Bacteria

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Content

- Cultures
- Classification
- Temperature relationships
- Oxygen relationships
- Fermentation and respiration
- Fermentation tests
- Digestion tests
- Pathogenicity
- Serological reactions
- Bacterial Variation
- Interrelationships
- Gas Vesicles and Vacuoles
- Characteristics
- Composition and molecular structure
- Function
- Endospores
- Structure and constituents
- Formation
- Breaking of dormancy
- Microcycle sporulation
- Appendages
- Flagella
- Pili
- Acellular stalks
- Prosthecae
- Motility
- Flagellar motion
- Taxis
- Gliding

- Bibliography
- Additional Readings

Extremely small—usually 0.3 to 2.0 micrometers in diameter—and relatively simple microorganisms possessing the prokaryotic type of cell construction. 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 eukaryotic organisms.

Bacteria have a practical significance for humans. Some cause disease in humans and domestic animals, thereby affecting health and the 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 also:* **Food engineering (/content/food-engineering/266000)**; **Food microbiology (/content/food-microbiology/267000)**; **Industrial microbiology (/content/industrial-microbiology/342000)**; **Medical bacteriology (/content/medical-bacteriology/412700)**; **Petroleum microbiology (/content/petroleum-microbiology/503000)**; **Soil microbiology (/content/soil-microbiology/632000)**; **Textile microbiology (/content/textile-microbiology/687600)**; **Zoonoses (/content/zoonoses/756900)**

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 also:* **Animal reproduction (/content/animal-reproduction/581200)**; **Prebiotic organic synthesis (/content/prebiotic-organic-synthesis/381010)**

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.

If conditions are suitable, each bacterium grows and divides, using food diffused through the gel, and produces a mass of cells called a colony-forming unit (cfu). Colonies always develop until visible to the naked eye unless toxic products or deficient nutrients limit them to microscopic dimensions. *See also:* **Axenic culture (/content/axenic-culture/066300)**; **Bacteriology (/content/bacteriology/069800)**; **Culture (/content/culture/173000)**

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. Three principal shapes of bacteria exist, spherical (coccus), rod (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. 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. *See also:* **Stain (microbiology) (/content/stain-microbiology/650400)**

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.

Many bacteria are enveloped in a capsule, a transparent gelatinous or mucoid layer outside the cell wall. Some form a heat- and drought-resistant spore, called an endospore, within the cell. Cytoplasmic structures such as reserve fat, protein, and volutin are occasionally visible within the bacterial cell.

The nucleus of bacteria is prokaryotic, 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 also:* **Bacterial genetics (/content/bacterial-genetics/068700)**

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.

Temperature relationships

Bacteria are said to be psychrophilic if their optimum temperature is below 60°F (20°C), mesophilic if it is 60–113°F (20–45°C), and thermophilic if it is above 113°F (45°C). Some hyperthermophilic bacteria can grow at temperatures as high as 167°F (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, although 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. *See also:* **Fermentation (/content/fermentation/253100)**

In respiration, as much as 50% of the food material and energy appears 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.

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 organisms 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.

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. However, 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.

Some bacteria obtain energy from the oxidation of reduced substances with compounds other than oxygen (O_2). The sulfate reducers use sulfate, the denitrifiers use nitrate or nitrite, and the methanogenic bacteria use carbon dioxide as the oxidizing agents, producing H_2S, nitrogen (N_2), and methane (CH_4), respectively, as reduction products. *See also:* **Bacterial physiology and metabolism (/content/bacterial-physiology-and-metabolism/069000)**

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 humans. Some bacteria cause only one disease, 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 also:* **Pathogen (/content/pathogen/492200)**

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 also:* **Antibody (/content/antibody/040100)**; **Bacterial taxonomy (/content/bacterial-taxonomy/069700)**; **Serology (/content/serology/616000)**

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 also:* **Lysogeny (/content/lysogeny/394000)**

Natural defenses against infections 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 antigens necessary for development of protective antibodies. 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. *See also:* **Disease (/content/disease/200100)**

