McGraw-Hill Encyclopedia of Science & Technology

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McGraw-Hill Encyclopedia of Science & Technology

5th Edition

AN INTERNATIONAL REFERENCE
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INCLUDING AN INDEX

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Organization of the Encyclopedia

This Encyclopedia presents pertinent information in every field of modern science and technology. There are two departures from previous editions in the organization of the 7700 alphabetically arranged articles. Inverted article titles have been largely eliminated to simplify sequencing in the volumes and in the index. Formerly scattered articles on certain subjects have been collected into larger comprehensive articles, so that the reader can gain a broader perspective by referring to only one page range. Often the reader can find information by simply choosing the volume bearing the appropriate letter for the subject.

As for the development of the material, broad survey articles for each of the disciplines or large subject areas give even the uninitiated reader the basic concepts or rudiments. From the lead article the reader may proceed to other articles that are more restricted in scope by utilizing the cross-referencing system. These cross references are set in small capitals for emphasis and are inserted at the relevant points in the text. In all, some 50,000 cross references are given. In a survey article such as **Petroleum engineering** the reader is directed to other articles such as OIL AND GAS WELL DRILLING, PETROLEUM RESERVOIR MODELS, and WELL LOGGING (MINERAL). The references may lead to subjects that have not occurred to the reader. For example, the article **Chlorine** has such diverse cross references as ANTIMICROBIAL AGENTS, BLEACHING, HALOGEN ELEMENTS, and HYPOCHLORITE.

The pattern of proceeding from the general to the specific has been employed not only in the plan of the Encyclopedia but within the body of the articles. Each article begins with a definition of the subject, followed by sufficient background material to give a frame of reference and permit the reader to move into the detailed text of the article. Within the text are all-capital, boldface, and italic subheadings which outline the article; they are intended to enhance understanding, and can guide the user who prefers to read selectively the sections of the long article.

Alphabetization of article titles is by word, not by letter, with a comma providing a stop in occasional inverted article titles (so that subject matter can be grouped):

Air
Air-cushion vehicle
Air mass
Air-traffic control
Air waves, upper synoptic
Aircraft fuel
Airfoil

Some article titles contain parenthetical information for clarification:

Cell (biology)
Land drainage (agriculture)

Copious illustrations, both line drawings and halftones, contribute to the utility, clarity, and interest of the text. Each illustration (as well as each table) is called out in the text to alert the reader at the proper point. Illustrations and tables, insofar as practical, appear on the page spread with their callouts.

As the International System of Units gains wider application, it has become imperative to include such units in the Encyclopedia. As appropriate, these SI units may be used exclusively in some articles or may be given as equivalents of U.S. Customary or metric units in other articles; sometimes conversion factors are used for simplicity, as in references to measurements in illustrations or tables.

The contributor's full name appears at the end of an article section or an entire article. Each author is identified in an alphabetical Contributors List in volume 15, which cites the university, laboratory, business, or other organization with which the author is affiliated and the titles of the articles written.

Most of the articles contain bibliographies citing useful sources. The bibliographies are placed at the ends of articles or sometimes at the ends of major sections in long articles. To utilize additional bibliographies, the reader should refer to related articles which are indicated by cross references.

Thus, the alphabetical arrangement of article titles, the subheadings, the cross references, and the bibliographies permit the reader to pursue a particular interest by simply taking a volume from the shelf. However, the reader can also find information in the Encyclopedia by using the Analytical Index and the Topical Index in volume 15. The Analytical Index contains each important term, concept, and person—150,000 entries in all—mentioned throughout the 14 text volumes. It guides the reader to the volume numbers and page numbers concerned with a specific point. The reader wishing to consult everything in the Encyclopedia on a particular aspect of a subject will find that the Analytical Index is the best approach. A broader survey may be made through the Topical Index, which groups all article titles of the Encyclopedia under 75 general headings. For example, under "Geophysics" 60 articles are listed, and under "Medicine and pathology" 280. The Topical Index thus enables the reader quickly to identify all articles in the Encyclopedia in a particular subject area.

A useful feature is the section "Scientific Notation in the Encyclopedia" in volume 15. It clarifies usage of symbols, abbreviations, and nomenclature, and is especially valuable in making conversions between the International System, U.S. Customary, and metric measurements.

Babbitt metal

A white alloy of tin, lead, antimony, and copper used as an antifriction metal in sleeves and bearings. Bearings of babbitt metal are used where high pressures need not be sustained and where high temperatures are not likely. The alloy is a moderately soft matrix carrying cubic crystals of a hard compound of either copper or lead with the antimony. Wear soon relieves the softer matrix, exposing the hard crystals which carry the load. Their small exposed area decreases friction, and the undercut matrix permits lubricant to circulate between crystals. *See* ANTIFRICTION BEARING; TIN ALLOYS.

[FRANK H. ROCKETT]

Bacillaceae

The family of the rod-shaped, endospore-forming bacteria. Species in this family range from organisms used in retting flax to those pathogenic for animals and humans, such as anthrax. The special features of the group are largely associated with spore production. The spore is formed within the vegetative cell and is therefore of the type known as an endospore. Its outstanding property is a capacity to tolerate conditions which destroy the vegetative stage. The two principal genera of this family are *Bacillus* and *Clostridium*. Other genera include *Sporolactobacillus*, *Desulfotomaculum*, and *Sporosarcina*.

Sporulation. This usually occurs only at the end of a period of vegetative multiplication. A vegetative cell produces only one spore. As the spore matures, it becomes impermeable to aqueous dyes and may thus be recognized in a stained sporangium. The shape and size of the spore and its position in the rod are characteristics of species (see illustration). When a spore has matured, it is liberated by the dissolution of the remnant of its parent cell. *See* BACTERIAL ENDOSPORES.

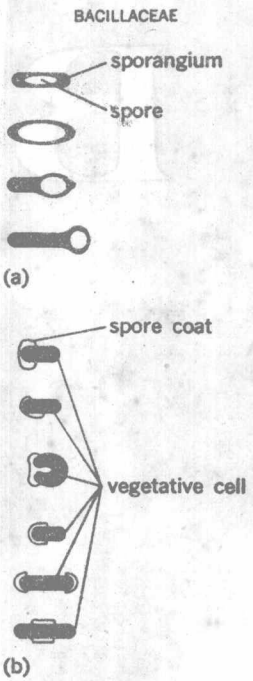
Endospore properties. The endospore is distinguished from the vegetative cell by its much lower water content, its greater refractive index, and its exceptional resistance to destructive agencies such as desiccation, heat, or disinfectants. In heat resistance, there is a wide variation among species. Some spores are destroyed in water at 90°C in a few minutes; the most resistant survive at 100°C in water or steam for periods longer than 24 hr.

Spore germination. Spore germination is provoked by a suitable food supply. In this event the spore absorbs water, loses its refractile character, becomes stainable with aqueous dyes, and loses its heat resistance. A vegetative rod then breaks out of the spore coat by one of the methods shown in the illustration, and the young cell proceeds to multiply by fission. In the case of several species, single substances such as L-alanine or glucose stimulate spore germination as effectively as a complete nutrient mixture. Such germination stimulants have the remarkable effect of compelling the spore to germinate, although the environment may be lethal to the vegetative form.

Bacillus. This genus comprises the organisms that grow aerobically. Some of them are capable of anaerobic growth if they are supplied with a fermentable sugar or with nitrate. The species show much diversity in temperature requirements, some being thermophiles capable of growth above 70°C.

Other characters by which the species may be recognized are the morphology at the time of spore formation, and biochemical features such as action on proteins and ability to produce acid, acid and gas, or acetoin from sugars. Organisms of this genus often come into prominence in the processing of foods where heat treatments eliminate nonsporing bacteria. The spores of *B. subtilis* and of the thermophile *B. stearothermophilus* are extremely resistant to heat. One species, *B. anthracis*, is the causative agent of anthrax. Other species are pathogenic for the larvae of the honeybee or other insects. *See* ANTHRAX.

Clostridium. The *Clostridium* comprise a group of strictly anaerobic species. Their vegetative cells are easily killed by oxygen, yet they frequently multiply in nature because aerobes afford them protection. The species differ in microscopical character and temperature requirements (some being thermophiles), and they show wide variations in chemical activity. Some ferment carbohydrates to a variety of products which in many cases include butyric acid. Others digest proteins actively and ferment the amino acids so produced. Still other species effect more specialized fermentations. Among the useful activities of clostridia are the retting of flax and other fiber-producing plants,



Variations in shape, size, and site of (*a*) endospore formation and (*b*) types of germination into vegetative cells.

the acetone-butanol fermentation of *C. acetobutylicum* and related organisms, and the fixation of nitrogen by *C. pasteurianum*. On the other hand, the action of these organisms on foods is invariably destructive, and several species are pathogenic for man or animals. For example, *C. botulinum* produces an exotoxin which is neurotoxic for man and animals if injected or ingested. *See* ACETONE-BUTANOL FERMENTATION; NITROGEN CYCLE.

Ecology. All Bacillaceae appear to have the same mode of life. A large reserve of dormant spores occurs in nature, principally in soil. Many of the spores are possibly of great age, especially in the case of organisms such as thermophiles, which only rarely meet conditions suitable for growth. If a spore is induced to germinate by the presence of food material, rapid multiplication may occur. When the food supply is exhausted, spores may again be formed, and they join the natural reserve. The short multiplication phase becomes possible in the refuse of plant and animal life, in foods, in the bowel of the animal in the case of clostridia, and in the tissues of animals in the case of pathogenic species. *See* BLACKLEG; BOTULISM; TETANUS.

