One important group of compounds that is in this catch-all class of lipids is the steroids. **Steroids** consist of four fused rings, three with six carbons and one with five, and with a hydroxide at one end and a hydrophobic “tail” at the other. Steroids are important regulatory chemicals in plants and animals. They are able to move through cell membranes formed by lipid bilayers. The sex hormones estrogen and testosterone are steroids, as are the fat-soluble vitamins A, D, and E. The most abundant steroid in animals is *cholesterol*. It forms an essential part of the cell membrane, affecting its fluidity. However, factors

related to diet and heredity can cause cholesterol to form obstructive deposits in blood vessels, causing strokes or heart attacks.



cholesterol

Another lipid that is important in biological wastewater treatment is *poly-β-hydroxybutyric acid* (PHB). This is used for energy storage by some bacteria.

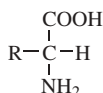


poly-β-hydroxybutyric acid

3.6.3 Proteins

Proteins have a central role in cell function. Like carbohydrates and lipids, they are involved in structure and in energy metabolism. More important is the function unique to proteins: Each of the thousands of enzymes in living things, each of which catalyzes a specific biochemical reaction, is a protein specialized for that task. In addition, they may act as biochemical regulators or hormones, such as insulin; transport chemicals such as hemoglobin, which transports oxygen in the blood; or they may be responsible for motility, as in the cilia and flagella of protists.

Proteins are composed of one or more chains of amino acid repeating units. Each individual chain is called a **polypeptide**. In turn, **amino acids** are compounds in which a central carbon is covalently bonded to three functional groups: an amine, a carboxylic acid, and a variable organic side group:



Many amino acids are found in nature, but only 20 are commonly part of proteins. In contrast to polysaccharides, proteins are formed not from one or two repeating units, but from all 20, and in any sequence. This makes possible a virtually unlimited variety of structure and of corresponding function. A chain of n amino acids can form 20^n different proteins. For a length of only five acids, this gives 3.2 million combinations. Typical chain lengths are from 100 to several thousand. Of course, only certain combinations actually occur. The human body has about 100,000 different proteins.

Table 3.6 shows the 20 amino acids commonly found in proteins. Some have simple side groups (e.g., glycine and alanine), others are complex (e.g., tryptophan). Two contain sulfur (cysteine and methionine). Some have ionizable side groups, such as the carboxylic

TABLE 3.6 Amino Acids Commonly Found in Proteins and Their pI Values

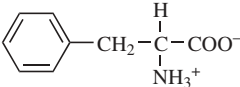
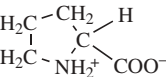
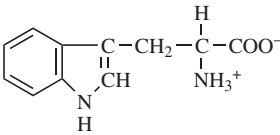
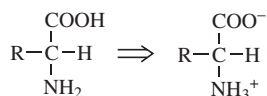
Name	Symbol	Structure	pI
Amino Acids with Nonpolar R Groups			
<i>Alanine</i>	Ala	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	6.00
<i>Isoleucine</i> ^a	Ile	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{CH}_2-\text{CH}-\text{C}-\text{COO}^- \\ \quad \\ \text{H}_3\text{C} \quad \text{NH}_3^+ \end{array}$	6.02
<i>Leucine</i> ^a	Leu	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{CH}-\text{CH}_2-\text{C}-\text{COO}^- \\ \quad \\ \text{H}_3\text{C} \quad \text{NH}_3^+ \end{array}$	5.98
<i>Methionine</i> ^a	Met	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{S}-\text{CH}_2-\text{CH}_2-\text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	5.74
<i>Phenylalanine</i> ^a	Phe		5.48
<i>Proline</i>	Pro		6.30
<i>Tryptophan</i> ^a	Trp		5.89
<i>Valine</i> ^a	Val	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{CH}-\text{C}-\text{COO}^- \\ \quad \\ \text{H}_3\text{C} \quad \text{NH}_3^+ \end{array}$	5.96
Amino Acids with Uncharged Polar R Groups			
<i>Asparagine</i>	Asn	$\begin{array}{c} \text{O} \quad \text{H} \\ // \quad \\ \text{H}_2\text{N}-\text{C}-\text{C}-\text{COO}^- \\ \quad \\ \quad \quad \text{NH}_3^+ \end{array}$	5.41
<i>Cysteine</i>	Cys	$\begin{array}{c} \text{H} \\ \\ \text{HS}-\text{CH}_2-\text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	5.07
<i>Glutamine</i>	Gln	$\begin{array}{c} \text{O} \quad \text{H} \\ // \quad \\ \text{H}_2\text{N}-\text{C}-\text{CH}_2-\text{CH}_2-\text{C}-\text{COO}^- \\ \quad \\ \quad \quad \text{NH}_3^+ \end{array}$	5.65

TABLE 3.6 (Continued)

Name	Symbol	Structure	pI
<i>Glycine</i>	Gly	$\begin{array}{c} \text{H} \\ \\ \text{H}-\text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	5.97
<i>Serine</i>	Ser	$\begin{array}{c} \text{H} \\ \\ \text{HO}-\text{CH}_2-\text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	5.68
<i>Threonine</i> ^a	Thr	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{C}-\text{CH}-\text{C}-\text{COO}^- \\ \quad \\ \text{OH} \quad \text{NH}_3^+ \end{array}$	5.60
<i>Tyrosine</i>	Tyr	$\text{HO}-\text{C}_6\text{H}_4-\text{CH}_2-\begin{array}{c} \text{H} \\ \\ \text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	5.66
Amino Acids with Acid R Groups (Negatively Charged at pH 6.0)			
<i>Aspartic acid</i>	Asp	$\begin{array}{c} \text{O}^- \\ \\ \text{C}=\text{O} \\ \\ \text{CH}_2-\begin{array}{c} \text{H} \\ \\ \text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array} \end{array}$	2.77
<i>Glutamic acid</i>	Glu	$\begin{array}{c} \text{O}^- \\ \\ \text{C}=\text{O} \\ \\ \text{CH}_2-\text{CH}_2-\begin{array}{c} \text{H} \\ \\ \text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array} \end{array}$	3.22
Amino Acids with Basic R Groups (Positively Charged at pH 6.0)			
<i>Arginine</i>	Arg	$\begin{array}{c} \text{H} \\ \\ \text{H}_3\text{N}^+-\text{C}-\text{NH}-\text{CH}_2-\text{CH}_2-\text{CH}_2-\text{C}-\text{COO}^- \\ \quad \\ \text{NH} \quad \text{NH}_3^+ \end{array}$	10.76
<i>Histidine</i>	His	$\begin{array}{c} \text{H} \\ \\ \text{HC}=\text{C}-\text{CH}_2-\text{C}-\text{COO}^- \\ \quad \quad \\ \text{H}^+\text{N} \quad \text{NH} \quad \text{NH}_3^+ \\ \quad \quad \quad \\ \quad \quad \quad \text{C} \\ \quad \quad \quad \\ \quad \quad \quad \text{H} \end{array}$	7.59
<i>Lysine</i> ^a	Lys	$\text{H}_3\text{N}^+-\text{CH}_2-\text{CH}_2-\text{CH}_2-\text{CH}_2-\begin{array}{c} \text{H} \\ \\ \text{C}-\text{COO}^- \\ \\ \text{NH}_3^+ \end{array}$	9.74

^aEssential amino acids.

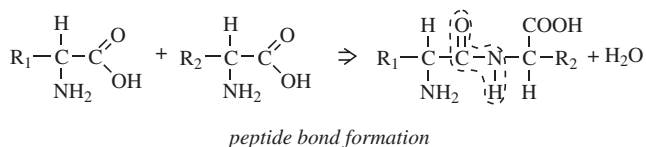
acids in aspartic acid and glutamic acid, or the basic amines of lysine, histidine or arginine. Amines, including the one connected to the central carbon, ionize by accepting an additional hydrogen ion at pH levels below a characteristic pK value. Because all amino acids have both an acidic and a basic functional group, all will have an ionic charge at either sufficiently high or low pH values. For some, it is possible at certain pH values for both groups to be ionized:



These behaviors are important in forming attractions between different parts of the protein molecule, affecting its shape. Table 3.6 also gives the **isoelectric point (pI)**, which is the pH at which the number of positive charges on the amino acid in solution equals the number of negative charges.