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 $in.^3$ or 16 ml of a culture may contain 50 billion bacteria), 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 also:* **Mutation (/content/mutation/441200)**

Interrelationships

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 cellulolytic bacteria with grazing animals, and of luminous bacteria with certain deep-sea fishes. *See also:* **Nitrogen fixation (/content/nitrogen-fixation/454100)**; **Population ecology (/content/population-ecology/538150)**

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

Gas Vesicles and Vacuoles

Gas vesicles are submicroscopic structures of cylindrical shape with conical ends. They were discovered in electron micrographs of gas vacuole–containing cyanobacteria. These studies revealed that the gas vesicles are the structural units which make up the gas vacuoles recognizable within the cells by ordinary light microscopy. Gas vesicles occur exclusively in prokaryotic microorganisms. *See also:* **Vacuole (/content/vacuole/725300)**

Characteristics

The gas vacuoles were first described for purple sulfur bacteria in 1888 and called hollow cavities; they were named gas vacuoles in 1895, when it was observed that they conferred buoyancy to the cells containing them. In the light microscope, gas vacuoles appear in the cytoplasm as refractile hollow cavities of irregular shape and pinkish shine.

The gas vesicles are homologous structures in all prokaryotic organisms. The size of the vesicles varies considerably in different systematic groups. In the cyanobacteria and green sulfur bacteria, the vesicles are about 70 nanometers in diameter and, on the average, 400 nm long (maximum length up to 1 micrometer). The gas vesicles of the purple sulfur bacteria and of several species and genera of chemotrophic bacteria are 100–200 nm wide but only up to 300 nm long. The widest gas vesicles, with a diameter of up to 300 nm, occur in the halobacteria.

The gas vesicle membrane is 2 nm thick and exhibits a ribbed fine structure from both the outside and the inside. The ribs are 4.5 nm wide and lie perpendicular to the long axis of the vesicle cylinder. The ribs apparently represent turns of a shallow spiral rather than stacks of concentric rings. The vesicle membrane, permeable to gases but impermeable to water, encloses a hollow space into which gases diffuse freely.

The gas vesicles are fairly rigid structures. However, when suspensions of cells with gas vacuoles are subjected to a sudden increase in pressure, the gas vesicles collapse and lose their gas-filled hollow spaces. Consequently, the gas vacuoles are no longer detectable by light microscopy and the cells lose their buoyancy.

Composition and molecular structure

Intact gas vesicles can readily be isolated from gently lysed cells by centrifugation, which causes the vesicles to float to the supernatant surface, where they are skimmed off. Chemical analysis of isolated gas vesicles from cyanobacteria and halobacteria shows that the vesicles consist exclusively of protein. Only one type of protein was found in the vesicles of cyanobacteria, while the vesicles of *Halobacterium* consisted of two very similar protein types. The molecular weights of the vesicle proteins are between 13,000 and 15,000. The amino acid composition of the vesicle proteins is fairly similar in all species. The proteins have in common a high proportion (more than 50%) of hydrophobic aliphatic amino acids and a low proportion of aromatic amino acids; both cysteine and methionine are absent. *See also:* **Centrifugation (/content/centrifugation/119700)**

It was established by x-ray and neutron diffraction studies that the gas vesicle membrane consists of a monolayer of the vesicle protein. Since the outside of the vesicles is hydrophilic and wettable while the inside is hydrophobic, the protein molecules must be positioned so that their hydrophobic aliphatic amino acids are located toward the inner surface of the vesicles. It is assumed that the hollow space of the vesicle arises simultaneously with formation and enlargement of the vesicle. The gases in the surrounding cytoplasm diffuse into the hollow space, while the hydrophobic inner surface of the vesicle prevents the penetration of water as well as the formation of water droplets inside the structure. *See also:* **Cell membranes (/content/cell-membranes/116500)**

Function

Good evidence exists for only one of several suggested biological functions for gas vesicles. The hollow space of the vesicles effectively decreases the specific weight of the cells and, therefore, provides buoyancy. Buoyancy can be of selective advantage only in nonturbulent aquatic habitats. In agreement with this, gas-vacuolated microorganisms are mainly encountered as planktonic cells in lakes and stagnant water bodies, while they are rarely found in soils.