[T. GIBSON]

Bacillary dysentery

An infectious disease of humans and primates which affects the large bowel and is caused by members of the genus *Shigella*. The organisms enter the body via the fecal-oral route (for example, from unclean hands) or through fecally contaminated water or food, and penetrate the intestinal mucosa only. The incubation time varies from 1 to 7 days. The characteristic symptoms are watery, watery-mucoid, or bloody diarrhea accompanied by fever, dehydration, abdominal cramps, and prostration. Most cases, however, are "subclinical" or mild. Short-term convalescent carriers are an important reservoir; long-term carriers are rare. The main diagnostic tool is the stool culture. *See* SHIGELLA.

Most infections occur in children, during the warm-weather months, under conditions of crowding and poor sanitation (for example, in custodial institutions), and are acquired by the fecal-oral route. In tropical and subtropical areas, the incidence is the highest, and the disease affects all age groups, may be more serious than it is in other areas (particularly if due to *S. dysenteriae*), and is often transmitted by water.

Effective treatment nowadays has to rely on the results of sensitivity testing of the strains involved, since some of them have acquired resistance to sulfonamides, ampicillin, and tetracycline. Many cases are self-limited. Prevention efforts must stress sanitation, cleanliness in handling food and water, and the use of handwashing facilities. *See* MEDICAL BACTERIOLOGY; SALMONELLA.

[ALEXANDER W. C. VON GRAEVENITZ]

Bibliography: F. H. Top and P. F. Wehrle (eds.), *Communicable and Infectious Diseases*, 8th ed., 1976.

Bacitracin

An antibiotic produced by *Bacillus licheniformis* (*B. subtilis*, strain Tracy). It is active against a wide variety of gram-positive bacteria and only a few gram-negative ones. The use of bacitracin is almost entirely limited to topical (including local injection and oral dosage) application because of the toxicity shown after systemic administration. It is therapeutically effective in the local treatment of a wide variety of infections such as furuncles, abscesses, infected wounds, carbuncles, and impetigo caused by staphylococci, streptococci, and certain other gram-positive bacteria. It is also used as a feed supplement for enhanced growth of chickens and swine. *See* STAPHYLOCOCCUS; STREPTOCOCCUS.

Chemistry. Bacitracin is normally marketed as a mixture of polypetides (bacitracin A, B, C, D, E, and F). The A component makes up the main part of the product with varying amounts of the other components. The component amino acids (some of which are D-amino acids) in these bacitracins are known, and their sequence in the molecule has been worked out for some.

Purified bacitracin is a white to light-brown powder, soluble in water and a variety of aqueous alcohols, including *n*-butanol and *sec*-butanol. Purified bacitracin has an activity of 60 units/mg with a molecular weight of about 1470 for bacitracin A.

Assay. The drug is assayed by a diffusion-plate assay using *Micrococcus flavus* or by a turbidimetric assay using a sensitive organism such as a hemolytic streptococcus. *See* BIOASSAY.

Antimicrobial activity. The antimicrobial activity resembles that of penicillin in that it is bacteriostatic for gram-positive bacteria, especially cocci, and the gram-negative gonococci, meningococci, and hemophilus type B. Most of these sensitive organisms are inhibited at concentrations between 0.0009 and 5.0 μg/ml. There is a synergistic action shown in combination with penicillin, and even penicillin-resistant strains may be inhibited by mixtures at levels which are well below the effective level for either drug alone. Resistance to bacitracin does not appear to develop during therapy but can be developed in vitro. *See* DRUG RESISTANCE; GRAM-NEGATIVE DIPLOCOCCI; HEMOPHILIC BACTERIA.

Pharmacology. Bacitracin is essentially nontoxic when used locally as an ointment, instilled in solution into the spine and skull, administered orally. In human therapy, intramuscular or intravenous injection exhibits some degree of kidney toxicity in a high percentage of patients. General allergic reactions to bacitracin are not encountered. After oral administration, no concentration in the blood can be demonstrated.

Use. Therapeutically effective results are obtained by local application of bacitracin as an ointment, or by instillation as a solution in infections of the eye, ear, nose, and throat or in infections of surgical and other wounds, and in vulvovaginitis, when caused by sensitive bacteria. It can also be injected in small doses into locally infected tissues such as furuncles, carbuncles, and abscesses. Its use in systemic infections is generally not recommended.

Production. Commercial production is carried out by means of fermentation with strains of *B. licheniformis* selected for high bacitracin production, for bacteriophage resistance, and for a rough

colony form (for ease in filtration). The inoculum is started from spores; flask stages and an inoculum tank stage follow. The final fermentation is conducted in 15,000–50,000-gal tanks on a medium composed of soybean meal or other high-protein seed meal as a protein source, a carbohydrate such as starch, and calcium carbonate or calcium lactate. The culture is vigorously aerated and may also be mechanically agitated. Optimum titers of bacitracin at 48-hr fermentation may be 3–4 g/liter or higher.

Recovery for medicinal use is by extraction of the filtered broth with butanol at pH 7 and back extraction into water with phosphoric acid at pH 2–3. After various purification steps the final concentrate may be spray-dried or the bacitracin may be precipitated as a zinc salt. Recovery for animal-feed supplement is usually by evaporation of the whole broth to a syrup in a multiple-effect evaporator followed by drum or spray drying. *See* ANTIBIOTIC.

[RALPH E. BENNETT]

Bibliography: B. Baker and F. Prescott, *Antimicrobial Agents in Medicine*, 1974; S. Hammond, *Antibiotics and Antimicrobial Action*, 1978; H. Smith (ed.), *Antibiotics in Clinical Practice*, 3d ed., 1977.

Background count

The number of counts that must be subtracted from an observed number of counts in an experiment where atomic or nuclear particles coming from a source are being enumerated. The background count may be due to cosmic rays; to natural radioactivity in the air, in the walls of the room, or in the counter itself; or to the scattered radiation in the vicinity of a source of nuclear particles, such as an accelerator or a nuclear reactor. The background normally continues to give counts during the experiment. To determine the background count, the source of true counts is removed, shielded, or turned off, and the number of counts during a given time is observed. This number is then converted to a background counting rate, which may be subtracted from the observed counting rate of the source to give the true counting rate. *See* RADIOACTIVITY.

[WILLIAM B. FRETTER]

Backing wind

A wind which changes direction in a counterclockwise sense, for example, a south wind changing to an east wind or an east wind changing to northerly. At a particular place, the wind gradually backs with time when a cyclone passes eastward on a path south of the observer's location. The wind characteristically backs with increasing height, on the west side of an extratropical cyclone. The meaning, in terms of changes of cardinal directions, is reversed in the Southern Hemisphere. The term backing wind is opposite in sense to veering wind.

[CHESTER W. NEWTON]

Backward-wave tube

A type of microwave traveling-wave tube in which energy on a slow-wave circuit flows opposite in direction to the travel of electrons in a beam. Chief characteristics of backward-wave tubes are regenerative feedback produced by interaction of circuit and beam, and a wide range of electrical tuning, easily produced by changing the beam voltage. Such tubes are useful as voltage-tuned oscillators for signal generators, as power sources for quick tuning transmitters, and as local oscillators in receivers for systems that have quick tuning transmitters. If backward-wave tubes are operated as regenerative amplifiers, they are useful as narrowband amplifiers in wide-range rapidly tuned receivers.

O-type backward-wave oscillator. An O-type backward-wave oscillator (or O-carcinotron) may be similar in appearance to a forward-wave traveling-wave tube. An electron gun produces an electron beam; this beam is focused longitudinally throughout the length of the tube. A slow-wave circuit interacts with the beam, and at the end of the tube a collector terminates the beam (Fig. 1). *See* TRAVELING-WAVE TUBE.

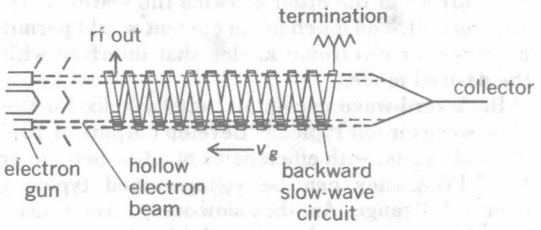


Fig. 1. O-type backward-wave oscillator (or O-carcinotron), which uses a helix as the slow-wave circuit and with a hollow cylindrical electron beam.

Energy in the slow-wave circuit travels from collector end toward the gun end of the tube. Hence, microwave energy is coupled out adjacent to the electron gun. At the collector end the slow-wave circuit is terminated with a matched load, usually internally, so that no microwave terminal is provided. For a tube in which the slow-wave circuit is a helix, the termination usually consists of lossy material sprayed on the collector end of the circuit.

The electron beam is usually hollow, the electrons thereby all being close to the helix. The electrons experience the strongest electric field from the microwave signal when they pass a gap between two helix turns. Electron velocity is adjusted so that any one electron experiences approximately the same phase of the microwave signal as it passes successive gaps. Hence, axial forces due to the microwave field cause some electrons to speed up and others to slow down as they travel past successive gaps. These accelerations and decelerations cause the electrons to bunch in the axial direction. Average velocity of a bunch is such that it drifts into a retarding electric field as it travels down the tube; thus the bunched beam transfers energy to the slow-wave circuit. This action provides continuous feedback along the tube, the beam providing a forward flow of energy and the circuit a backward flow.