The fact that all amino acids contain nitrogen explains the importance of that element to all organisms. Nitrogen limitations can cause growth problems in biological wastewater treatment and in natural ecosystems. Humans also have a nutritional requirement for proteins. We can form many of the amino acids from other compounds. However, we cannot synthesize the following eight, which are called **essential amino acids**: *isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine*. These must be provided in the diet daily, since free amino acids are not stored in the body. The absence of any one causes protein synthesis to stop. Most animal proteins contain all eight, but many plant proteins do not, or do not have them in balanced amounts. For this reason vegetarians need to be aware that they must eat vegetables in combinations that eliminate deficiencies. For example, rice is deficient in lysine but has sufficient methionine, whereas beans are low in methionine but contain adequate lysine. However, beans and rice together in a diet supply a complete protein supply.

Amino acids form polypeptides by covalently bonding the carbon from the carboxylic acid group to the nitrogen of the amine, with loss of a water molecule. The result is called a **peptide bond**:



Because of the amino acid functional groups, proteins also possess charges in solution, which vary with pH. Like individual amino acids, proteins have an isoelectric point. These can range from less than 1.0 for pepsin, the digestion enzyme that must act under acidic conditions in the stomach, to 10.6 for cytochrome *c*, which is involved in cellular respiration.

Unlike polysaccharides, which can have random lengths and random branching, each peptide is a single chain with a precise sequence of amino acids. Changing even a single amino acid can destroy the ability of the resulting protein to perform its function. Furthermore, the peptide chain must arrange itself into a complex shape, which is determined by the exact amino acid sequence, and often by the method by which the cell machinery

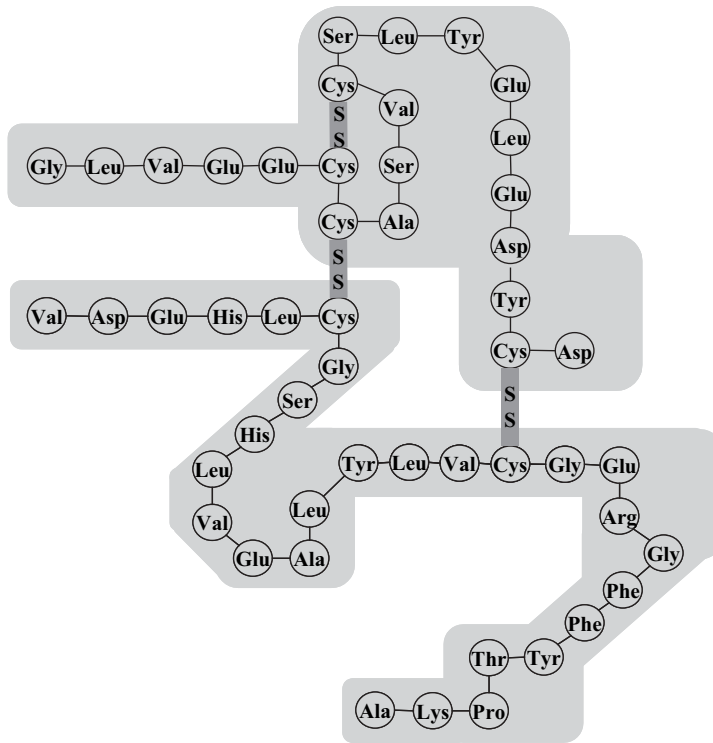


Figure 3.10 Tertiary and quaternary protein structure as shown in bovine insulin. This protein consists of two polypeptide chains joined by two disulfide bonds. Another disulfide bond within the smaller chain contributes to the molecule's shape. (Based on Bailey and Ollis, 1986.)

constructs the protein. The structure of a protein has three or four levels of organization. The **primary level** is the actual amino acid sequence. The **secondary level** refers to relatively local arrangements such as coiling into a helix or folding into a pleated sheet. The helix is held together by hydrogen bonds between the peptide bonds of every fourth amino acid. The **tertiary level** of organization is larger-scale folding and coiling, to give the overall shape to the molecule. Some proteins will exhibit the **quaternary level** of structure, in which several polypeptides are linked together by a variety of attractions, including hydrogen bonds, ionic attraction, or covalent disulfide linkage between cysteine amino acids on the two peptides. Hemoglobin, for example, consists of four polypeptide units. Figure 3.10 shows an example of protein structure. If the protein forms a compact, water-soluble state, which the majority of proteins do, they are called **globular proteins**. **Fibrous proteins** are elongated and often function in structural applications in connective tissue, contractile tissue, or as part of the hair or skin in mammals.

Proteins molecules often have other chemical compounds, called **prosthetic groups**, included in their structure, usually through noncovalent bonding. Often, they include metal ions. Hemoglobin contains four organic prosthetic groups, each containing an iron atom. Other proteins may contain chromium, copper, or zinc, for example. This is one of the reasons that humans and other organisms have a nutritional requirement for some heavy metals.

Since the higher levels of protein structure depend on relatively weak bonds such as hydrogen bonds, they are easily disrupted by increasing temperature or by changing pH or ionic strength. Such changes may result in conversion of the protein to a non-functional form, which is said to be **denatured**. These changes are often reversible. For example, hair can be curled by wrapping it around a rod and heating. This breaks hydrogen bonds, which re-form upon cooling, “freezing” the protein in the new shape. However, there is tension in the hair fibers, and with time the hydrogen bonds gradually rearrange into their former relationship, losing the curl. A “permanent” rearrangement can be made by using chemical treatment, which breaks disulfide bonds between cysteine residues in hair proteins, then re-forms them in the curled shape. A common example of irreversibly denaturing proteins by heat is the cooking of eggs. Heat disrupts the globular albumin proteins, which do not return to their native state upon cooling.

Enzymes are protein catalysts that increase biochemical reaction rates by factors ranging from 10^6 to 10^{12} over the uncatalyzed reactions. They often include non-amino acid portions that may be organic or consist of metallic ions. These are called **cofactors**.

Most enzymes are named with the suffix *-ase*. For example, *lipase* is an enzyme that digests lipids. Another enzyme is *lactase*, which catalyzes the breakdown of milk sugar, the disaccharide *lactose*, into monosaccharides glucose and galactose. Many adults, and almost all non-Caucasian adults, lose their ability to produce lactase after early childhood. However, some bacteria, including *Escherichia coli*, produce a different lactose-digesting enzyme. Adults lacking lactase who eat milk products have abdominal disturbances when the bacteria in the gut begin to produce gas using the lactose.

Enzymes are very specific; each catalyzes one or only a few different reactions, which is sensitively controlled by its shape. It is remarkable that contrary to reactions in aqueous media in the laboratory, enzyme-catalyzed reactions produce few side reactions. Equally remarkable is the fact that, with enzymes, a wide variety of reactions are promoted at mild conditions of temperature, pressure, and pH.

Each enzyme has at least one **active site**, the location on the molecule that binds with the **substrate(s)** (the reactants in the catalyzed reaction). The active site attracts the substrate(s) and holds it, usually by physicochemical forces. Two major mechanisms by which enzymes increase reaction rates are (1) by bringing the reactants close together, and (2) by holding them in an orientation that favors the reaction (Figure 3.11). It is also thought that enzymes can act by inducing strain in specific bonds of bound substrates, making certain reactions favorable.

Since the shape of a molecule is so sensitive to its environment, the cell can turn reactions on or off by changing conditions (e.g., pH) or by providing or withdrawing a cofactor or inhibitory compound. Figure 3.12 shows how a cofactor could promote binding of a single substrate with an enzyme. The cofactor binds first with the enzyme, changing the shape of the active site. This allows the substrate to bind, forming the complex. As with all proteins, denaturing stops the function of any enzyme.