Since the vesicle membrane is permeable to gases, the pressure of the gas in the vesicles is always equal to the atmospheric pressure at the surface of the aquatic habitat. The rigid structure of the vesicle membrane maintains the hollow space of the vesicle against both the turgor pressure of the cells and the hydrostatic pressure of the water at the depth in which the cells float. Depending on the critical pressure that is tolerated by the vesicle membrane of a given species, a kind of buoyancy regulation is feasible by either formation or collapse of gas vesicles. For certain planktonic cyanobacteria (for example, *Oscillatoria agardhii*) which develop their maximum population density at a certain depth in stratified lakes, buoyancy regulation has been experimentally established. When at growth-limiting light intensities the turgor pressure of the cells is low, newly forming gas vesicles cause the cells to rise in the water column. At higher light intensities in the vertical light gradient, a rising turgor pressure may cause part of the gas vesicles to collapse and, consequently, cause the cells to stop rising or even to sink. At the population maximum, gas vesicles render the cells neutrally buoyant.

Under certain conditions in nutrient-rich eutrophic lakes, gas-vacuolated cyanobacteria may become overbuoyant by an excess of gas vesicles. In this case, masses of cells appear at the surface and form a water bloom. *See also:* **Eutrophication (/content/eutrophication/247000)**

Norbert Pfennig

Endospores

Endospores are resistant and metabolically dormant bodies produced by the gram-positive rods of *Bacillus* (aerobic or facultatively aerobic) and *Clostridia* (strictly anaerobic), by the coccus *Sporosarcina*, and by certain other bacteria. Spore-forming bacteria are found mainly in the soil and water and also in the intestines of humans and animals. Some spore-formers are found as pathogens in insects; others are pathogenic to animals and humans. Endospores seem to be able to survive indefinitely. Spores kept for more than 50 years have shown little loss of their capacity to germinate and propagate by cell division.

The endospore appears as a light-refractile body inside another cell (sporangium), as shown in **Fig. 1**. Each sporangium produces one endospore with a characteristic size, shape, and position within the cell.

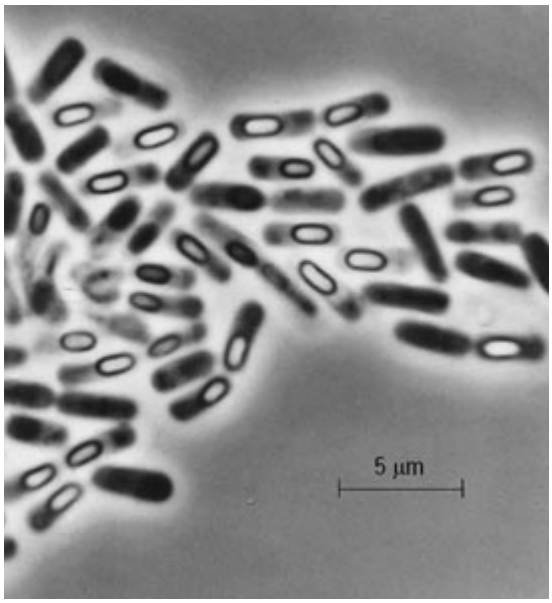

Fig. 1 Sporulating cells of *Bacillus cereus*. (*Photomicrograph by F. C. Fitz-James*)

Structure and constituents

The mature spore has a complex structure which contains a number of layers. The outermost envelope, surrounding the spore, is called the exosporium and is a thin, membranous covering. Beneath the exosporium lies the spore coat, which is composed of several layers, largely of a protein nature; each is about 2–2.5 nm thick. Beneath these is a thin membrane which separates the spore coat from an area of low electron density called the cortex. The cortex is primarily a modified peptidoglycan structure. It occupies approximately half the volume of the spore. A wall and a thin membrane separate the cortex from the cytoplasm of the dormant spore. The internal structures of the spore appear similar to those seen in the cytoplasm of vegetative cells, as shown in **Fig. 2**.