To examine the synchronism condition for backward-wave interaction, consider two successive gaps of a helix. The time required for an elec-

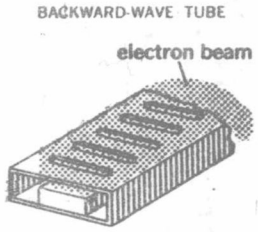


Fig. 2. Karp circuit, used at millimeter wavelengths.

tron to travel from the first gap to the second equals p/u_o, where p is helix pitch, and u_o is electron velocity. During this transit time, a microwave signal of frequency f on the helix will have changed its phase at any one gap by $2\pi fp/u_o$. In addition, at any instant the microwave fields at the two adjacent gaps differ in phase by $2\pi fp/v_g$, where v_g is the velocity at which microwave energy travels along the helix toward the gun. Thus, an electron in moving from the first to the second gap experiences a total field phase change of ϕ. This is defined in the equation below, where synchronism occurs when

$$2\pi fp/u_o + 2\pi fp/v_g = \phi$$

phase change ϕ is exactly one cycle or 2π radians. Frequency of oscillation f can be controlled by changing electron velocity u_o, which depends on the helix-to-cathode voltage.

As in any feedback oscillator, gain must exceed internal losses. To obtain this minimum required gain, beam current is raised above a value called the start-oscillation current. Normally, operation is at a current in the order of twice the start-oscillation current. Too much beam current would permit higher-order electronic modes that interfere with the desired mode.

Backward-wave oscillators with a helix for the slow-wave circuit typically develop outputs of 10–200 milliwatts, with efficiencies of a few percent or less. Frequency can be voltage-tuned typically over a 2:1 range. Another slow-wave circuit, used at millimeter wavelengths, is the Karp circuit (Fig. 2).

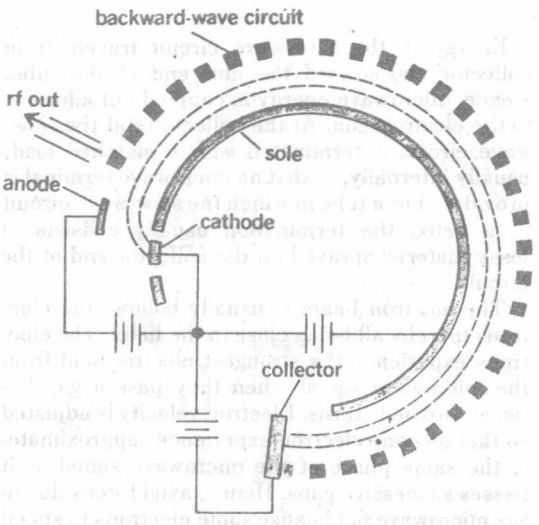


Fig. 3. M-type backward-wave oscillator with the beam focused by a static magnetic field directed into the plane of the page.

M-type backward-wave oscillator. An M-type backward-wave oscillator (or M-carcinotron) is similar in principle to the O-type, except that focusing and interaction are through magnetic fields, as in magnetrons. In the M-type oscillator (Fig. 3), a transverse magnetic field and a static radial electric field between sole and backward-wave circuit structure confine the beam to the interaction space. Either the voltage connected to the sole or

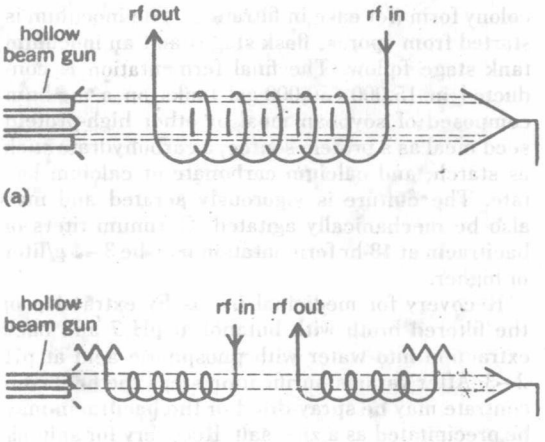


Fig. 4. Backward-wave amplifiers. (*a*) Single-circuit type. (*b*) Cascade type, used for increased stability.

to the slow-wave circuit tunes the frequency. *See* MAGNETRON.

The commonest slow-wave circuit is an interdigital structure, consisting of an array of vertical bars alternating up and down. Efficiency of the M-type tube is considerably higher than that of the O-type tube, typical efficiencies being 20–30%. However, noise and spurious output power are also greater in the M-type tube. Continuous output powers of several hundred watts are typical.

Backward-wave amplifier. When either type tube is operated with currents below the start-oscillation value, narrow-band regenerative amplification is obtained. Amplifier frequency is electrically tunable over a wide range by change of beam voltage. Input to a backward-wave amplifier is at the collector end and output is at the gun end (Fig. 4). Separation of the slow-wave circuit into two or more parts enhances stability. A cascade backward-wave amplifier has a stable gain in excess of 20 dB, a bandwidth of a fraction of a percent, a tuning range easily of 2:1, and a noise figure as low as 3.5 dB. *See* MICROWAVE TUBE.

[J. W. GEWARTOWSKI]

Bibliography: J. W. Gewartowski and H. A. Watson, *Principles of Electron Tubes*, 1965; A. L. Lance, *Introduction to Microwave Theory and Measurements*, 1964; S. Ligo, *Microwave Devices and Circuits*, 1980.

Bacteria

Extremely small—usually 0.3–2.0 microns (μ) in diameter—and relatively simple microorganisms possessing the procaryotic type of cell construction. Although traditionally classified within the fungi as "Schizomycetes," they show no phylogenetic affinities with the fungi, which are eucaryotic organisms. The only group that is clearly related to the bacteria are the blue-green algae. *See* MICROORGANISMS; PROTOPHYTA; SCHIZOMYCETES; SCHIZOPHYCEAE.

Bacteria are found almost everywhere, being abundant in soil, water, and the alimentary tracts of animals. Each kind of bacterium is fitted physiologically to survive in one of the innumerable habitats created by various combinations of space,

food, moisture, light, air, temperature, inhibitory substances, and accompanying organisms. Dried but often still living bacteria can be carried into the air.

One of the few locations in which bacteria are not usually found is within the cells of other healthy organisms, though even this is subject to exceptions, as there are many bacteria that do live intracellularly in a number of eucaryotic organisms.

Bacteria have a practical significance for man. Some cause disease in man and domestic animals, thereby affecting his health and economy. Some bacteria are useful in industry, while others, particularly in the food, petroleum, and textile industries, are harmful. Some bacteria improve soil fertility. *See* FOOD ENGINEERING; FOOD MICROBIOLOGY; INDUSTRIAL MICROBIOLOGY; MEDICAL BACTERIOLOGY; SOIL MICROBIOLOGY; ZOONOSES.

As in higher forms of life, each bacterial cell arises either by division of a preexisting cell with similar characteristics, or through combination of elements from two such cells in a sexual process. The earlier idea, that full-fledged bacteria arise from nonliving material by spontaneous generation, has been disproved by careful elimination of living bacteria from the nonliving material. This does not eliminate the possibility that, sometime during evolution of the universe, life was derived from the nonliving. Separation of matter into living and nonliving is arbitrary, though useful and unambiguous when transitional states are not under consideration. *See* LIFE, ORIGIN OF; REPRODUCTION (ANIMAL).

Pure cultures. Descriptions of bacteria are preferably based on the studies of pure cultures, since in mixed cultures it is uncertain which bacterium is responsible for observed effects. Pure cultures are sometimes called axenic, a term denoting that all cells had a common origin in being descendants of the same cell, without implying exact similarity in all characteristics. Pure cultures can be obtained by selecting single cells, but indirect methods achieving the same result are more common. These involve separating the bacteria from each other and keeping their progeny separate. This is done on a streak plate. The nutrient culture medium is solidified with a gelling agent, usually agar. The tip of a fine sterile wire is dipped into a suspension of the mixed bacteria and streaked over the surface of gelled nutrient agar in a flat covered dish, the petri plate. During streaking the number of bacteria on the needle becomes so reduced (by rubbing off on the agar) that single bacteria are by chance left on the gel at considerable distances from all other cells (Fig. 1). Another method is to inoculate the suspension of mixed bacteria into melted nutrient medium, which is cooled to just above the solidification temperature in order not to kill the inoculated cells; the medium is then solidified. *See* AXENIC CULTURE; PURE CULTURE.

With either method, if conditions are suitable, each bacterium grows and divides, using food diffused through the gel, and produces a mass of cells called a colony. Colonies always develop until visible to the naked eye unless toxic products or deficient nutrients limit them to microscopic dimensions.

Since a colony might arise from more than one cell, and thus from dissimilar cells, it must be picked out, diluted, and subcultured. This process is repeated until daughter colonies are alike and contain only one cell type as judged by microscopic examination. Slight differences in the microscopic or submicroscopic structure of the individual bacterial cells often affect their appearance as a colony. When the desired bacterium is so scarce that the chance of separating it from others is slight, the material to be tested is inoculated into an enrichment culture, which provides environmental conditions better suited to the desired bacterium than to contaminants. *See* ELECTIVE CULTURE.

Classification. The morphology, that is, the shape, size, arrangement, and internal structures, of bacteria can be distinguished microscopically and provides the basis for classifying the bacteria into major groups. Stains are used to visualize bacterial structures otherwise not seen, and the stain reaction with Gram's stain provides a characteristic used in classifying bacteria.