Enzymes may also require **coenzymes**, which are molecules that function by accepting by-products of the main reaction, such as hydrogen. Coenzymes differ from cofactors and from enzymes themselves in that they are consumed by the reaction (although they may be regenerated in other reactions). Examples include NAD and FAD, discussed below. Some cofactors and coenzymes cannot be synthesized by mammals and must be included in their diet, making them what we call *vitamins*.

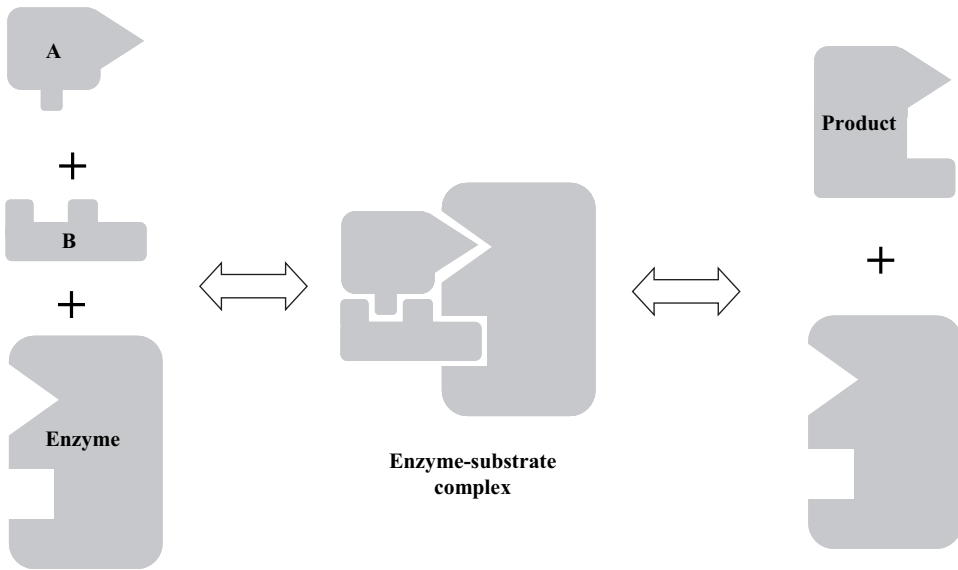


Figure 3.11 Enzyme control of proximity and orientation of substrates.

Another important protein function is their use as binding proteins. Hemoglobin is an example of a binding protein that transports oxygen in the blood. Other binding proteins are active in the immune system, which responds to foreign substances in animals. The cell membrane is studded with proteins that function in communicating substances

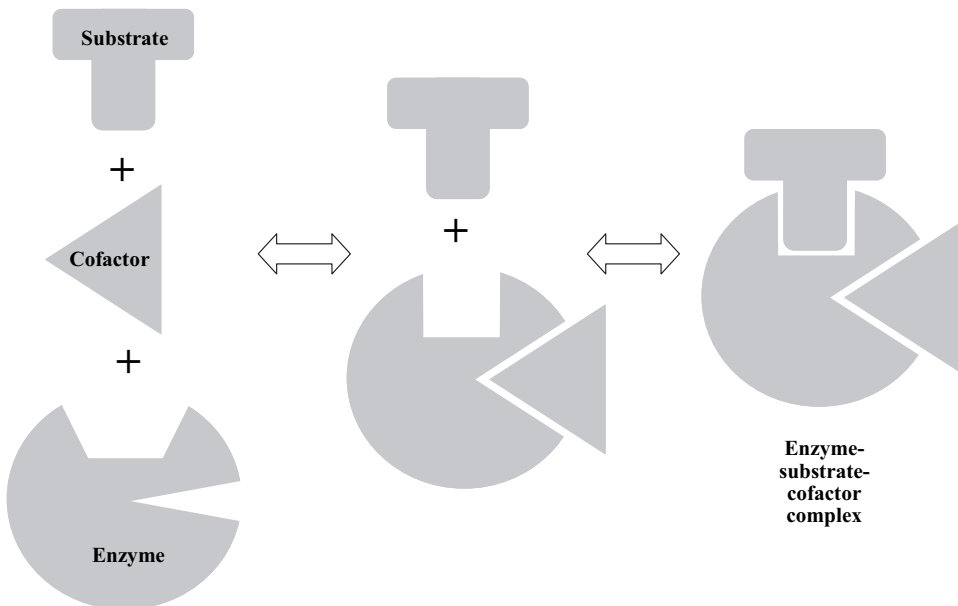


Figure 3.12 Hypothetical enzyme mechanism involving a cofactor.

and signals into and out of the cell. Cell membrane proteins are also a point of attack for infectious agents such as viruses, or may bind with drugs, leading to reactions that produce their characteristic effects.

3.6.4 Nucleic Acids

Nucleic acids do not form a large portion of the mass of living things, but make up for this in importance by being central to reproduction and control of cell function (DNA and RNA) and as the single most important compound in energy metabolism [adenosine triphosphate (ATP)]. DNA and RNA are linear polymers of nucleotides; ATP is a single nucleotide.

A **nucleotide** is a compound consisting of three parts:

pyrimidine or purine base + ribose or deoxyribose sugar + one or more phosphates

The **pyrimidines** are based on a six-membered ring containing two nitrogens. Only the following three pyrimidines are found in DNA and RNA: *thymine*, *cytosine*, and *uracil* (Figure 3.13). **Purines** have an additional five-membered ring fused to the pyrimidine. Only two purines are used in DNA and RNA, *adenine* and *guanine*. Nucleotides using these bases are labeled with their first letter: A, G, U, C, or T. The five-carbon sugars are bonded to the base, and the phosphate(s) are connected to the sugar via an ester.

A **nucleoside** is the same as a nucleotide, without the phosphate. The nucleoside formed from adenine and ribose is called **adenosine**. The nucleoside formed from thymine and deoxyribose is called **thymidine**.

Besides forming a chain of phosphates, the phosphate portion of the molecules can form ester bonds to two nucleotide sugars, forming a linear polymer with the phosphates and sugars as a “backbone” and the bases as branches (Figure 3.14).

Deoxyribonucleic acid (DNA) and **ribonucleic acid** (RNA) are polymers formed from nucleotides. In DNA the sugars are deoxyribose; in RNA the sugars are ribose. Another important difference between these polymers is that DNA does not contain uracil, while RNA never includes thymine. In other words, DNA includes only A, G, C, and T; RNA has only A, G, C, and U.

RNA is present only as a single chain. However, two strands of DNA form a fascinating structure called the **double helix**, discovered by Watson and Crick in 1953. It happens that thymine and adenine on two different strands can form two hydrogen bonds in just the right position relative to each other, and cytosine and guanine on two complementary strands form three such bonds (Figure 3.14). Thus, the sequence of bases on one strand determines the sequence on the other. The two complementary strands are held together by a large number of hydrogen bonds, making the pairing very stable. The resulting structure resembles a ladder, with each sugar–phosphate backbone making one side of the ladder, and the base pairs forming the rungs. A purine is always opposite a pyrimidine, to keep the lengths of the rungs all the same. In addition, the ladder has a right-hand twist to it, making a complete turn every 10 “rungs” or base pairs, producing the famous double helix structure.