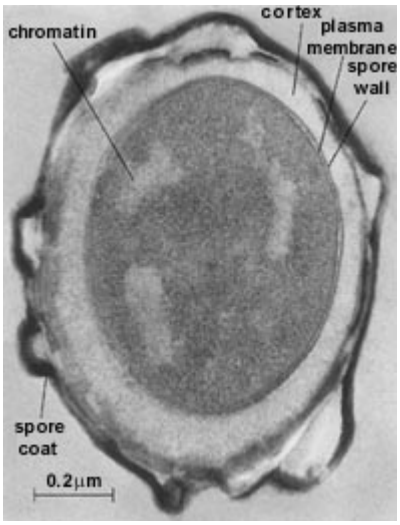

Fig. 2 Section of resting spore of *Bacillus megaterium*. (*Electron micrograph by C. F. Robinow*)

The unique properties of bacterial spores are their extreme resistance to heat, radiation from ultraviolet light and x-rays, organic solvents, chemicals, and desiccation. The most conspicuous chemical component is a chelating agent called dipicolinic acid (2,6-pyridine dicarboxylic acid), which constitutes 5–15% of the dry weight. This compound is absent from vegetative cells. Spores also differ from vegetative cells in containing higher levels of divalent metals and disulfide bonds and little, if any, free water.

Formation

The capacity of a bacterial cell to form a spore is under genetic control, although the total number of genes specific for sporulation is not known. The actual phenotypic expression of the spore genome depends upon a number of external factors. For each species of spore-forming bacteria, there exist optimum conditions for sporogenesis which differ from the optimal conditions for vegetative growth. These conditions include pH, degree of aeration, temperature, metals, and nutrients. Limitations in a variety of substances in the medium can initiate the process of sporulation. Sporulation is an ordered sequence of morphological and biochemical events leading to the formation of a mature spore. Commonly observed stages of sporulation are, in order of appearance, antibiotic release, cortex synthesis, increased light refractility, dipicolinic acid synthesis, formation of coats, resistance to octanol, resistance to heat, and release of the spore from the mother cell.

Sporulation is strongly influenced by the carbon and nitrogen sources available. Metabolizable nitrogen compounds generally repress sporulation. Glucose, in the presence of an available nitrogen source, effectively represses the initiation of spore formation; in general, carbon and nitrogen sources which are rapidly metabolized favor vegetative growth, whereas carbon and nitrogen sources which are more slowly metabolized stimulate spore formation.

Breaking of dormancy

The three processes involved in the conversion of the spore into a vegetative cell are (1) activation (usually by heat or aging), which conditions the spore to germinate in a suitable environment; (2) germination, an irreversible process which results in the loss of the typical characteristics of a dormant spore; and (3) outgrowth, in which new classes of proteins and structures are synthesized so that the spore is converted into a new vegetative cell.

Germination

Germination is an irreversible process in which a number of simultaneous events take place, shortly after the exposure of activated spores to specific stimulants (amino acids, sugars, and nucleotides). Germination is accompanied by a swelling of the spore, either rupture or absorption of the spore coat, and loss of a number of typical properties of the spore. Among these last-mentioned events are a loss of resistance to environmental stress, a loss of refractility, an increase in permeability, a release of spore components (dipicolinic acid, calcium, spore peptides), and an increase in metabolic activity. As a whole, the process is degradative and probably involves a number of enzymes.