The submicroscopic differences that distinguish many bacterial genera and species are due to structures such as enzymes and genes that cannot be seen. The nature of these structures is determined by studying the metabolic activities of the bacteria. Data are accumulated on the temperatures and oxygen conditions under which the bacteria grow, their response in fermentation tests, their pathogenicity, and their serological reactions. There are also modern methods for determining directly the similarity in deoxyribonucleic acids between different bacteria. *See* BACTERIAL TAXONOMY.

Stains and staining reactions. Many bacterial structures not otherwise visible, such as shape, flagella, and spores, can be differentiated with various staining techniques. The most common staining procedure is the Gram's stain, in which crystal violet and iodine form a violet-colored complex with cell material. The complex is not extracted by alcohol and acetone from gram-positive cells, and these appear violet. The complex is extracted from gram-negative cells, which stain red when the counter-stain safranin is added. While gram-negative organisms are constant in their reaction, gram-positive organisms may, in older cultures, appear gram-negative. *See* STAIN (MICROBIOLOGY).

Shape and arrangement. Three principal shapes of bacteria exist, spherical (coccus), rod shape (bacillus), and twisted rod (spirillum). The coccus may be arranged in chains of cocci as in *Streptococcus*, or in tetrads of cocci as in *Sarcina*. The rods may be single or in filaments (Fig. 2).

Motility. Many bacteria are not motile. Of the motile bacteria, however, some move by means of tiny whirling hairlike flagella extending from within the cell. Others are motile without flagella and have a creeping or gliding motion. Spiral forms are usually polarly flagellated, that is, with flagella at the end of the cell. Cocci (spheres) are rarely flagellated. Rod-shaped bacteria may lack flagella, or have polar or peritrichous (around the entire surface of the cell) flagella (Fig. 2). *See* BACTERIAL MOTILITY.

Cell wall and endospore. Many bacteria are en-

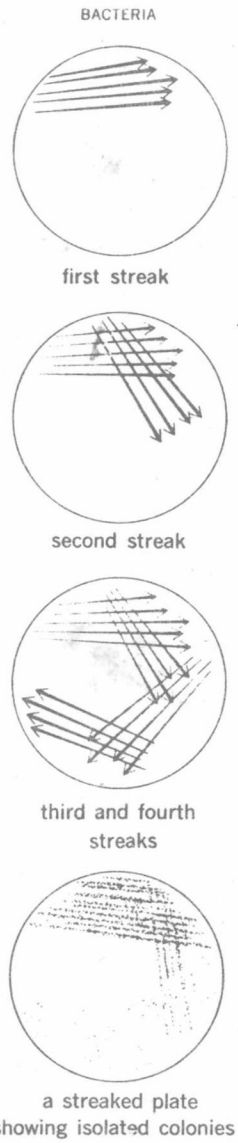


Fig. 1. Streak-plate technique used to isolate bacterial colonies.

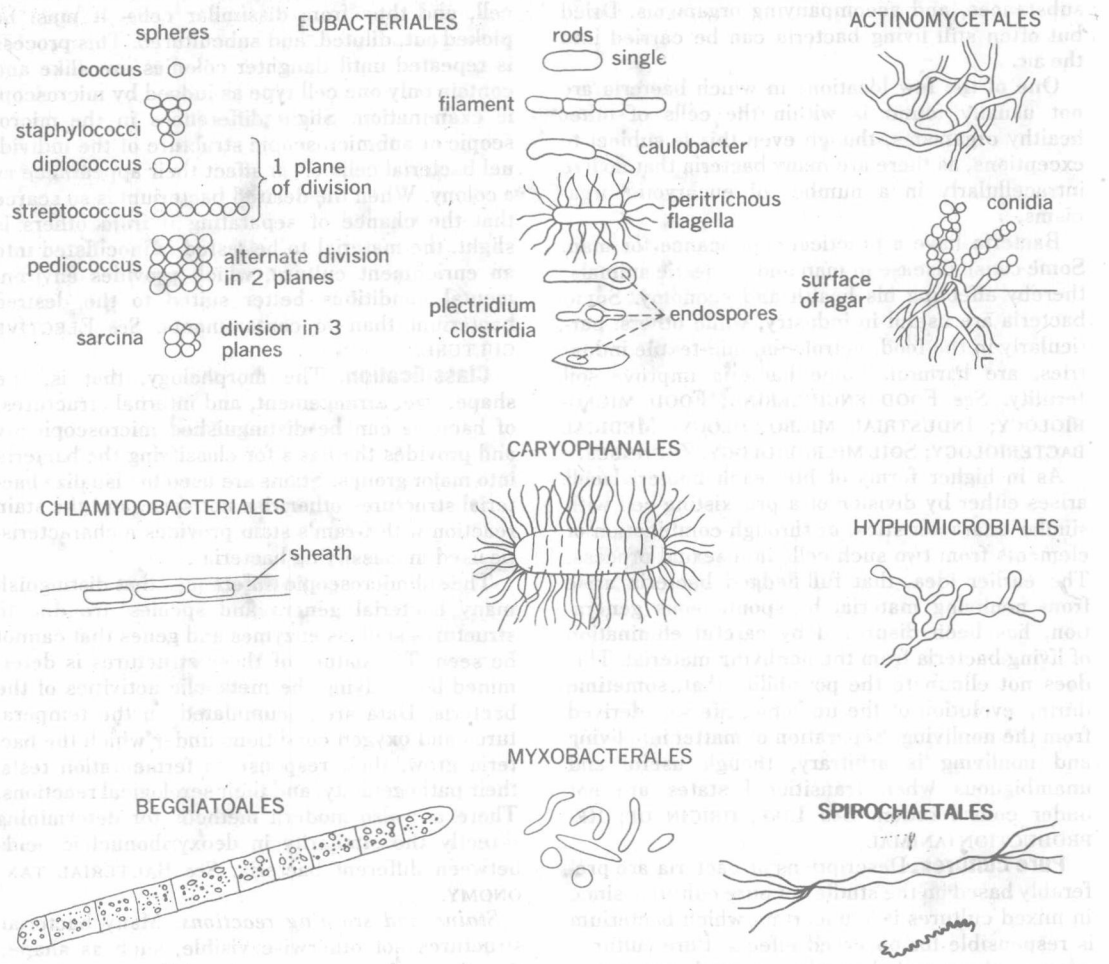


Fig. 2. Morphological features of representative bacteria in eight orders of Schizomycetes.

veloped in a capsule, a transparent gelatinous or mucoid layer outside the cell wall. Some, chiefly rods in the family Bacillaceae, form within the cell a heat- and drought-resistant spore, called an endospore. Endospores are spherical to oval in shape and sometimes develop to a size that swells the cell to a drumstick shape (plectridium) if the endospore is located terminally, or to a spindle shape (clostridium) if it is located centrally. Cytoplasmic structures such as reserve fat, protein, and volutin are occasionally visible within the bacterial cell. *See* BACTERIAL ENDOSPORES.

Nucleus. The nucleus of bacteria is procaryotic, that is, not separated from the rest of the cell by a membrane. It contains the pattern material for forming new cells. This material, deoxyribonucleic acid (DNA), carrying the information for synthesis of cell parts, composes a filament with the ends joined to form a circle. The filament consists of two DNA strands joined throughout their length. The joining imparts a helical form to the double strand. The double-stranded DNA consists of linearly arranged hereditary units, analogous and probably homologous with the "genes" of higher forms of life. During cell division and sexual reproduction, these units are duplicated and a complete set is distributed to each new cell by an orderly but as yet unelucidated mechanism. *See* BACTERIAL GENETICS.

Temperature relationships. Bacteria are said to be psychrophilic if their optimum temperature is below 20°C, mesophilic if it is 20–45°C, and thermophilic if it is above 45°C. Some bacteria can grow at temperatures as high as 75°C. Others, which are not killed but which cannot grow at high temperatures, are called thermoduric.

Oxygen relationships. Bacteria are said to be aerobic if they require oxygen and grow best at a high oxygen tension, usually 20% or more. Microaerophilic bacteria need oxygen, but grow best at, or may even require, reduced oxygen tensions, that is, less than 10%. Anaerobic bacteria do not require oxygen for growth. Obligatorily anaerobic bacteria can grow only in the complete absence of oxygen.

Fermentation and respiration. Fermentation is a term used to indicate processes in which foodstuffs are decomposed in the absence of oxygen. Respiration is the comparable aerobic process, in which oxygen is one of the foods. Some oxygen-utilizing microorganisms cannot completely oxidize the food to water and carbon dioxide, and

often form acids as a product of this type of aerobic food utilization. These incomplete oxidative processes are sometimes called fermentations, though they are actually examples of limited respiration. As in all chemical rearrangements, some of the available energy in both respiration and fermentation is dissipated as heat. The remainder is stored in the form of the materials that make up living cells.

In respiration as much as 50% of the food material and energy appear as bacterial cell material and the remainder as carbon dioxide, water, and heat. In fermentation the lack of O_2 decreases the energy supply available through rearrangement of the food, and less food (up to 15%) is converted to cells. Less heat is dissipated, and fermentation products are formed, such as CO_2, hydrogen, methane, ethanol, acetone, glycerol, and formic, acetic, propionic, butyric, lactic, and succinic acids. These products, when combined with oxygen by aerobes to form water and carbon dioxide, yield energy equal to the difference between the energy available in respiration and in fermentation.