Notice from Figure 3.14 that the point of attachment at one end of the chain of nucleotides is carbon 5 of the sugar, and at the other end it is carbon 3. This gives a direction to

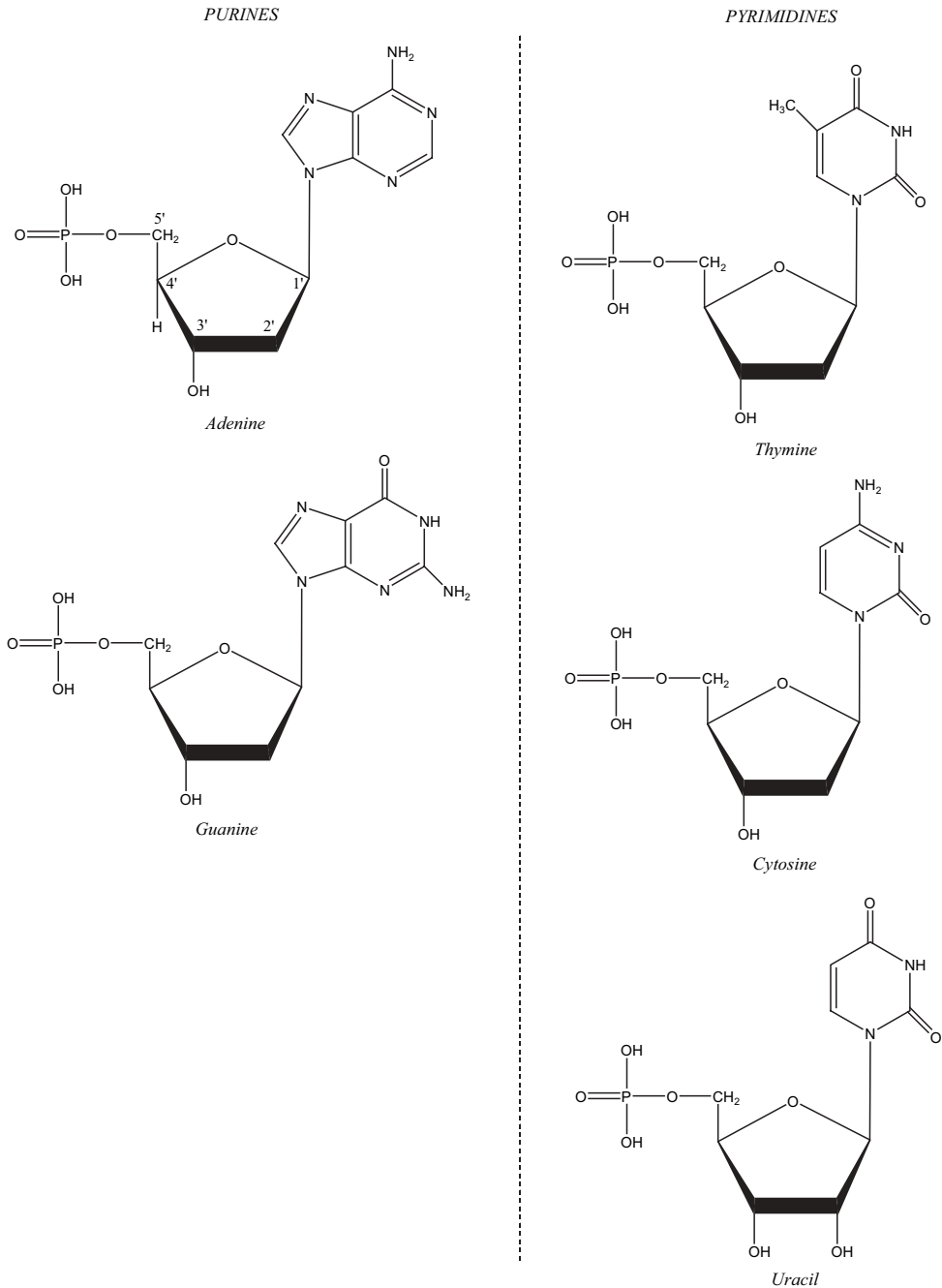


Figure 3.13 Nucleotide structures.

the chain. The ends are labeled 3' and 5'. You can also see that the complementary DNA chains run in opposite directions.

The importance of DNA is that it carries all of the genetic information of all living things. The information is coded in the sequence of bases in the DNA molecule. The two strands, although different, are complementary and carry the same information. That

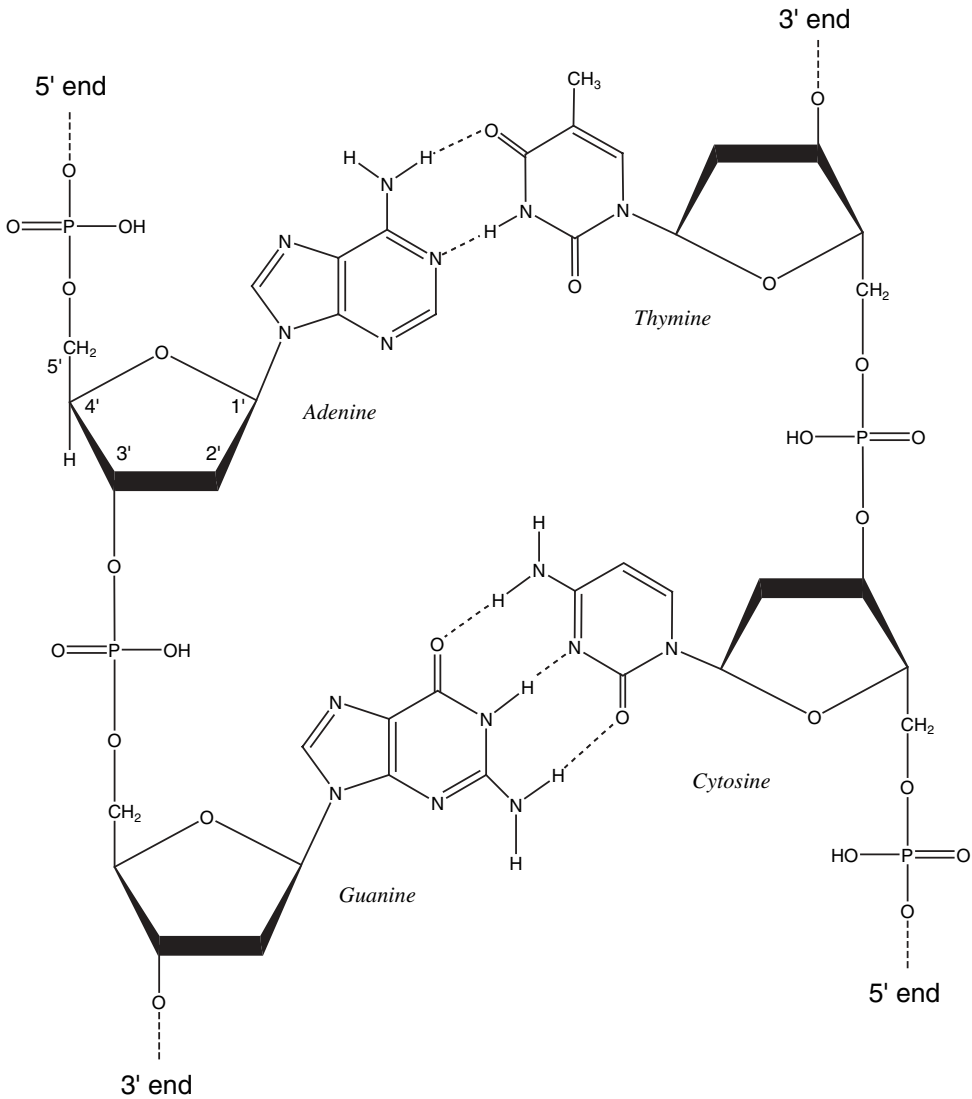


Figure 3.14 DNA molecule section showing the phosphate-sugar “backbone.”

is, if one strand has the bases ATGCCACTA, the other strand must be TACGGTGAT, to form the following pairings:



What does DNA code for? Very simply, by specifying the sequence of amino acids, it contains instructions for the construction of all the proteins that the organism can make. Recall that proteins can have 20 different amino acids. So how can four nucleotide bases code for all 20? The answer is that the DNA bases code in groups of three.

The sequence for the bottom strand in the example above, and the corresponding amino acid sequence, is

DNA :	TAC	–	GGT	–	GAT
AA :	methionine	–	proline	–	leucine

As mentioned above, RNA uses uracil in place of thymine and ribose sugar instead of deoxyribose. In addition, it is a single strand. The major function of RNA is to communicate the DNA code from the cell nucleus to the cytoplasm, where proteins are synthesized. More details on the mechanisms involved are provided in Section 6.2.1. RNA has another function, recently discovered. It can act as a catalyst, similar to protein enzymes. RNA with this capability are called **ribozymes**. One school of thought holds that because RNA can act as both a genetic template and as a catalyst, it may be that when life originated, it was based on RNA for both of those functions.