Outgrowth

Germination is followed by a period of biosynthetic activity called outgrowth. The endospore coat breaks, and the cortex disappears (degraded by hydrolytic enzymes). A new cell emerges from the spore coat and eventually matures into a vegetative form, as shown in **Fig. 3**. During this period, new proteins and structures characteristic of vegetative cells are synthesized. Outgrowth terminates at the time of cell division and return to vegetative growth. The conditions for outgrowth are usually different from those supporting germination. Germination and outgrowth have different optimum temperatures, and most spores need nutrients for outgrowth that are not required for germination.

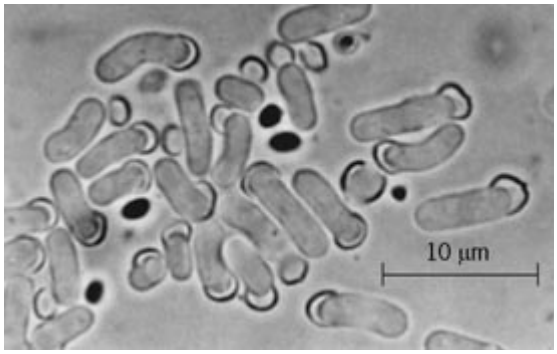

Fig. 3 Germination of spores of *Bacillus megaterium*. (*Photomicrography by F. C. Fitz-James*)

Microcycle sporulation

Spores may be germinated under nutrient-limited conditions. When faced with insufficient nutrients for proliferation, the new vegetative cell does not divide but instead enters the sporulation process, a shortcut leading to the formation of a mature spore.

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Appendages

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

Flagella

A bacterial flagellum has three parts, a long helical filament (about 0.01 micrometer in diameter), a short proximal hook (about 0.05 µm long), and a basal body, composed of a rod and a set of rings (about 0.02 µm in diameter) embedded in the cell wall and cytoplasmic membrane. The filament is a polymer or crystal composed of several thousand subunits per turn. Its shape can be changed by altering the structure of the subunit (the protein flagellin), the pH, ionic strength, temperature, or dynamic load. It dissolves in acids or in

bases or when heated. Cultured in a solution containing pure monomeric flagellin, the filament grows in one direction at a constant rate. When attached to the living cell, it grows at the free end at a rate that decreases exponentially with length. Evidently, monomeric flagellin passes through the center of the filament and crystallizes on it at the distal end. The proximal hook is made up of a second protein, and the basal body is built up of another dozen or so different proteins. In a gram-positive bacterium, the basal body has two rings, an M ring embedded in the cytoplasmic membrane and an S ring found just outside this membrane. Common gram-negative bacteria have two additional rings, thought to serve as a bushing that carries the rod through the outer membrane. The M ring appears to be the rotor, the S ring the stator, the rod the drive shaft, the proximal hook a flexible coupling, and the filament a propeller.

Howard C. Berg

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 “male” cell of strains capable of conjugation produces a sex pilus that enables it to attach to an appropriate “female” 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.

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 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 4** shows an unnamed aquatic bacterium that forms rosettes (the rosette shown has 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.

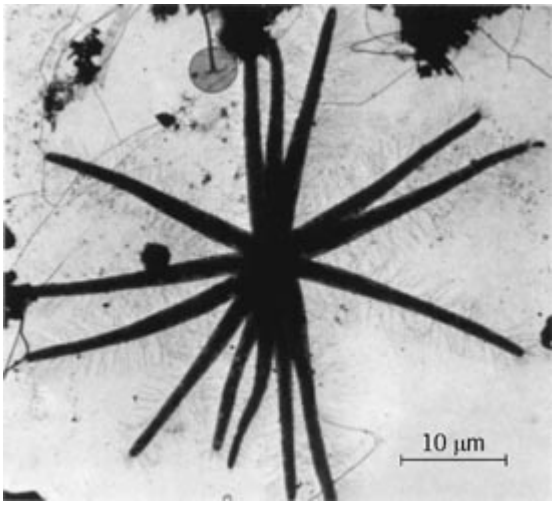

Fig. 4 Electron micrograph of a rosette-forming bacterium found in ponds and lakes.

Acellular stalks

Flagella and pili are too fine to be observed using ordinary light microscope 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. 5**. 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.

