II. PENGGOLONGAN MIKROBA

Taksonomi Mikroba

Ringkasan

Mikroba sangat beragam dalam hal ukuran, bentuk, fisiologi, dan cara hidup. Pokok bahasan ini akan mengenalkan prinsip-prinsip umum dan menyajikan ringkasan skema klasifikasi terbaru. Pada bahasan berikutnya, berbagai kelompok mikroba akan dijelaskan lebih rinci.

Kompetensi

Setelah membaca pokok bahasan ini Saudara diharapkan dapat:

1. menjelaskan logika dibalik ilmu taksonomi
2. menjelaskan tiga domain organisme (Bacteria, Archaea, and Eucarya)
3. menjelaskan arti kata spesies dan dasar penggolongan organisme ke dalam spesies
4. menjelaskan cara organisme digolongkan
5. menjelaskan beragam karakteristik yang digunakan dalam taksonomi dan menerangkan mengapa asam nukleat mungkin indikator filogeni dan keterkaitan mikroba
6. menjelaskan skema klasifikasi yang digunakan dalam *Bergey's Manual of Systematic Bacteriology*
7. menjelaskan sifat dinamis taksonomi bakteri dan tipe data baru yang mendukung perubahan pengklasifikasian organisme

Konsep-konsep penting yang dipelajari dalam pokok bahasan ini meliputi:

1. Agar supaya dapat memahami keragam organisme, perlu untuk mengelompokan organisme yang sama dan mengorganisasikan kelompok ini dalam penataan hirarki tanpa tumpang tindih. Taksonomi adalah ilmu yang mengkaji klasifikasi biologis.
2. Kelompok prokariotik (archaeobacteria dan eubacteria) muncul pertama kali, kemudian kelompok eukarot.; organisme tersebut dikelompokkan dalam dalam tiga domain: Eubacteria (Bacteria), Archaea, and Eucarya. Ketiga domain ini berbeda satu sama lain dalam urutan rRNA dan banyak karakter yang lain.
3. Kelompok taksonomik dasar adalah spesies, yang ditentukan baik dalam hal reproduksi seksual maupun kemiripan umum..
4. Klasifikasi didasarkan atas analisis huhungan evolusi (klasifikasi filogenetik atau filetik) atau kemiripan (klasifikasi fenetik). Hasil analisis ini seringkali diringkas dalam diagram mirip pohon yang disebut dendogram.
5. Karakteristik fisiologis, metabolik, ekologis, genetik, dan molekuler secara keseluruhan berguna dalam taksonomi karena semua mencerminkan organisasi dan aktivitas genom..Urutam asam nukleat diduga merupakan indikator filogeni dan hubungan mikroba terbaik.
6. Bergey’s Manual of Systematic Bacteriology edisi pertama adalah fenotipik dan membagi bakteria berdasarkan atas karakter yang mudah ditentukan seperti bentuk, sifat pewarnaan Gram, hubungan oksigen, dan motilitas. Edisi keduanya, dengan lima volume dan 30 seksinya, diorganisasikan secara filogenetik dan membagi prokariot ke dalam dua domain dan sekurang-kurangnya 14 kingdom.

7. Taksonomi bakteri berubah sangat cepat sejak masuknya data baru, khususnya data yang diperoleh menggunakan teknik molekuler seperti komparasi struktur RNA ribosomal dan urutan kromosom. Hal ini akan mengarah ke klasifikasi fiogenetik baru..

Garis Besar Pokok Bahasan

I. Pendahuluan Umum dan Ringkasan
   A. Taksonomi adalah ilmu klasifikasi biologis
      1. Klasifikasi adalah penataan organisme ke dalam kelompok-kelompok (taksa)
      2. Nomenklatur adalah pemberian nama untuk kelompok-kelompok taksonomi
      3. Identifikasi adalah penentuan isolat tertentu pada takson tertentu
   B. Peranan taksonomi mikroba
      1. Memungkinkan ilmuwan mengorganisasikan sejumlah besar pengetahuaannya
      2. Memungkinkan ilmuwan membuat prediksi dan kerangka hipotesis tentang organisme
      3. Menempatkan organisme dalam kelompok-kelompok bermakna dengan memberi nama secara tepat, jadi akan mempermudah komunikasi ilmiah.
      4. Penting untuk identifikasi mikroorganisme secara tepat.
   C. Sistematik adalah kajian ilmiah organisme dengan tujuan akhir untuk mengkarakterisasi dan menempatkan organisme dengan cara yang teratur
   D. Taksonomi mikroba saat ini sedang memasuki perode perubahan besar yang disebabkan oleh penggunaan teknik molekuler