Several nucleotide monomers are important participants in biochemical reactions. More is said in Section 5.1.3 about *adenosine triphosphate* (ATP) and its central role in energy metabolism. The cell uses a number of other nucleotides. Cyclic adenosine monophosphate (cAMP) is involved in regulation of cell metabolism. Adenine is combined with other organic molecules to form a number of coenzymes, including:

flavin adenine dinucleotide (FAD)

nicotinamide adenine dinucleotide (NAD)

nicotinamide adenine dinucleotide phosphate (NADP)

guanosine triphosphate (GTP)

These compounds are important in the mechanisms for many biochemical processes, including photosynthesis and respiration, as discussed below.

3.6.5 Hybrid and Other Compounds

Hybrid compounds are those composed of a combination of two or more types of compounds, such as sugar combined with protein or with lipid. Some have already been discussed; examples are some proteins with their prosthetic groups; the nucleotides themselves, which contain sugars; and the nucleic acid coenzymes.

In addition, sugars commonly combine covalently with lipids and proteins. Many are important in cell membranes. For example, *peptidoglycans* have the interesting property that they form a two-dimensional polymer (covalently bonded in both the x and y directions) so that they encapsulate bacterial cells with a single huge macromolecule. Lipopolysaccharides include bacterial cell membrane components called **endotoxins**, which are responsible for powerful toxic effects in animals. Bacteria important in wastewater treatment secrete a coating of polysaccharides and lipopolysaccharides that enables them to flocculate into large aggregates or to form slime layers called **biofilms**. This improves their ability to capture particulate food matter.

Lipoproteins are noncovalently bound lipids and proteins. Since lipids are insoluble in water, they are transported in the blood by being associated with proteins in this way. In other words, proteins act as a “detergent” to solubilize lipids, including cholesterol. Despite cholesterol’s bad reputation related to disease of the circulatory system, it is an essential component of animal cell membranes and a precursor for steroid hormones and

bile acids (which aid in lipid digestion). However, people with high levels of cholesterol in the blood tend to have higher incidences of **arteriosclerosis**, the narrowing and blocking of arteries by cholesterol deposits. This can lead to strokes and heart attacks. Blood lipoproteins can be separated into fractions distinguished by density. One of the fractions is low-density lipoprotein (LDL). Blood cholesterol is concentrated in the LDL fraction, resulting in its being labeled as “bad” cholesterol. A high LDL level is associated with the intake of saturated fats and alleviated by the intake of monounsaturated fats.

Lignin is a polymer of various aromatic subunits, such as phenylpropane. It is produced by woody plants as a resin, bonding the cellulose fibers into a tough composite.

3.7 DETECTION AND PURIFICATION OF BIOCHEMICAL COMPOUNDS

The tremendous amount that is known about biochemistry may seem somewhat mysterious without an appreciation for the methods used to gain it. A brief description of some of the techniques used to purify and detect biochemical compounds may help with understanding how this body of knowledge came about.

Thin-layer chromatography is done with paper or a glass plate coated with silica powder or other adsorbent material. A solution containing a mixture of biochemical compounds, ranging from amino acids and nucleic acids to polypeptides, is placed in a spot near one corner. One edge is then placed in contact with a solvent, which carries the compounds along the plate as it is drawn up by capillary action. Compounds with various physicochemical properties move at different speeds. This spreads the compounds out in a line along one edge. That edge is then placed in a different solvent, which moves the compounds across the plate in the other direction. This distributes the individual compounds from the mixture across the two dimensions of the plate (Figure 3.15). The resulting spots can be made visible by chemical treatment or can be removed for further experiments.

If the molecules are electrically charged, such as amino acids and polypeptides at the appropriate pH, one of the solvent steps can be replaced with an electrostatic field to move the compounds. This is called **electrophoresis**.

Large molecules and subcellular particles can be separated by sedimentation. This is done in an **ultracentrifuge**, which creates accelerations up to 400,000g by spinning as fast as 75,000 rpm. Molar masses of large macromolecules can be determined from their sedimentation rate. Particle size is often given in terms of its settling velocity in a centrifuge, measured in **Svedberg units**.

Immunoassay uses antibodies to form a precipitate with specific compounds. *Antibodies* are special proteins produced by the body to bind with foreign substances so that they can be made harmless. Each antibody is highly specific, binding only to a single substance and binding extremely tightly in what is called a *lock-and-key relationship*. Molecular biology techniques have enabled the production of large quantities of antibodies of a specific type, called **monoclonal antibodies**. They are used for research purposes as well as to detect specific hormones in pregnancy tests and tests for prostate cancer. Immunoassay is a highly sensitive and selective detection method. Its use has been extended to organic pollutants and even to heavy metals.

The power of the methods described above is often increased by the use of **radioisotope labeling**. In this technique, radioactive compounds such as ^3H , ^{14}C , ^{32}P or ^{33}P , and ^{35}S are incorporated into substrates, making it easy to detect the products incorporating

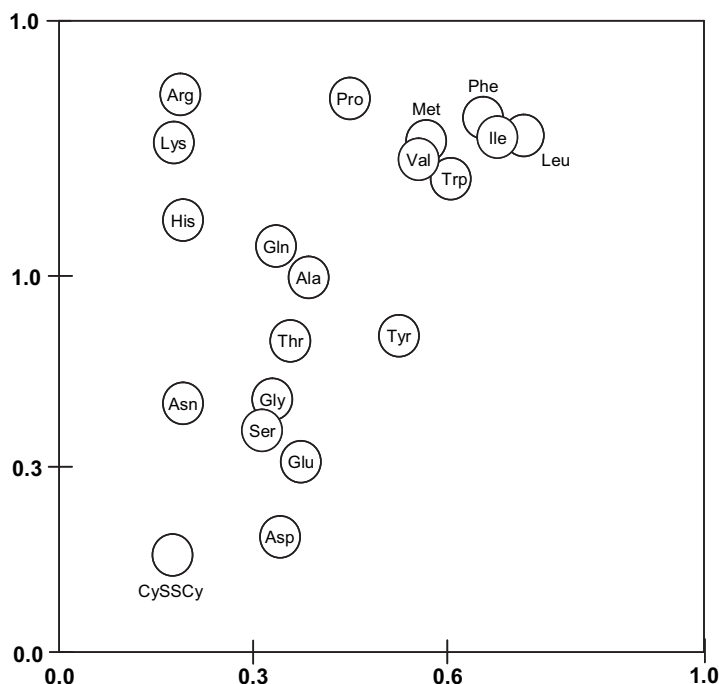


Figure 3.15 Two-dimensional thin-layer chromatograph separation of amino acids. (Based on White et. al., 1973.)

them. The radioactivity makes compounds easier to detect in small quantities. For example, exposing plants to carbon dioxide with carbon-14, and then analyzing plant matter periodically for radioactive compounds is a way to elucidate the steps in photosynthesis as the ^{13}C appears in one compound and then another. **Radioimmunoassay** can detect compounds such as hormones or drugs in blood plasma at quantities as low as several picograms (10^{-12} g).

Other analysis techniques, based on the methods of molecular biology, are discussed in Chapter 6.

PROBLEMS

- 3.1. Write symbol-and-stick diagrams for CO_2 , NH_4 , 1,1,1-TCA (1,1,1-trichloroethane), TCE (trichloroethylene), and formic acid (CH_2O_2).
- 3.2. Glucose, starch, and glycogen are very similar chemically. How will wastewater containing a high concentration of one or the other affect a biological wastewater treatment plant differently? How would the same wastewater affect a stream differently? Assume that the chemical oxygen demand (COD) of each wastewater is similar.
- 3.3. A rule of thumb for biological wastewater treatment plant nutrition is that for every 100 mg of oxygen demand there should be 5 mg of nitrogen. (a) Would a wastewater

containing either only glycine or only leucine need a nitrogen supplement? **(b)** Which of the 20 amino acids is most balanced in this respect? [*Hint:* Answer by computing the theoretical oxygen demand for each substrate and compare to the mass concentration of nitrogen. The theoretical oxygen demand for $C_cH_hO_oN_n$ is $c + (h-3n)/4 - o/2$ moles of oxygen per mole of substrate. Convert this to grams of oxygen per gram of substrate by the molar mass of O_2 (32 g/mol), dividing by the molar mass of the substrate.] Computing oxygen demand is discussed in detail in Section 13.1.3.