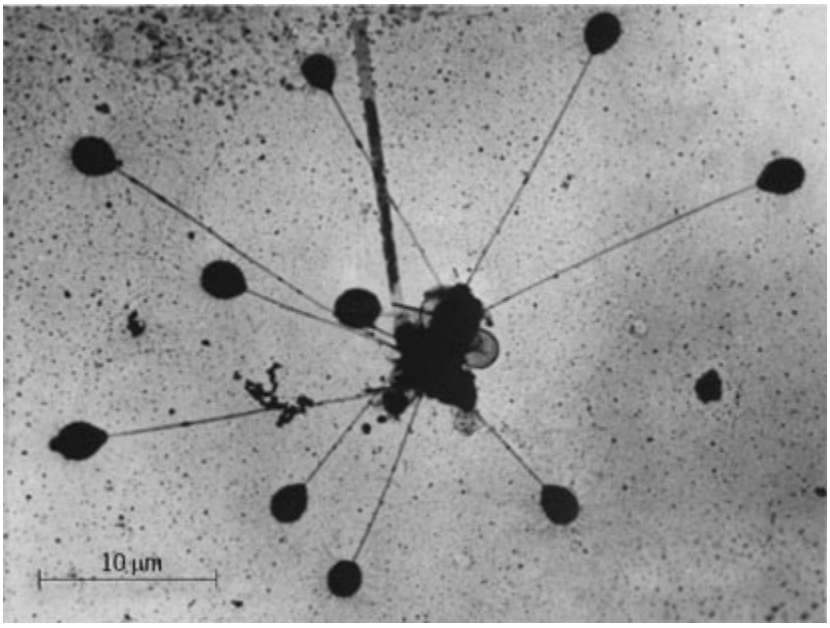

Fig. 5 Electron micrograph of a rosette of a budding bacterium of the *Blastocaulis-Planctomyces* group; note small bud on cell at lower left. Pili can be seen emanating from each cell.

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.

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 organisms, prosthecae enable them to take up nutrients more quickly in the dilute environments in which they reside.

To provide some insight into the nature of these bacteria, the life cycles of several of those most thoroughly studied are described below.

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. 6**). *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.

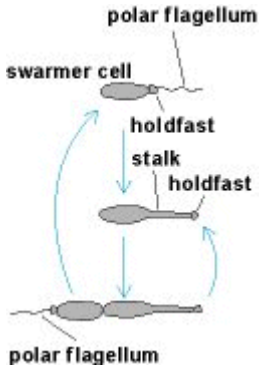

Fig. 6 Life cycle of *Caulobacter* species.

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. 7**). 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.

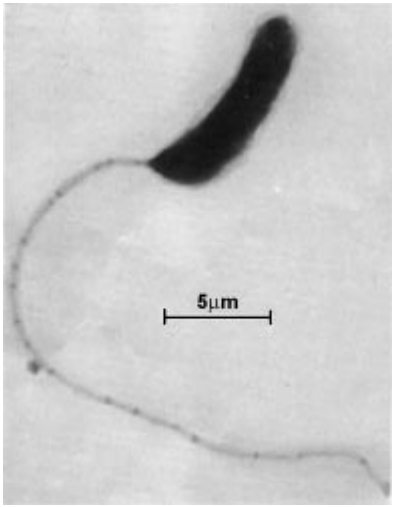

Fig. 7 Electron micrograph of a *Caulobacter* cell showing numerous crossbands on the prostheca; each crossband was formed when a daughter cell was produced.

Hyphomicrobium

The genus *Hyphomicrobium* is distinctive because of its prosthecae and because of its division by budding. Like *Caulobacter*, it undergoes, for a bacterium, a rather complex life cycle including flagellated, nonprosthecate cells and prosthecate, nonmotile cells (**Fig. 8**). 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. Therefore, the life cycle of this bacterium is more complex than that of *Caulobacter*.