Fermentation tests. Fermentation tests, which use liquid media, each medium containing a different nutrient, aid in classifying bacteria. Gas or acids or both are always formed when carbohydrates are fermented. Acid is detected by including an indicator of acidity in the culture medium; a small inverted tube is used to trap any gas emitted. Other useful tests measure the acidity (pH) developing during fermentation and the range of acidity permitting growth. *See* FERMENTATION.

Fermentation of proteins yields products similar to those from carbohydrates plus large quantities of nitrogenous products, such as ammonia and amines. Since ammonia and amines are weak bases, a protein fermentation causes alkalinity instead of acidity. The ability of an organism to ferment carbohydrate or protein is tested by inoculating the organism into milk containing litmus indicator, called litmus milk. The culture is incubated and then examined for color changes denoting acidity or alkalinity.

Digestion tests. Tests for digestion of protein, starch, fats, cellulose, pectin, and many other insoluble materials disclose other physiological characteristics useful in classification. Ability to digest protein (peptonization) is often tested by examining litmus milk cultures for an increase in transparency, caused by digestion of casein, the protein responsible for the white opacity of milk. The digestion of gelatin, another protein, may be detected by liquefaction.

Other metabolic reactions of bacteria include the oxidation of ammonia to nitrate by nitrifying bacteria, oxidation of sulfur to sulfates by sulfur bacteria, and oxidation of ferrous to ferric iron by iron bacteria. Some of the products formed within the cell in these oxidations react with carbon from carbon dioxide, with hydrogen from water, and with other elements to form new cells. *See* CHLAMYDOBACTERIALES; NITROBACTERIACEAE; THIOBACTERIACEAE.

The purple sulfur bacteria and the green sulfur bacteria also form new cells from inorganic compounds, but the hydrogen is obtained by splitting water with light (photolysis) instead of with chemical energy. These bacteria form an oxidized substance as the second product of the photolysis of water, as do green plants. But the former cannot convert this to oxygen, which the latter do; hence the photosynthetic bacteria can photosynthesize only if an oxidizable compound, such as hydrogen (H_2), hydrogen sulfide (H_2S), or a suitable organic substance, is present with which the oxidized moiety is continually reduced. *See* BACTERIAL PHOTOSYNTHESIS; RHODOBACTERIINEAE.

Some bacteria obtain energy from the oxidation of reduced substances with compounds other than oxygen (O_2). The sulfate reducers use sulfate, the denitrifiers nitrate or nitrite, and the methanogenic bacteria carbon dioxide as the oxidizing agents, producing H_2S, nitrogen (N_2), and methane (CH_4), respectively, as reduction products.

Pathogenicity. Pathogenicity, the ability to cause disease, is another property used in establishing the relationship between various groups of bacteria. Some bacteria produce disease only in certain species; for example, *Neisseria gonorrhoeae* will cause gonorrhea only in man. Some bacteria cause only one, while others may cause several diseases. An example of the former is *Corynebacterium diphtheriae*, which causes diphtheria; *Staphylococcus aureus* belongs to the latter category, and may cause boils, osteomyelitis, and pneumonia. *See* PATHOGEN.

Serological reactions. Serological reactions are very useful in distinguishing closely related bacteria. If two bacteria, A and B, differ, some of their proteins and other complex molecules also differ. When cells of A are injected into an experimental animal, such as a rabbit, some of their constituent molecules (especially proteins) cause production in the rabbit's blood of special proteins called antibodies. Each of these can combine specifically with the molecular species that caused its production. If, after a suitable incubation period, blood is drawn from the animal (in the case of a rabbit usually from an ear vein) and allowed to clot, a clear yellow liquid (blood serum) is extruded as the clot shrinks. It contains antibodies against each protein in the injected A cells. If B cells in excess are added to this antiserum, each B protein occurring also in A reacts with its corresponding antibody, thereby removing from the serum all antibodies against proteins common to both A and B. Addition of A cells gives a further reaction if A contains proteins not found in B. With reciprocal absorption of B antiserum with A cells, and testing with B cells for antibodies restricted to B, any differences in the A and B cells can be detected. *See* ANTIGEN-ANTIBODY REACTION; SEROLOGY.

Natural defenses against infections. These depend in part on serological mechanisms. When bacteria enter animal hosts containing antibodies against them, the bacteria become coated with antibodies and are then susceptible to engulfment and digestion (phagocytosis) by host cells. Chicks, mice and rats, aseptically removed from the shell or uterus, can be reared bacteria-free. These axenic animals, when mature, are highly susceptible to infection by bacterial types harmless to normal animals. Antibodies carried over from the mother protect very young animals and, by the time maternal antibodies are depleted, normally reared offspring have developed their own. The isolation of axenic animals deprives them of the bacterial anti-

gens necessary for development of protective antibodies. *See* GERMFREE VERTEBRATE.

Every ancestor of living organisms survived bacterial attacks to reach maturity. The resistance, selected in this manner, is the factor most commonly concerned in defense against infections

Bacterial variation. Variation in the characteristics of a single cell occurs during cell division, but since cells in a culture divide at different times, unless artificially synchronized, the average for the entire cell population is constant, as long as the environment is constant. A change in any limiting factor in the environment causes a change in the population. In nature environmental changes are often cyclic, and bacteria undergo accompanying changes in morphology interpreted by some as a life cycle. The applicability of this term to bacteria has been disputed.

An extremely small proportion of living organisms undergo sudden genetic changes, usually involving only one characteristic of the cell, which are transmitted through many generations. Because of the tremendous number of bacteria (1 ml of a culture may contain as many bacteria as there are humans on Earth), their mutations are common in cultures as well as in nature. If, in a given environment, a mutation enables its possessor to grow and divide more rapidly than the type from which it arose, the mutants ultimately predominate. The characteristics of the population are changed by the environment through selection of cells most fitted to survive, rather than by a direct action on all cells as discussed in the preceding paragraph. *See* MUTATION.

Dissociation. Bacterial pathogens have been observed that form a protective capsule which may belong to one of several different serological types. Noncapsulated mutant cells occasionally arise. In the animal they are destroyed by phagocytes, but on artificial media they survive and produce colonies with a rough surface. Such strains are called rough or *R* forms to distinguish them from the capsulated, smooth or *S* types. Heavy inoculation of an *R* strain into a susceptible animal causes a change to an *S* strain since any reverse mutant (that is, a mutation from *R*) *S* cell can multiply, whereas the *R* cells are consumed by phagocytes. Pretreatment of the injected *R* cells with an extract of *S* cells or growing *R* cells in a medium with an extract of *S* cells induces reversion to an *S* strain, serologically identical with the one used to prepare the extract. *See* LYSOGENY; PNEUMOCOCCUS.

Interrelationships with other organisms. Interrelationships may be close and may involve particular species. Examples are the parasitic association of many bacteria with plant and animal hosts, and the mutualistic association of nitrogen-fixing bacteria with leguminous plants, of celluloytic bacteria with grazing animals, and of luminous bacteria with certain deepsea fishes. *See* ECOLOGICAL INTERACTIONS.

Bacteria are also active in other less intimate, but no less important, natural interrelationships. Bacterial decomposition of the dead bodies of animals, and especially plants, releases for reuse by living plants the carbon dioxide needed in photosynthesis. Many other chemical activities relate bacteria to other organisms through the world pool of materials essential to life, to which all organisms contribute and from which they draw their food.

[ROBERT E. HUNGATE]

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Bacterial appendages

On the basis of structure and function, bacteriologists recognize several types of bacterial appendages: flagella, pili, acellular stalks, and prosthecae.

Flagella. Of the appendages associated with bacteria, the flagellum, which is responsible for motility, is the best known and most thoroughly studied. It consists of a protein fibril about 10–20 nanometers in diameter and several micrometers in length. It is anchored within the cell membrane of the organism; the cell produces motility by "shaking" the flagellum in a characteristic manner. The mechanism by which the chemical energy of metabolism is translated into movement is not yet understood. Not all motile bacteria have flagella, and in those that do, the number and location vary with the species. *See* BACTERIAL MOTILITY.

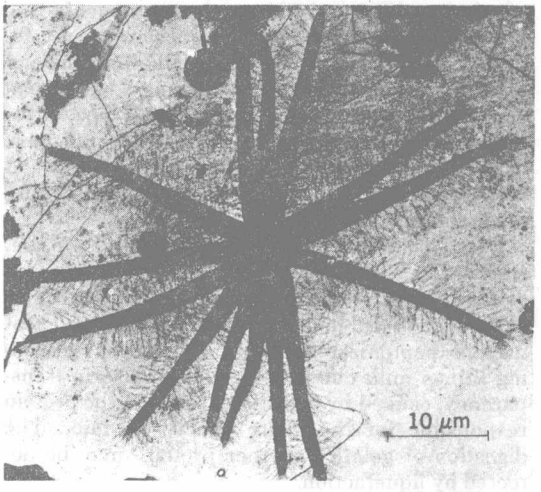

Fig. 1. Electron micrograph of a rosette-forming bacterium found in ponds and lakes.

Pili. The pilus is also a proteinaceous appendage but differs from the flagellum in that it has a hollow core, is generally finer (ranges in width from 3 to 30 nm), and does not cause motility. Nonetheless, several important functions have been attributed to this structure. The most thoroughly documented function performed by pili is their role in bacterial sexual conjugation. The so-called "male" cell of strains capable of conjugation produces a sex pilus that enables it to attach to an appropriate "fe-

male" cell containing the specific receptor site for the pilus. Only when cells of these two mating types are physically attached by the pilus can genetic material be transferred from the male to the female cell. *See* BACTERIAL GENETICS.