- 3.4.** List all the elements that are more electronegative than carbon.
- 3.5.** For each of the acids listed in Table 3.3, compute the fraction that would be undissociated at pH 7.4, the normal pH of human blood.

REFERENCES

- Bailey, J. E., and D. F. Ollis, 1986. *Biochemical Engineering Fundamentals*, 2nd ed., McGraw-Hill, New York.
- Fried, G. H., 1990. *Schaum's Outline: Theory and Problems of Biology*, McGraw-Hill, New York.
- Kimball, J. W. <http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/>, and <http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/R/Radioimmunoassay.html>.
- Pauling, Linus, 1970. *General Chemistry*, 3rd ed., W.H. Freeman, San Francisco.
- Smith, E. L., R. L. Hill, I. R. Lehman, R. J. Lefkowitz, P. Handler, and A. White, 1983. *Principles of Biochemistry*, 7th ed., McGraw-Hill, New York.
- White, A., P. Handler, and E. L. Smith, 1973. *Principles of Biochemistry*, 5th ed., McGraw-Hill, New York.

4

THE CELL: THE COMMON DENOMINATOR OF LIVING THINGS

Cells were discovered by Robert Hooke of England in the mid-seventeenth century, and named by him after the small dormitory-style rooms inhabited by monks. He first saw cell wall remains in thin slices of cork, using a microscope. Around the same time, Anton van Leeuwenhoek of Holland advanced the art of building microscopes, achieving magnification up to 500 times. With these he was able to make detailed studies of living cells. Further study led to the development in the nineteenth century of **cell theory**:

- All living things are composed of one or more cells.
- Cells are the basic units of living things and are the site for the reactions of life.
- Under today's conditions, all cells come from preexisting cells.

The first tenet encompasses everything from single-celled bacteria to large animals and trees that can have trillions of cells. The second tenet recognizes that individual parts of cells are not by themselves viable. This tenet also excludes viruses from being classified as living things, since they do not metabolize. The third tenet leaves open the possibility of cells arising spontaneously under the conditions of the primitive Earth.

The light microscope opened a new world to examination, literally under our noses. Typical cell sizes are about 1 μm for bacteria to 10 μm for most human cells. The human eye can resolve down to only about 100 μm (0.1 mm). The light microscope extends resolution down to 0.2 μm [200 nanometers (nm)], which is half the wavelength of violet light. An advance similar in magnitude to Hooke and Leeuwenhoek's microscopes occurred in the 1960s with the development of electron microscopes. These can magnify by 30,000 to 100,000 times, yielding resolution down to 2 nm. This is enough to resolve some of the larger macromolecules such as proteins and nucleic acids. Another

leap was made in 1986, with the development of the atomic force microscope, which can resolve individual atoms and has been used to detect the shape of the DNA helix. These imaging tools, together with biochemical techniques, have led to continual advances in **cytology**, the study of cells.

4.1 PROKARYOTES AND EUKARYOTES

As mentioned in Section 2.4, the highest level of biological classification, the domain, is based on cell type. Bacteria are made of the simpler prokaryotic cell; protists, fungi, plants, and animals are eukaryotic. Prokaryotes are smaller than eukaryotic cells and lack any internal membrane-bound structures. Eukaryotes have organelles, which are specialized structures within the cell that are surrounded by their own membranes, almost like cells within a cell. Some organelles, such as mitochondria, even have their own DNA.

It is thought that prokaryotes are relatively primitive life-forms and that eukaryotes may have evolved from a symbiotic association in which an early form of prokaryotic cell incorporated other prokaryotes internally. For example, a large anaerobic prokaryote may have incorporated an aerobic bacterium. The latter eventually became mitochondria, the site of aerobic respiration in eukaryotes.

Table 4.1 shows some of the similarities and differences between prokaryotic and eukaryotic cell structures. Figure 4.1 illustrates a typical bacterial (prokaryotic) cell. The nuclear region is not surrounded by a membrane, as it is in eukaryotes. Photosynthetic bacteria include thylakoid membrane structures, an exception to the rule of not having internal membranes. Granules are structures that contain storage projects such as lipids or starches. Bacterial cells are typically about 1 μm in size.

Table 4.1 Contrast Between Prokaryotic and Eukaryotic Cells

Structure	Prokaryotes		Eukaryotes	
	Archaeans	Bacteria	Plants	Animals
Cell wall	No peptidoglycan; some have glycoprotein or protein walls	Peptidoglycan	Cellulose	None
Cell membrane	Lipid bilayer ether-linked branched hydrocarbon chains	Phospholipid bilayer composed of ester-linked straight hydrocarbon chains		
Motility	Flagella	Flagella	Flagella	Flagella or cilia
Genetic material	Single circular DNA	Single circular DNA	Several linear DNA molecules	
Ribosomes	Yes	Yes	Yes	Yes
Membranous organelles	Absent	Few: e.g., thylakoids for photosynthesis in cyanobacter	Nuclear envelope, endoplasmic reticulum, mitochondria, Golgi apparatus, lysosomes, centrioles Chloroplasts and central vacuoles	

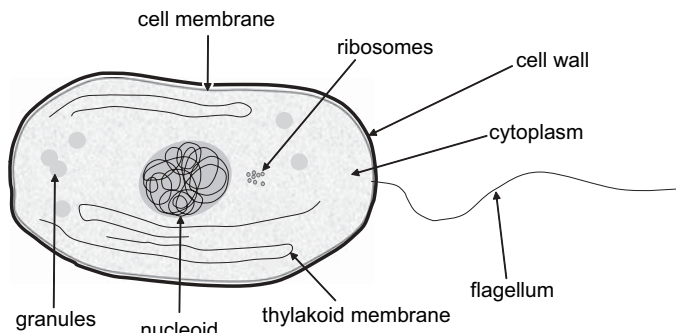


Figure 4.1 Structure of a prokaryotic cell.

Figure 4.2 shows typical plant and animal (eukaryotic) cells. These cells are much more complicated. The nuclear region (nucleus), endoplasmic reticulum, mitochondria, Golgi apparatus, chloroplasts in photosynthetic organisms, and a number of other structures are all surrounded by their own membranes. Eukaryotic cells are usually much larger than prokaryotic cells, on the order of $10\ \mu\text{m}$ in size.

Functionally, prokaryotes are capable of a much wider range of basic metabolic processes, including many of environmental importance. These include many processes that catalyze key pathways of the biogeochemical cycles. All chemoautotrophs (organisms that obtain energy from inorganic chemicals) are prokaryotes. These include bacteria that oxidize minerals, such as Fe(II) , NH_3 , H_2S , and others. Other major processes limited to prokaryotes are nitrogen fixation and denitrification. Furthermore, with few exceptions, only prokaryotes are capable of using electron substitutes for oxygen, such as nitrate, sulfate, or carbonate, and can live their entire life cycles in the absence of oxygen. However, prokaryotes are specialized, and none can do all of these processes, and most do very few. What specialized advantage do eukaryotes have? One answer is that only eukaryotes form multicellular organisms.

4.2 THE BIOLOGICAL MEMBRANE

In many areas of science, it is at the interface where things get interesting, and difficult. Chemical reactions in homogeneous gas or liquid phases are complex enough, but when an interface is present, even the notion of chemical concentration is oversimplified. For example, the pH near the surface of a colloid can vary with distance from the surface. Surface-active agents will distribute themselves differently between the surface and the bulk fluid. Many surfaces act as catalysts. They can be gatekeepers, affecting the transport of substances between phases. The phospholipid bilayer membrane is the major interface formed by living things. It is the structure that separates “inside” from “outside.” By increasing the complexity of the system, it also increases its possibilities.