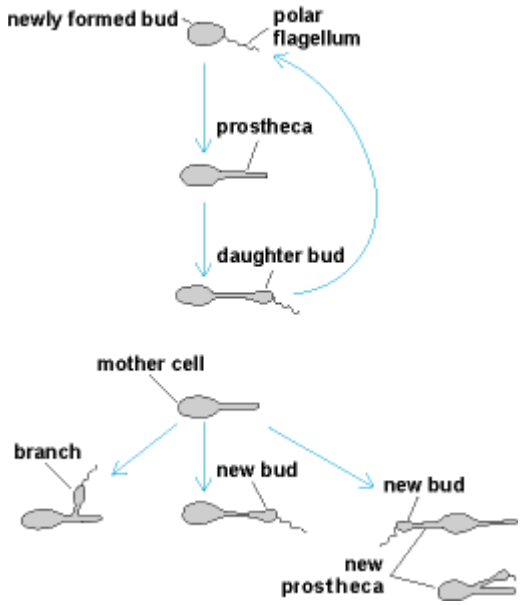

Fig. 8 Life cycle of *Hyphomicrobium* species.

Prosthecomicrobium

Bacteria in the genus *Prosthecomicrobium* have approximately 20 conical 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. 9**). 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 more. 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*.

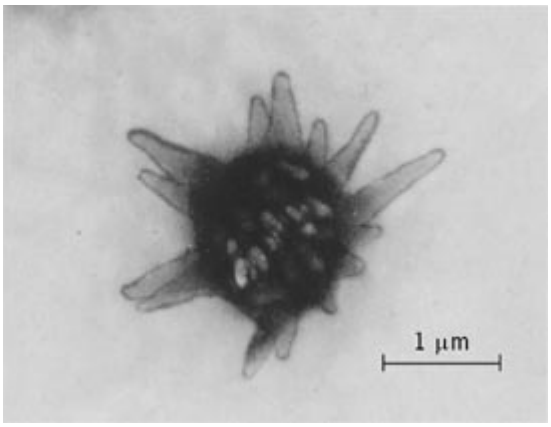

Fig. 9 Electron micrograph of *Prosthecomicrobium pneumaticum*. Note the 14 prosthecae extending from the cell, and the transparent gas vesicles inside the cell.

Ancalomicrobium

Like *Prosthecomicrobium* cells, cells of the genus *Anacalomicrobium* have several prosthecae per cell, although the number rarely exceeds eight (**Fig. 10**). This nonmotile bacterium produces an outgrowth from one position on the cell surface. This outgrowth, or bud, differentiates to form 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.

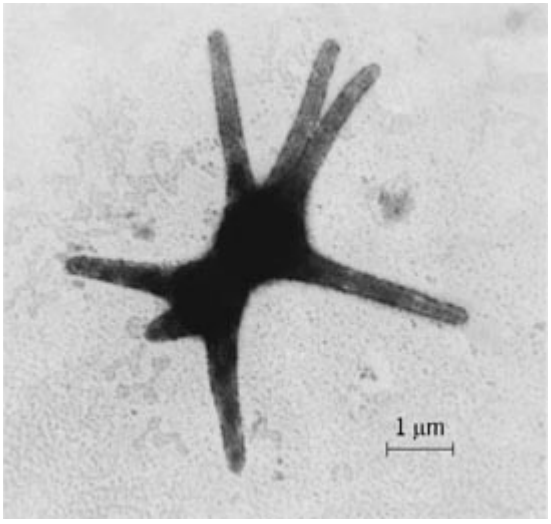

Fig. 10 Electron micrograph of *Ancalomicrobium adetum*. The cell has seven prosthecae.

James T. Staley

Motility

Motile bacteria swim or glide. Common gram-positive and gram-negative organisms swim by rotating flagellar filaments that project from the surface of the cell and extend several micrometers into the surrounding medium. Spirochetes, another group of gram-negative organisms, swim by rotating filaments that run between the protoplasmic cylinder and the outer membrane. Gliding bacteria, a third major group of gram-negative organisms, do not swim or have flagella but creep when in contact with solid surfaces.