Pili have also been implicated in the attachment of bacteria to unrelated organisms. For example, piliated strains of *Neisseria gonorrhoeae*, the bacterium which causes the venereal disease gonorrhea, are more frequently pathogenic (disease-causing) than nonpiliated strains. It is thought that the piliated strains can use the pili to attach more strongly to host tissues. Certain viruses that infect bacteria attach to specific pili during the initial stages of infection.

Immotile aquatic bacteria commonly possess pili. Figure 1 shows an unnamed aquatic bacterium that forms rosettes (the rosette shown had 14 cells which are joined together at a common center). Each cell has more than 100 very fine pili emanating from it. The role of these structures in such aquatic bacteria is not known.

Acellular stalks. Flagella and pili are too fine to be observed using ordinary light-microscopic techniques of observation. Most acellular stalks, on the other hand, are sufficiently wide to be seen by these classical procedures. For this reason it should not seem surprising that stalks were observed long before pili and flagella were seen. Indeed, the stalked bacterium *Gallionella ferruginea* was one of the first bacteria described. Interestingly, however, early investigators thought that the stalk was the bacterium because it was enormous compared to the small, bean-shaped cell which was readily dislodged from its position at the tip of the stalk. *Gallionella* is commonly found in iron springs, where the stalk becomes heavily encrusted with iron oxides that impart a rust-colored appearance. Although these bacteria have been grown in pure culture, the difficulties encountered in cultivating them have precluded extensive studies of their biology. Pure-culture studies indicate that the stalk is made up of several small fibrils, possibly pili, that are extruded during growth from the concave side of the cell. The iron appears to be precipitated in a sheath that surrounds the fibers.

The *Blastocaulis-Planctomyces* group also has members with acellular stalks. One example is shown in Fig. 2. This is a rosette containing nine ovoid cells borne at the tips of acellular stalks which are connected together at a common center. The cells reproduce by budding at the opposite, nonstalked pole of the cell. Note also that each cell has numerous pili in addition to the single stalk.

In both of the examples cited above, the appendage is an excretion of the cell and for this reason is termed extracellular or acellular.

Prosthecae. Unlike acellular stalks, the prostheca is an appendage that is actually part of the cell; that is, it is bounded by some or all of the layers of the cell envelope (cell wall and cell membrane). Frequently, species that have these appendages also have nonprosthecate cells that serve as stages in the life cycle of the organism. These nonprosthecate cells are usually motile by flagella and undergo predictable developmental stages during which prosthecae differentiate and daughter cells are formed. Thus, these bacteria are among the simplest unicellular organisms in which cellular developmental processes can be studied at the molecular level. To provide some insight into the nature of these bacteria, the life cycles of several of those most thoroughly studied are described below.

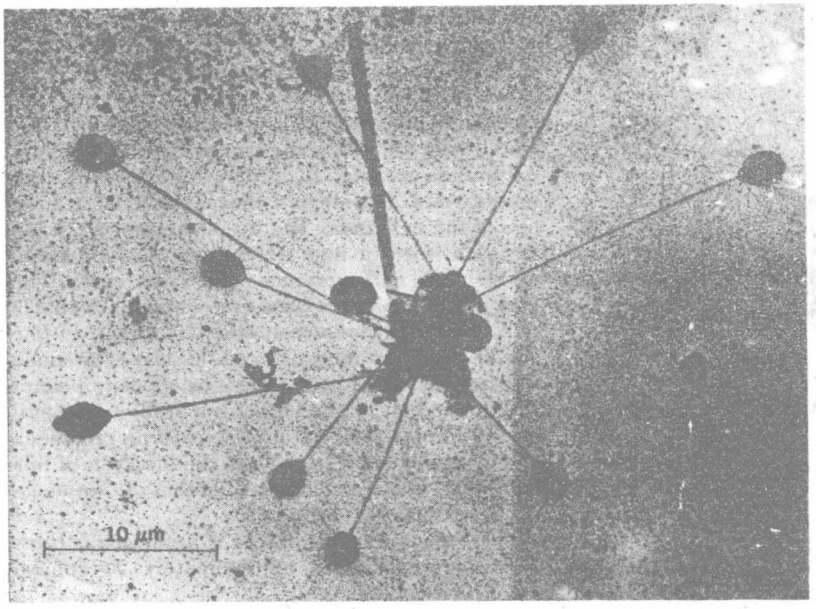

Fig. 2. Electron micrograph of a rosette of a budding bacterium of the *Blastocaulis-Planctomyces* group; note small bud on cell at lower left. Pili can be seen emanating from each cell.

Caulobacter. The best-known genus of prosthecate bacteria is *Caulobacter*. These bacteria have a single prostheca, termed a stalk, that extends from one end of the cell (Fig. 3). *Caulobacter* cells undergo division at their nonstalked pole by binary fission to produce a daughter cell that has a single flagellum. The daughter cell, which has no stalk, becomes motile and separates from the mother cell. After separation, the daughter cell, called a swarmer cell because of its motility, normally attaches to a solid substratum by a sticky holdfast material located at the base of the flagellum. In time the cell loses its motility and synthesizes a stalk at the flagellum-base position so that the holdfast is borne at the tip of the stalk. It is now a mature cell that elongates and produces swarmer cells of its own.

It has been discovered that the age of a *Caulobacter* cell can be estimated by counting the number of crossbands in the stalk of the cell. These crossbands can be seen when cells are observed with the electron microscope (Fig. 4). Apparently, each time a cell undergoes binary fission, the mother cell synthesizes a crossband in its stalk. Therefore, the age of the cell can be estimated by counting these structures in the same manner that the annual rings of a tree can be used to determine its age. This is the only bacterium whose age can be determined by direct examination of the organism. *See* CAULOBACTERACEAE.

Hyphomicrobium. The genus *Hyphomicrobium* is distinctive not only because of its prosthecae but also because it divides by budding. Like *Caulobac-*

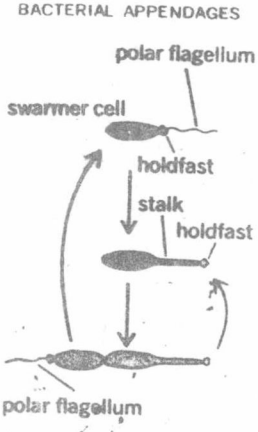

Fig. 3. Life cycle of *Caulobacter* species.

ter, it undergoes, for a bacterium, a rather complex life cycle including flagellated, nonprosthecate cells and prosthecate, nonmotile cells (Fig. 5). Newly formed oval buds are motile by subpolar flagella. Some species have holdfast material associated with the cell that permits them to attach to particulate material. Eventually the buds lose their motility and develop prosthecae, invariably from one of the cell ends. The tip of the prostheca enlarges to form a bud which separates from the mother cell and undergoes the same cycle. The mother cell, however, has several options available to it: (1) It may produce another bud from the same site at the tip of its prostheca; (2) it may produce another prostheca at the same or opposite pole of the cell and form a bud at its tip; or (3) it may produce a branch from its already existing prostheca and form a bud at its tip. Thus, the life cycle of this bacterium is more complex than that of *Caulobacter*. *See* HYPHOMICROBIALES.

Prosthecomicrobium. Bacteria in the genus *Prosthecomicrobium* have approximately 20 conical

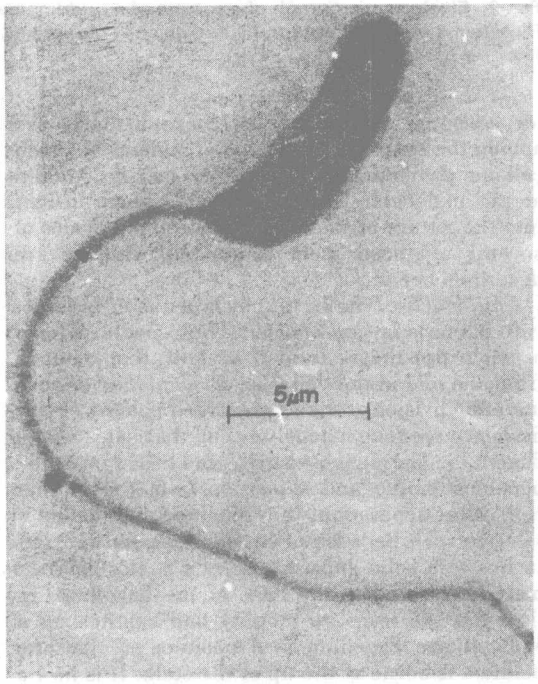

Fig. 4. Electron micrograph of a *Caulobacter* cell showing numerous crossbands on the prostheca; each crossband was formed when a daughter cell was produced.

prosthecae that extend in all directions from the cell, giving the organism the appearance of a bur of a cocklebur plant when observed in the microscope (Fig. 6). The appendages vary in length from one species to another, being as short as 0.2 μm or as long as 1.0 μm, or longer. The bacteria reportedly divide by binary fission. Although both motile and nonmotile cells are found in some strains, not all strains have motile stages, and in those that do, it is not known whether the motile stage is part of the life cycle, as in the case of *Caulobacter* and *Hyphomicrobium*.