The biological **membrane** is a flexible sheet forming a closed surface, whose basic structure is formed of a phospholipid bilayer (see Figure 4.3). The capability of phospholipids to form enclosed bilayer vesicles spontaneously was described in Section 3.7.2. The outer membrane of all cells is called the **plasma membrane** or **cell membrane**. Similar membranes also enclose cell organelles such as the mitochondria or the nucleus in eukaryotic cells.

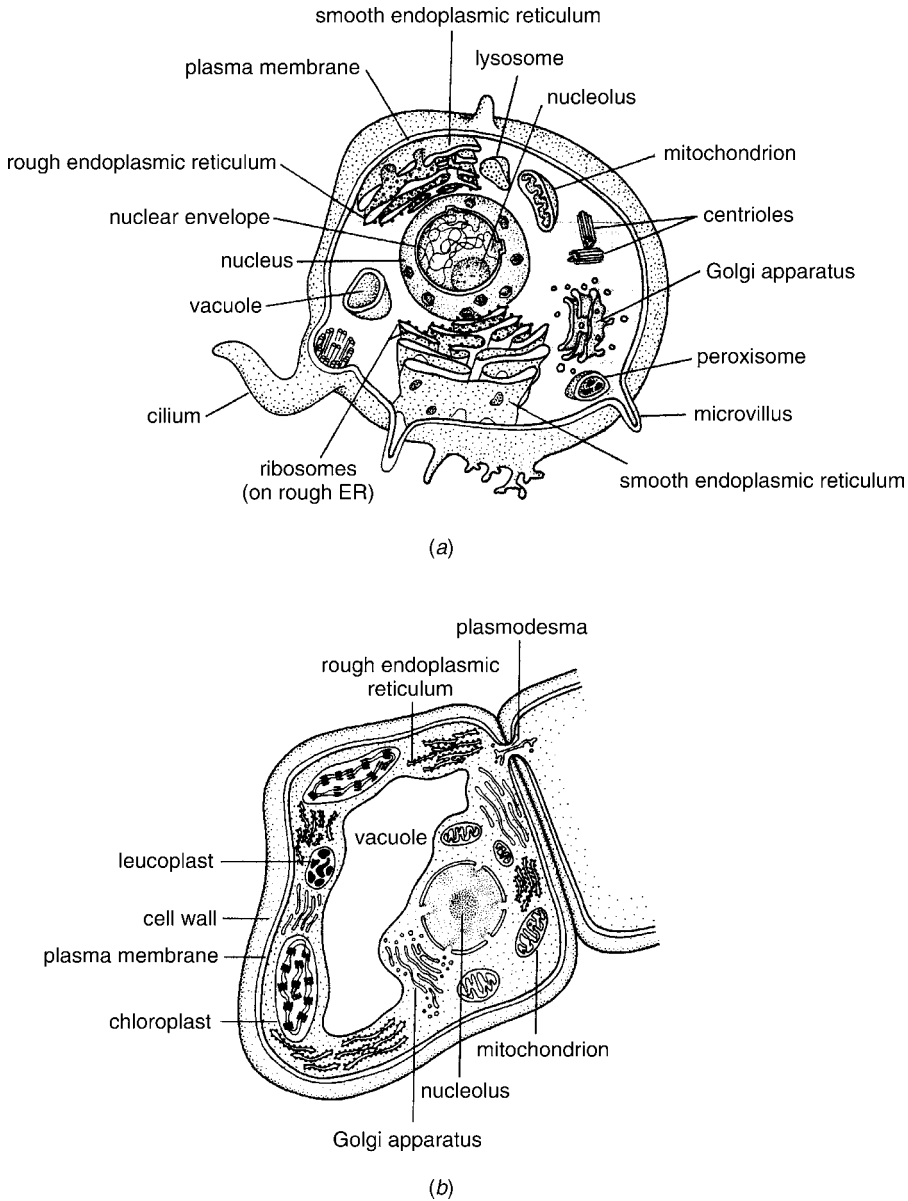


Figure 4.2 Animal (a) and plant (b) cells. (From Fried, 1990. © The McGraw-Hill Companies, Inc. Used with permission.)

Besides being flexible, the phospholipid molecules can move freely within the plane of the membrane, a behavior described as a *two-dimensional fluid*. Other molecules are intimately associated with the membrane. Eukaryotic membranes can contain large amounts of cholesterol, which increase the fluidity of the membrane. Fatty acids serve the same function in prokaryotes. Globular proteins are embedded in the membrane, somewhat like icebergs floating in the sea. Some penetrate both surfaces of the membrane and participate in the transport of substances across it. Others are embedded in one or the

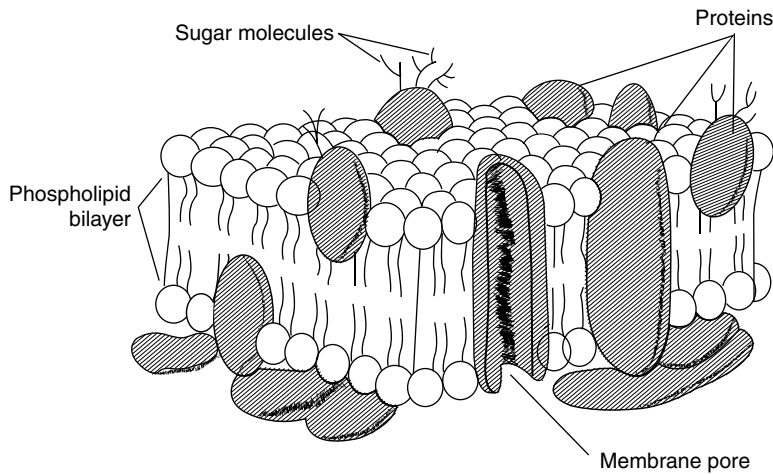


Figure 4.3 Plasma membrane structure. (From Van De Graaff and Rhees, 1997. © The McGraw-Hill Companies, Inc. Used with permission.)

other surface and function as chemical receptors or catalytic sites. Biological membranes are asymmetrical. The external surface of the plasma membrane and the internal surface of organelles have carbohydrates bonded to them, forming glycolipids and glycoproteins.

The plasma membrane of archaean cells is chemically distinct from eubacterial or eukaryotic cell membranes. Instead of being composed of lipids made from straight-chain fatty acids bonded to glycerol by ester bonds, archaean membrane lipids are made of the branched hydrocarbon *isoprene* bonded to glycerol by ether bonds. This structure is thought to give archaean greater physical and chemical resistance to the relatively unfavorable environmental conditions in which they are often found.

Membranes are typically less than 10% carbohydrate by mass; the rest of the membrane mass is about equally divided between protein and lipid. In animals, about half the lipid is phospholipid and half is cholesterol.

The membrane controls the transport across it of both substances and information. Information is transported in the sense that substances, called **ligands**, can bind to **receptors** composed of transmembrane proteins (proteins that penetrate both sides) on one side of the membrane, producing a change in its conformation on the other side. The altered protein can then affect other reactions. This sends a signal across the membrane without a substance actually crossing over. Examples of this are the intercellular messengers called *hormones*. Insulin, for example, binds to a receptor and causes two separate effects. Primarily, it stimulates plasma membrane mechanisms for the transport of glucose, some ions, and amino acids. Second, it results in changes in intracellular metabolism that result in increased synthesis and storage of protein, glycogen, and lipid. Some toxic substances act by binding with receptors, either by stimulating an inappropriate response directly, or by competing with normal ligands.

4.3 MEMBRANE TRANSPORT

Membranes also control the transport of substances. This is one of the essential functions of life: the maintenance of different conditions between the interior and exterior of the

cell, the distinction between the self and the rest of the world. Many toxic substances also must be transported across membranes to achieve their effect.

The simplest mechanism is **passive transport**, the movement of a chemical from an area of relatively high concentration, through a membrane, to an area of low concentration, by means of molecular diffusion. The transport occurs only when a concentration difference exists between the aqueous phases on the two sides of the membrane. To diffuse across a membrane, a chemical must first dissolve in it. Then, random molecular motion results in a net movement toward the side with the lower concentration. However, molecules that are polar, such as ions or sugars, have very low solubility in the nonpolar interior of the phospholipid bilayer. Thus, the transport of such compounds through the membrane is very slow by this mechanism.