II. Evolusi dan Keragaman Mikroba
   A. Bumi berumur kira-kira 4,6 milyar tahun dan sisa-sisa fosil sel prokariotik berumur 3,5-3,8 milyar tahun terdapat dalam stromatolit dan batuan sedimen.
      1. Stromatolit adalah batuan berlapis yang dibentuk dari penggabungan sedimen mineral menjadi hamparan mikroba (*microbial mats*)
      2. Prokariot pertama mungkin bersifat anaerob.
      3. Sianobakteri aerobik mungkin muncul 2,5-3,0 milyar tahun yang lalu.
   B. Hasil penelitan Carl Woese dan kawan-kawan menyarankan bahwa organisme dibagi dalam tiga domain:
      1. Eukaria-meliputi seluruh organisme eukariotik
      2. Bakteria-terdiri dari organisme prokariotik yang mempunyai rRNA bakterial and lipid membran terutama berupa diasil gliserol eter.
      3. Archaea-terdiri dari organisme prokariotik yang mempunyai rRNA archaeal dan lipid membran terutama berupada isoprenoid gliseral dieter atau turunan diglesrol tetraeter.
   C. Sel eukariotik modern yang muncul kurang lebih 1,4 milyar tahun yang lalu berasal dari prokariot.
      1. Hipotesis I: perkembangan kloroplast dan mitokondria merupakan pelipatan (invaginasi) membran plasma dan kemudian membentuk ruang- ruang (compartmentalization) dengan fungsi tertentu.
      2. Hipotesis II (hipotesis endosimbiotik) menyarankan sebagai berikut:

a. Proses pertama pembentukan sel eukariot adalah pembentuk nukleus (mungkin fusi bakteri dan archaea purba)
b. Kloroplast dibentuk ketika bakteri fotosintetik yang hidup bebas bersimbiosis dengan sel eukariotik primitif (sianobakteria dan proklron disarankan sebagai kandidat yang paling kuat).
c. Mitokondria mungkin terbentuk melalui proses yang sama (tetua Agrobacterium, Rhizobium, dan riketsia menjadi kandidatnya)

3. Hopotesis endosimbiotik mendapat dukungan kuat dari penemuan sianobakterium yang berendosimbiotik dengan protista biflagelata (Cyanophora paradoxa); sianobakterium berfungsi sebagai chloroplast Cyanophora paradoxa; endosimbiotik ini kernal sebagai sianel (*cyanelle*)

III. Tingkatan Taksonomi (*Taxonomic Ranks*)

A. Tingkatan taksonomi (dari bawah ke atas) adalah: spesies, genus, famili, ordo, klas, dan kerajaan (kingdom); Namun, ahli mikrobiologi seringkali menggunakan nama seksi (suatu pengelompokan yang kurang formal) yang bersifat deskriptif untuk kelompok-kelompok organisme tertentu, seperti metanogen, *purple bacteria*, bakteri asam laktat, dan lain-lain.

B. Kelompok taksonomi dasar adalah **spesies**

1. Spesies prokariotik tidak didefinikan atas dasar kecocokan (*compatibility*) reproduktif seksual (sebagaimana pada organisme tingkat tinggi) tetapi didasarkan atas perbedaan fenotipik dan genotipik; spesien prokariotik adalah koleksi galur (*strain*) yang mempunyai banyak kesamaan sifat yang stabil dan berbeda secara nyata dengan sekurang-kurang beberapa kelompok galur lain.
2. Galur adalah populasi organisme yang dapat dibedakan dari sekurang-kurang beberapa pupulasi lain dalam suatu kategori taksonomik, galur dianggap berasal dari organisme tunggal atau isolat kultur tunggal.
   a. Biovar – berbeda secara biokimiawi atau fisiologis
   b. Morfovar – berbeda secara morfologi
   c. Serovar – berbeda sifat antigenik
3. Galur tipe (*Type strain*) adalah galur suatu spesies yang dikaji pertama kali (yang paling rinci dikarakterisasi), galur ini tidak harus anggota yang paling mewakili.
4. Genus adalah kelompok spesies (satu atau lebih) yang telah ditentukan dengan sangat baik yang secara jelas terpisah (berbeda) dari genera lain.

C. Dalam sistem nomenklatur binomial yang diajukan oleh Carl von Linne (Carolus Linnaeus), huruf pertama nama genus ditulis dengan huruf besar dan epitet spesifik ditulis dengan huruf kecil pada huruf pertamanya (e.g., *Escherichia coli*); dalam artikel ilmiah, huruf pertama genus dapat disingkat penulisan penulisan setelah digunakan setelah ditulis lengkap pada penulisan sebelumnya. (contoh, *E. coli*).