Some species in this genus and in *Ancalomicrobium*, discussed below, have been found to contain

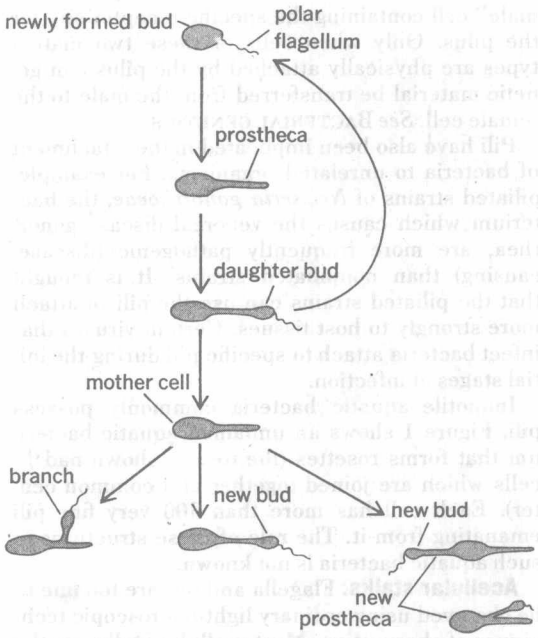

Fig. 5. Life cycle of *Hyphomicrobium* species. Newly formed buds are motile by a subpolar flagellum. The buds enlarge and differentiate to form a prostheca from one pole. A daughter bud is produced at the tip of the prostheca, and it repeats the life cycle. The mother cell has several options: a new bud may be produced from the same site; a new prostheca and bud may be formed from the opposite or same pole; or a branch may be formed on the existing prostheca.

gas vacuoles. These structures appear as bright, refractile areas within the bacterium; each comprises numerous intracellular vesicles that contain gas. Each vesicle is a small cylinder whose ends terminate in conical tips. The vesicle is bound by a protein membrane that permits only gases to pass to the inside. Thus, when the cell synthesizes these structures, the density of the cell is reduced because part of the cytoplasm is displaced with gas. By regulating the amount of cell volume made up by the gas vesicles, the cell can regulate its buoyancy and therefore its position in the water

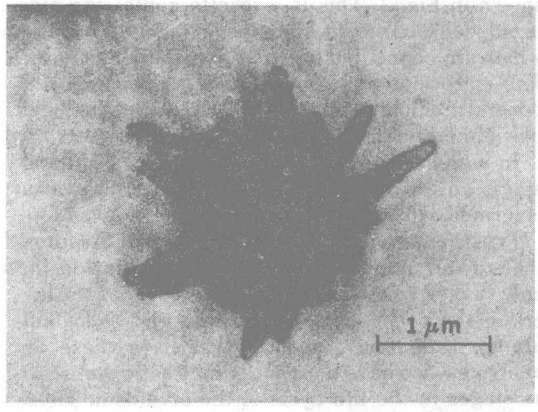

Fig. 6. A picture of *Prosthecomicrobium pneumaticum* taken with the electron microscope. Note the 14 prosthecae extending from the cell, and the transparent gas vesicles inside the cell.

column of stratified lakes. If more vesicles are produced, the cell rises, whereas if fewer are produced, the cell sinks. Gas vesicles are found only in certain aquatic bacteria and appear to play a role in regulating the incidence of light exposure available for photosynthesis.

Ancalomicrobium. Like *Prosthecomicrobium* cells, cells of the genus *Anacalomicrobium* have several prosthecae per cell, although the number rarely exceeds eight (Fig. 7). This nonmotile bacterium produces an outgrowth from one position on the cell surface. This outgrowth, or bud, differentiates to form from two to four prosthecae, each about 3 μm long. These appendages occasionally form branches analogous to those of *Hyphomicrobium*, but buds are not produced at the tips.

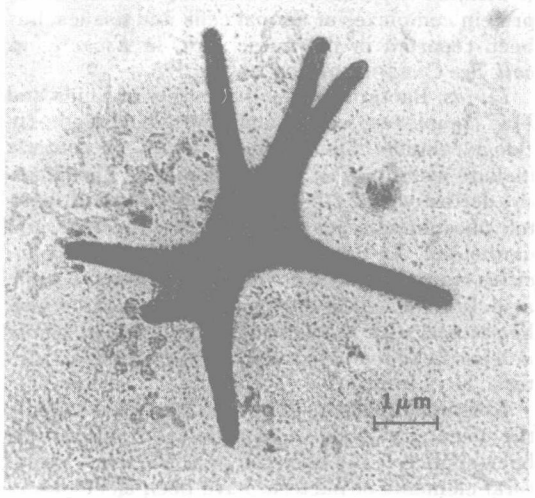

Fig. 7. A picture of *Ancalomicrobium adetum* taken with the electron microscope. Note that the cell has seven prosthecae.

Function. There are two hypotheses which have been advanced by workers in this field to explain the function of prosthecae: (1) These structures serve to act as "wings" by preventing the cells that have them from settling out of the water column in aquatic habitats; and (2) by increasing the membrane surface area of the organism, prosthecae enable it to take up nutrients more quickly in the dilute environments in which they reside. As yet, however, the question of function has not been resolved. *See* BUDDING AND APPENDAGED BACTERIA. [JAMES T. STALEY]

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Bacterial cell chemistry

That branch of bacteriology concerned with the description of the various components of the cell in chemical terms.

Chemical composition. The overall chemical composition of the bacterial cell is very similar to that of all other types of cells of animals, plant, and microbial origin, which are capable of growth and replication. Bacteria thus possess the proteins ribonucleic acid (RNA) and deoxyribonucleic acid (DNA), which are the major classes of chemical constituents. These are required for the biochemical activities and the continuity and expression of the genetic characteristics of the cell. All cells possess a plasma membrane structure responsible for permeability properties, and one of the universal features of cellular membranes is their protein-lipid nature. Thus bacteria contain lipids of the phospholipid class as essential chemical constituents of their cell membranes. Although sterols, such as cholesterol, are widely distributed in nature, occurring in membranous structures from animal, plant, and higher microbial cells, they have not been found in bacteria (except the Mycoplasma group of pathogenic bacteria) or blue-green algae. On the other hand, carotenoids, which are also lipid-soluble compounds, are found in many bacteria and in the closely related blue-green algae. Lecithin is one of the commonest phospholipids in higher organisms, and although it is found in several bacterial groups, it occurs much less frequently in the bacteria. The other major class of chemical components of cells, the carbohydrates or polysaccharides, also occurs in a wide variety of bacterial groups.

Many of the unusual compounds of biological origin have been found in bacterial cell structures and products. Although bacterial proteins appear to be quite normal with respect to the variety and isomeric form of the amino acid building blocks, the cell walls, certain capsules, and antibiotics formed by bacteria possess peptides containing D isomers of amino acids, such as alanine, glutamic and aspartic acids, and phenylalanine. The amino acid diaminopimelic acid, first detected and isolated from the bacterium *Corynebacterium diphtheriae* in 1950, was subsequently found to be one of the characteristic cell wall amino acids of many bacterial species. It occurs in the wall peptidoglycan but is not an amino acid component of the bacterial proteins. *See* AMINO ACIDS; ANTIBIOTIC; BACTERIAL PIGMENTATION; CAROTENOID; CELL MEMBRANES; STEROL.

Cell walls of bacteria contain one of the most distinctive bacterial products, the amino sugar muramic acid (3-0-carboxyethyl-glucosamine), in combination with glucosamine in the peptidoglycan polymer forming the rigid wall structure. The distribution of muramic acid in nature is confined to the bacteria, blue-green algae, and rickettsias. It has not been detected in higher microorganisms or in plant and animal cells. The amino sugars generally found in higher organisms are glucosamine, galactosamine, and the sialic acids. In addition to these amino sugars and muramic acid, bacteria also contain a variety of other amino sugars in their polysaccharide and lipopolysaccharide structures. Polysaccharides of the pneumococcus capsular substances and lipopolysaccharides of gram-negative bacteria have been shown to contain the following variety of amino sugars: mannosamine, fucosamine, pneumosamine (an amino-dideoxytalose), amino uronic acids, amino dideoxy sugars, and diamino sugars. The bacterial lipopolysaccharides also contain a unique class of sugars, the dideoxy sugars—colitose, abequose, paratose, and tyvelose. The other very characteristic product of the lipopolysaccharides is the sugar acid ketodeoxyoctonic acid. Bacterial cell walls also possess

a group of polymers called the teichoic acids, whose occurrence so far is confined to bacteria. The teichoic acids are polymers of ribitol or glycerol phosphate with additional compounds such as glucose, *N*-acetylglucosamine, and D-alanine linked to the polyol backbone. The D-alanine in the teichoic acid is linked through an ester bond and thus represents another example of the unusual features of the bacterial wall compounds. *See* AMINO SUGAR.

The lipids of bacteria contain the common fatty acids found in lipids from other types of cells. However, bacteria lack the ability to form polyunsaturated fatty acids and thus differ from higher microorganisms, plants, and animals. Certain bacteria contain high proportions of branch-chain fatty acids in their lipids. Other unusual features of the bacterial lipids include the occurrence of lipoamino acids in a variety of species and the derivatives of glycerol diether, in the extremely halophilic bacterium *Halobacterium cutirubrum*.

From this survey it is evident that bacterial cells contain a number of distinctive chemical constituents, many of which have been found in the cell's capsules, walls, or membrane structures. Despite the presence of the variety of unusual compounds in the major classes of chemical structures in bacteria, the quantitative chemical analyses are broadly similar to those for other cell types. Thus, on a weight basis, bacteria contain 70–90% water, and a mineral content of 1–10%. Much of the mineral matter is accounted for by potassium, sodium, calcium, magnesium, and phosphorus. Proteins and nucleic acids, the major organic constituents of bacteria, are present in more constant amounts than other organic compounds, such as the lipids and carbohydrates. Protein, determined by the percentage of nitrogen, accounts for 40–60% of the dry weight of the bacterial cell. The nucleic acid content is 10–20%. The amounts of carbohydrate and lipid vary widely and are dependent on the growth conditions. Carbohydrate content is 10–30% and that of lipids 1–50%.