Flagellar motion

Each flagellum is driven at its base by a reversible rotary motor; the filament rotates rigidly clockwise or counterclockwise; it does not wave or beat. To demonstrate this, a cell can be fixed to a glass slide by one of its flagellar filaments: the cell body spins alternately clockwise and counterclockwise. Mutants exist that spin in only one direction. Their motion has been followed for millions of revolutions; therefore, a bacterial flagellum does not wind up and unwind—it truly rotates. The flagella are not powered by the high-energy phosphate compounds that drive muscles, but rather by a proton flux. The passage of about a thousand protons from the outside to the inside of the cell carries the motor through one revolution. When connected to the proximal hook, the motor spins about 100 revolutions per second; when also connected to the filament, it spins about half as fast. When loads are light, the motor appears to run at constant speed; when loads are heavy, it runs at constant torque.

The style of locomotion of a bacterium depends on the size and shape of its body and its mode of flagellation. A rod-shaped cell with one or more flagella at either pole (monotrichous or lophotrichous flagellation, either monopolar or bipolar) swims forward or backward in the direction of its long axis. The body rotates (rolls) in a direction opposite to the direction of rotation of the flagella. Thrust generated by the flagellar filaments is balanced by viscous drag due to translation of the cell body, and torque generated by the filaments is balanced by viscous drag due to the roll.

If the cell body is corkscrew-shaped (as in *Spirillum*), the roll also contributes to the thrust. This is the primary mechanism for locomotion in most spirochetes (for example, the genus *Spirochaeta*), which are long thin helical organisms with loosely attached outer membranes. The rotation of the filaments underneath this membrane is thought to cause the surface of the cell to move circumferentially. Viscous drag, in turn, causes the cell body to roll about its long axis, and the cell screws its way through the medium. This mode of locomotion is particularly effective in gel-like media. *Leptospira*, having a more tightly fitting outer membrane, generates torque by gyrating its ends—the anterior end in a spiral configuration, the posterior end in a hook configuration; additional thrust is gained from propagation of the anterior spiral wave.

Rod-shaped cells with flagella arising at random points on their sides (peritrichous flagellation) swim as in a random walk. When their flagella spin counterclockwise, they coalesce into a synchronous bundle that pushes the cell steadily forward: the cell is said to run. When the flagella spin clockwise, the bundle flies apart, and the flagella turn independently, moving the cell this way and that in a highly erratic manner: the cell is said to tumble. These modes alternate, and the cell executes a three-dimensional random walk. A variety of species swim in this way, including *Bacillus subtilis*, *Salmonella typhimurium*, and *Escherichia coli*.

Taxis

Bacteria change the direction in which they swim in response to changes in their environment: they accumulate in regions that they find favorable. Different cells respond to light, heat, oxygen, and a variety of chemicals; and are said to be phototactic, thermotactic, aerotactic, and chemotactic, respectively. Cells of *E. coli*, for example, swim into capillary tubes filled with dilute solutions of simple sugars and amino acids. They do this by biasing their random walk. Runs that happen to carry a cell up the gradient are extended, while those that happen to carry it down the gradient are not. The cells monitor concentrations as a function of time; they compare the occupancy of specific receptors over the past second or so with the occupancy a few seconds before that. The memory required for this comparison involves receptor carboxymethylation. If current receptor occupancy exceeds past occupancy, as indicated by a relatively low level of methylation, the probability that the flagella spin counterclockwise increases and the probability that they spin clockwise decreases.

Gliding

Cells of some gliding bacteria, for example, *Myxococcus*, aggregate to form fruiting bodies. This behavior requires intracellular communication; the way in which one cell glides depends on its contacts with other cells. *Myxococcus* glides very slowly, about 2 μm per minute; other gliding bacteria, for example, *Cytophaga*, glide more rapidly, up to 2 μm per second. The organelles of locomotion for these bacteria have not been identified.

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