IV. Sistem Klasifikasi

A. Klasifikasi Alami (*Natural classification*) – penataan organisme ke dalam kelompok-kelompok yang anggota-anggotanya mempnyai banyak kesamaan sifat dan mencerminkan sebanyak mungkin sifat biologis organsme.

B. Sistem (Phenetic systems) adalah mengelompokkan organisme didasarkan atas kesamaan secara keseluruhan:
   1. Seringkali berupa suatu sistem alami yang didasarkan atas kesamaan karakter.
   2. Tidak tergantung pada analisis filogenetik
   3. Menggunakan "*unweighted traits*"
   4. Sistem terbaik jika membandingkan sebanyak mungkin sifat (attributes).

C. Taksomi Numerik (*Numerical taxonomy*):
   1. Informasi sifat suatu organisme dikonversikan ke bentuk yang sesuai untuk analisis numerk dan dibandingkan menggunakan komputer
   2. Ada atau tidaknya sekuran-kurangnya 50 (sebaiknya beberapa ratus) karakater dibandingkan; karakter tersebut di antaranya karakter morfologi, biokimiawi, dan fisiologi)
   3. Koefisien asosiasi ditentukan di antara karakter-karakter yang dimiliki oleh dua organisme
      a. Koefisien kesesuaian sederhana (*Simple matching coefficient*) – proporsi yang sesuai (match) baik untuk karakter yang ada maupun tidak ada.
      b. Koefisien Jaccard (*Jaccard coefficient*) – mengabaikan karakter-karakter yang tidak ada pada kedua organisme
      c. Nilai-nilai tersebut diatur untuk membentuk matriks kesamaan (*similarity matrix*); organisme dengan kesamaan tinggi dikelompokkan bersama dalam fenon (phenons)
      d. Perbedaan (*significance*) fenon tidak selalu jelas terlihat tetapi fenon dengan kesamaan 80% seringkali dianggap satu spesies (bakteri).
   4. Menggunakan *unweighted traits*
   5. Sistem terbaik jika membandingkan sebanyak mungkin karakter (*attributes*)

A. Sistem filogeneti (filetik) {Phylogenetic (phyletic)-pengelompokan organisme didasarkan pada hubungan evolusioner
   1. Untuk prokariot adalah sulit untuk mengetahui hubungan evolusi karena kekurangan catatan fosil yang baik.
   2. Pembandingan langsung materi genetik dan produk gen seperti rRNA dan protein dapat digunakan untuk mengatasi kesulitan tersebut di atas.

I. Karakter utama yang digunakan dalam taksonomi
   A. Karakter klasik (*Classical characteristics*)
      1. Karakter morfolofi (*Morphological characteristics*)- mudah untuk dianalisis, stabil secara genetis, variasi tidak besar terhadap perubahan lingkungan; seringkali menjadi indikasi yang baik untuk hubungan filogenetik.
      2. Karakter fisiologis dan metabolik (*Physiological and metabolic characteristics*)- berkaitan langsung dengan enzim dan protein transport (produk gen) dan oleh karenanya secara tidak langsung menunjukkan perbandingan genom mikroba.

3. Karakter ekologi (*Ecological characteristics*) – meliputi pola siklus hidup, hubungan simbiotik, patogenitas, preferensi habitat, dan kebutuhan pertumbuhan.
4. Analisis genetik (*Genetic analysis*) – meliputi kajian pertukaran gen kromosomal melalui konjugasi dan transformasi; proses ini jarang terjadi antar genera; harus hati-hati untuk mengindari kesalahan yang disebabkan adanya karakter dari plasmid.

B. Karakter Molekuler (*Molecular characteristics*)
1. Pembandingan protein (*Comparison of proteins*)-berguna sebab merefleksikan informasi genetik organisme, analisisnya melalui:
    a. Penentuan urutan asam amino protein
    b. Perbandingan mobilitas elektroforesis
    c. Penentuan reaktivitas silang imunologis (*immunological cross-reactivity*)
    d. Perbandingan sifat enzimatis
2. Komposisi basa asam nukleat
    a. Kandungan G+C dapat ditentukan atas dasar suhu leleh (Tm) – suhu (panas) yang mengakibatkan untai ganda molekul DNA memisah)
    b. Secara taksomi berguna karena variasi dalam genus biasanya kurang dari 10% tetapi variasi di antara genera jauh lebih besar, berkisar 25-80%
3. Hibridisasi asam nukleat (Nucleic acid hybridization)
    a. Menentukan tingkat homologi urutan
    b. Suhu inkubasi mempengaruhi tingkat homologi urutan yang diperlukan untuk membentuk hibrid stabil
4. Penentuan urutan asam nukleat (Nucleic acid sequencing)
    a. Gen rRNA adalah paling ideal untuk perbandingan sebab urutan basa gennya mengandung urutan yang stabil secara evolusioner (lestari) dan urutan bervariasi
    b. Sekarang ini, genom prokariotik lengkap telah ditentukan; perbandingan langsung urutan genom lengkap akan menjadi sangat penting dapam taksonomi prokariotik