Proteins and peptides. Most of the cellular proteins formed by bacteria are similar in amino acid composition to those of other organisms. The extracellular proteins secreted by gram-positive bacteria show one conspicuous difference from many other proteins in that they are devoid of, or exceptionally low in, the amino acid cysteine. Thus it appears that these proteins lack the S-S type of bridges linking the peptide chains together. In addition to the polypeptide antibiotics, the bacterial cell produces unusual peptide structures. The substance forming a thick, viscid layer, or capsule, surrounding the cells of *Bacillus anthracis* is a polymer of D-glutamic acid. *See* PROTEIN.

Nucleic acids. As in other cells, the bacterial cell contains both RNA and DNA. The RNA is largely in the form of ribosomes (RNA-protein particles) of somewhat smaller dimensions than those found in higher organisms. The DNA of the bacterial cell gives the Feulgen reaction, which is the cytochemical basis for the demonstration of the bacterial nucleus. The DNA in bacteria is not enclosed within a nuclear membrane as it is in other types of cells. The base composition (G+C, guanine+cytosine) values vary from one bacterial species to another and range from 20% to 74%. *See* NUCLEIC ACID.

Carbohydrates. A great variety of carbohydrates are synthesized by bacteria. They range from simple polymers of glucose, such as the cellulose produced by *Acetobacter xylinum*, to complex substances composed of a number of sugar units, such as glucose, galactose, rhamnose, and amino sugars. Unusual features of certain bacterial carbohydrates include the presence of the D isomer of arabinose in some, the occurrence of heptose sugars, and the detection of new amino sugars. Neuraminic acid, an important constituent of carbohydrate-protein complexes of animal cells and tissues, has been reported in polymeric form in *Escherichia coli*. *See* CARBOHYDRATE.

Lipids. Bacteria produce a variety of lipids and lipid complexes, waxes, fats, glycolipids, and peptidoglycolipids. Phospholipids found in bacteria include lecithin (phosphatidyl choline); phosphatidyl derivatives of ethanolamine, serine, and inositol; phosphatidic acid; phosphatidyl glycerol, and cardiolipin. An unusual lipid first detected in *Bacillus megaterium* is a polymer of β-hydroxybutyric acid. It is present in the form of granules that may be stained with the fat-soluble dye Sudan black, and has been found in many different kinds of bacteria. *See* LIPID.

Chemical anatomy of bacterial cells. Anatomy, the science of bodily and cellular structure, has been applied to the bacterial cell. The major structural elements of bacteria have been isolated and chemically characterized. This method of studying the chemical anatomy of the bacterial cell avoids the difficulties of applying cytochemical tests, such as the Feulgen reaction, to such small cells.

Flagella. The filamentous, locomotive appendages of bacteria are composed of flagellin, a protein related chemically and physically to the hair-like proteins of other organisms. *See* BACTERIAL MOTILITY; CILIA AND FLAGELLA.

Capsules. The thick, mucous envelope, or capsule, may be composed of polypeptide or carbohydrate material. The viscous capsular carbohydrates may be composed of a variety of sugars, including hexoses, pentoses, methylpentoses, uronic acids, and amino sugars.

Cell walls. Bacteria possess a rigid wall structure that defines the shape of each cell. The principal structural component of the wall is a covalently bonded peptidoglycan, the glycan portion of which consists of alternating molecules of *N*-acetylmuramic acid and *N*-acetylglucosamine linked by $\beta 1 \rightarrow 4$ glycosidic bonds. The peptide component is linked by an amide bond to the muramic acid. Alanine, D-glutamic acid, lysine, or diaminopimelic acid form the basic part of the peptide, and in some bacterial walls these peptide strands may be cross-linked by either glycine, alanine, or threonine peptide bridges or sometimes all three. In the gram-positive bacteria, the teichoic acids and polysaccharides may be covalently linked to the rigid peptidoglycan.

The wall, or more strictly speaking, the cell envelope, of the gram-negative bacteria is a more complex structure with a rigid layer of peptidoglycan upon which the lipopolysaccharide-protein-lipid complexes are anchored. The peptidoglycan has the basic building blocks of the structure

found in the walls of gram-positive organisms.

Protoplasmic membrane and mesosome. The plasma membrane and its intrusions within the cell (called the mesosome) are composed of 20–30% lipid and 50–70% protein. In some instances small amounts of carbohydrate have been found in isolated membranes. Virtually all of the cell's lipid, phospholipid, carotenoid, and electron-transport components are localized in the membrane-mesosome structures. The membranes contain a variety of proteins separable by polyacrylamide gel electrophoresis.

Enzyme action on bacterial structures. Enzymes have been used for the selective removal of surface slime, capsular polysaccharides, and the bacterial cell wall. Lysozyme, an enzyme obtained from egg white, specifically degrades the cell wall of some species. Other enzymes from the streptomyces group will attack the walls of lysozyme-resistant bacteria. Many of these enzymes have a specific action on the peptide cross bridges in the peptidoglycan. When the bacterial wall is digested with the cell wall–degrading enzymes in a sucrose medium, the bacterial protoplast is liberated. The protoplast can be further degraded by the action of proteolytic and lipolytic enzymes on the membrane structure. *See* BACTERIAL PHYSIOLOGY; ENZYME; LYSOZYME. [MILTON R. J. SALTON]

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Bacterial coenzyme

Organic molecules that participate directly in a bacterial enzymatic reaction and may be chemically altered during the reaction. Although many enzymes do not need specific cofactors, the majority of bacterial endoenzymes do. These cofactors may be simple inorganic cations such as magnesium, manganese, or calcium, which are commonly referred to as activators, or more complex organic molecules. The latter are called coenzymes.

Coenzymes are the functional units, also called prosthetic or active groups, of an enzyme. Their catalytic activity depends on their association with a protein moiety, the apoenzyme or carrier, which is responsible for the high degree of specificity of the complex, or holoenzyme. Many of these combinations are readily dissociable:

$$\text{Holoenzyme} \rightleftharpoons \text{coenzyme} + \text{apoenzyme}$$

Good examples of such enzymes are the pyridine nucleotide enzymes whose coenzymes are nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP); and the flavin nucleotide enzymes, whose coenzymes are flavin mononucleotide and flavin adenine dinucleotide (FMN and FAD). These coenzymes act as hydrogen acceptors and can, in combination with a wide variety of specific apoenzymes, catalyze the dehydrogenation of a large number of substrates. *See* COENZYME.

Some holoenzymes, particularly the iron-porphyrin enzymes such as catalases, peroxidases, and cytochromes, can be dissociated only by drastic means; their coenzymes are far more firmly bound to the protein. This is in keeping with the much more restricted range of their activity, which appears to be limited to specific reactions that are common to the majority of bacteria and other living organisms. *See* BACTERIAL ENZYME; DIPHOSPHOPYRIDINE NUCLEOTIDE (DPN); ENZYME; TRIPHOSPHOPYRIDINE NUCLEOTIDE (TPN).

Coenzymes and growth factors. The universal occurrence in the metabolism of all living organisms of hydrogenations, dehydrogenations, transhydrogenations, aminations, deaminations, transaminations, and various other general reaction types implies that the coenzymes for these processes must be present in the cells. Since 1940 this has cast a new light on the often-encountered special nutrient requirements, especially for vitamins of the B group. These vitamins are now recognized as substances that are structurally closely allied to coenzymes. Thus the ability of a particular bacterium to develop only if supplied with a certain B vitamin can be readily interpreted to mean that the organism cannot synthesize the corresponding coenzyme from other substances. For example, *Hemophilus influenzae* cannot synthesize NAD, and must consequently be supplied with the intact coenzyme before it can grow. Other organisms can synthesize the pyridine nucleotides if they are provided with simpler building blocks, such as nicotinamide or nicotinic acid. If a bacterium can grow in a medium devoid of such building blocks, the implication is that it can perform the synthesis of the coenzyme from still more remote, and often quite simple, ingredients. Where this has been experimentally tested, the results have been uniformly positive. *See* CULTURE MEDIA.

Many organisms have become obligatory parasites because of a spontaneous loss in their ability to synthesize a needed vitamin. As a result, such organisms become completely host-dependent for a source of growth factors. This has been the basis for the development of current ideas on physiological specialization and evolution. *See* VITAMIN.

Function. The mode of action of coenzymes generally involves their role as temporary acceptors for particular atoms or atom groups derived from a substrate, and subsequently as donors of the same entities to another kind of acceptor under the influence of specific apoenzymes. This is shown in the illustration, where H_2A represents an appropriate oxidizable substrate and A its oxidation product.

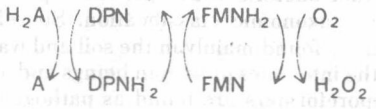

Diagram of role of pyridine nucleotide and flavin nucleotide coenzymes in hydrogen transfer.

Similar diagrams can be constructed to illustrate the role of adenosinetriphosphate (ATP) as a phosphorylating agent with the production of adenosinediphosphate (ADP), and the subsequent reformation of ATP from ADP with phosphate groups produced in special positions during metabolism;