Water also moves across membranes by passive transport. The movement is from low solute concentration to high solute concentration. Realize that the higher the concentrations of solutes (ions, proteins, sugars, etc.), the lower the concentration of solvent (water, in this case). From the point of view of the water, the movement is from high concentration (of the water) to low concentration. The passive transport of water due to its concentration gradient is called **osmosis**.

Consider a membrane that is permeable to neutral molecules such as water but impermeable to ions and that separates a solution of fresh water from salt water. The water will move by osmosis from the fresh water (which has a higher water concentration) to the salty side. The flow continues until equilibrium is achieved. If the pressures are equal, osmotic equilibrium means that the concentration of particles is the same on both sides. However, if the system is held at constant volume, the flow results in an increase in pressure on the salty side. The pressure difference across the membrane at equilibrium, π , is related to the difference in the molar concentration of total particles, Δc , by a version of the ideal gas law:

$$\pi = \Delta c RT \quad (4.1)$$

The effect of particle concentration is approximately independent of charge or size. For example, a 0.1 *M* solution of sodium chloride has the same osmolarity as a 0.2 *M* solution of glucose, because the sodium chloride dissociates to form 0.2 mol of ions per liter.

The concentration of particles expressed in moles per liter is called the **osmolarity** (Osmol/L). For example, blood plasma has a total particle concentration of about 325 mmol per liter (mOsmol/L). This produces an osmotic pressure of about 6000 mmHg (7.9 atm). (This is similar to the osmotic pressure of the ocean during the Precambrian Era, when animals with closed circulation evolved. Since then, the osmotic pressure of seawater has continued to increase about 3.5-fold.) If two solutions with different osmolarities are separated by a barrier to the solutes such as a plasma membrane, the lower-concentration solution is said to be **hypotonic** to the other. The higher-concentration solution is said to be **hypertonic**. If the two solutions have the same osmolarity, they are **isotonic**.

Because of osmotic pressure, the total concentration of particles inside a cell must be almost equal to that outside. Otherwise, water would cross the membrane, causing the cell to either shrink or to swell and burst. Plant and bacterial cells are surrounded by rigid cell walls that protect them from bursting, and can therefore exist in a hypotonic solution. A hypertonic solution, however, will cause them to shrink within their cell walls. Cells that have osmotic pressure are said to be **turgid**.

Plasma membranes have pores consisting of embedded proteins. In most cells, these allow molecules up to a molar mass of 100 to 200, including water itself, to pass by filtration. The membranes of capillary (blood vessel) cells have larger pores, which allow molecules up to molar mass 60,000 to pass.

Molecules too lipophobic for passive diffusion or too large for filtration may still enter the cell by specialized transport systems. These include four types of carrier-mediated transport: facilitated diffusion, active transport, co-transport, and countertransport. In **facilitated diffusion** the problem of lipophobicity is solved by forming a complex between the solute and a protein in the membrane (the *carrier*). Random molecular motion then transports the complex to the other face, where the solute is released and the protein is freed for reuse by other molecules. Facilitated diffusion has two important differences from passive diffusion: (1) Because there are a limited number of carriers, at high solute concentrations the carrier protein can become saturated, resulting in a maximum flux. Passive diffusion is limited only by the concentration gradient. (2) Facilitated diffusion is more selective than passive diffusion, since the solute must be able to form a complex with the carrier, and it can be inhibited by competition. An important compound that is carried across membranes by this mechanism is glucose. If it weren't for protein transporters, membranes would be impermeable to glucose. The hormone insulin affects the permeability of muscle and adipose tissue membranes by increasing the amount of transporter proteins in those membranes.

Passive transport, whether membrane or film theory, membrane filtration, or facilitated transport is a physicochemical process and requires no expenditure of energy by the cell. Instead, the cell relies on the free energy of the concentration gradient. Another form of carrier-mediated transport, **active transport**, involves the use of metabolic energy in the form of ATP. Active transport can occur when a membrane-spanning carrier absorbs the substrate from one side of the membrane and uses energy from ATP to pass the substrate through a channel and exude it at the other side. A second active transport mechanism can involve the consumption of a substrate on one side of the membrane, coupled with its production at the other side. The substrate is not really transported across the membrane, but the effect is as though it has been. An example of the latter mechanism is the "transport" of protons across the membrane of bacteria or mitochondria in the respiration process.

Active transport is an important mechanism for the transport of natural biochemical compounds in living things. It is the way they obtain nutrients and eliminate waste products. It is also a mechanism for the uptake and excretion of toxins. For example, lead is absorbed by active transport in the intestines. Active transport can move chemicals against a concentration gradient. Active transport has the following characteristics:

1. Chemicals can be moved against electrochemical gradients.
2. Like facilitated diffusion, active transport can be saturated and shows a maximum flux.
3. Also like facilitated diffusion, active transport is highly selective and exhibits competitive inhibition.
4. Active transport requires energy and so can be inhibited by metabolic poisons.

Active transport is exploited to transport water passively across membranes by osmosis. For example, the large intestine removes water from its lumen (interior) by using active

transport to remove sodium. This decreases the osmolarity in the lumen, and water passively diffuses out to the higher-osmolarity tissues surrounding it. When solutes are transported across a membrane, water will follow if the membrane is permeable to water.

Cotransport and **countertransport** involve two substrates being brought across the membrane by the same carrier at the same time, either in the same direction or in opposite directions, respectively. At least one of the substrates must be transported downgradient and provides the energy to transport the second substrate. For example, a sodium gradient can drive the cotransport of glucose into a cell. A countertransport mechanism exchanges chloride for bicarbonate in the kidney. Since these mechanisms are carrier mediated, they can also be saturated.

Another type of specialized transport, limited to eukaryotes, is **endocytosis**, in which particles are engulfed by cells. The cell accomplishes this by surrounding the particle with part of the plasma membrane, which then pinches off inside the cell, forming a vesicle. If the particle is solid, the process is called **phagocytosis**; if liquid, it is called **pinocytosis**. The protozoan *amoeba* feeds by phagocytosis and the lungs use it to clear themselves of inhaled particulates, incidentally taking up any associated toxins.

More details on some membrane transport processes, including ways of describing them mathematically, are given in Section 18.2.

4.4 EUKARYOTIC CELL STRUCTURE AND FUNCTION

The emphasis here is on eukaryotic cells. More details on prokaryotic cells are given in Chapter 10.

Plants, some fungi, some protists and most prokaryotes form a **cell wall** outside their plasma membrane. The basic structure in plants is composed of cellulose fibers (cotton is a pure form of cellulose). Besides maintaining cell shape and preventing a cell from rupturing due to osmotic forces, a cell wall provides structural rigidity to multicellular plants. Many plants also lay down a secondary cell wall, which includes lignin, inside the primary wall. *Lignin* is a polymer of aromatic subunits whose presence increases the toughness of wood. Lignin biodegrades much more slowly in the environment than cellulose does. The degradation products of lignin are thought to be the major source of *humic substances*, which are the predominant forms of organic matter in soil. The humic substances, in turn, give topsoil its beneficial properties for plant growth and are responsible for the great capacity for soils to absorb nutrients as well as many types of pollutants.

Animal cells protect themselves against rupturing from osmotic forces partly by manipulating those forces. Multicellular animals can control the osmotic pressure of their intercellular fluids. In addition, they produce a network of collagen fibers. **Collagen** consists of polypeptide strands twisted into a ropelike structure. About 25% of the protein in mammals is collagen, and tendons are mostly collagen.

The basic matrix of the cell interior is the gel-like **cytoplasm**, in which the other cell materials and structures are suspended, including the organelles. A three-dimensional lattice of protein fibers called the **cytoskeleton** gives structure to the cytoplasm and helps orient organelles. Inside cells, the largest and most obvious structure is the **nucleus**, which contains most of a cell's DNA. In eukaryotes the nucleus is separated from the cytoplasm by a **nuclear membrane**, which consists of *two* phospholipid bilayer