II. Penilaian filogeni mikroba (*Assessing Microbial Phylogeny*)

A. Kronometer molekuler (Molecular chronometers)- asumsi bahwa laju perubahan adalah konstan merupakan asumsi yang tidak tepat; mungkin asumsi yang tepat, laju perubahan gen tertentu adalah konstan

B. Pohon filogenetik (*Phylogenetic trees*)
1. membuat percabangan yang menghubungkan titik (nodes), yang merupakn unit taksonomi, seperti spesies atau gen; akar pohon merupakan titik yang bertindak sebagai tetua (nenek moyang) untuk seluruh organisme yang sedang dianalisis.
2. dibuat dengan membandingkan urutan molekuler dan perbedaan dinyatakan sebagai jarak evolusioner; kemudian organisme dikelompokkan untuk menentukan tingkat hubungan; atau tingkat hubungan dapat diduga dengan analisis parsimony yang mengasumsikan bahwa perubahan evolusioner organisme tertentu terjadi sepanjang jalur terpendek dengan perubahan paling sedikit terhadap tetuanya.

C. rRNA, DNA, dan protein sebagai indikator filogeni

1. Koefisien asosiasi (*Association coefficients*) dari kajian rRNA adalah suatu ukuran tingkat hubungan (relatedness)
2. Urutan penanda oligonukleotida (*Oligonucleotide signature sequences*) terdapat di sebagian besar atau seluruh anggota kelompok filogenetik tertentu dan jarang atau tidak pernah ada di dalam kelompok lain bahkan yang dekat sekali pun; berguna pada tingkat kingdom atau domain.
3. Kajian kesamaan DNA jauh lebih efektif pada tingkat genus dan spesies
4. Urutan protein kurang dipengaruhi oleh perbedaan kandung G+C pada organisme tertentu
5. Analisis tiga tipe molekult tidak selalu menghasilkan pohon evolusi yang sama.

D. Taksonomi polifasik (*Polyphasic taxonomy*)

1. Menggunakan kisaran luas informasi fenotipik dan genotipik untuk mengembangkan skema taksonomi
2. Teknik dan informasi yang digunakan tergantung pada tingkat resolusi taksonomi yang diinginkan (contoh, teknik serologis baik untuk mengidentifikasi galur, tetapi tidak baik untuk tingkat genera atau spesies.

III. Pengelompokan utama kehidupan (The Major Divisions of Life)

A. Domain

1. Woese dan kawan-kawan menggunakan kajian rRNA untuk mengelompokkan seluruh organisme ke dalam tiga domain.
   a. Bakteri – meliputi sebagian besar prokariot; dinding sel mengandung asam muramik; lipid membran mengandung asam lemak rantai lurus yang diikatkan oleh ikatan ESTER.
   b. Archaea – prokariot yang kekurangan asam muramik, mempunyai lipid yang mengandung rantai alifatik bercabang yang dihubungkan oleh ikatan ETER, kekurangan timidin pada tangan T molekul tRNA, mempunyai RNA polimerase jelas (distinctive), dan mempunyai ribosom dengan komposisi dan bentuk berbeda dengan yang terdapat di bakteri
   c. Eukaria – mempunyai yang struktur organ yang dilapisi oleh membran yang lebih kompleks.
2. Beberapa pohon filogenetik berbeda telah diusulkan yang menghubungkan domain utama; beberapa pohon yang diusulkan tidak medukung pola tiga domain.
3. Salah satu kesulitan dalam mengkonstruksi suatu pohon filogenetik adalah transfer gen horisontal yang sering terjadi secara luas; pohon yang lebih benar, mungkin menyerupai jejaring dengan banyak percabangan lateral yang menghubungan bermacam-macam anak cabang (*trunks*)

B. Kingdom

1. Sistem lima kingdom yang diusulkan oleh Whittaker, yang pada awal diterima secara luas, adalah:

a. **Hewan**-eukariot multiseluer dan tidak berdinding sel dan nutrisi *ingestive*.
b. **Tumbuhan**-eukariot multiseluler berdinding sel dan nutrisi fotoautotropik (*photoautotrophic nutrition*)
c. **Jamur** (Fungi)-eukariot multiseluler dan uniseluler berdinding sel dan nutrisi absorptif (*absorptive nutrition*)
d. **Protista**-eukariot uniseluler dengan bermacam-macam mekanisme nutrisi
e. **Monera** (Prokariot)-seluruh organisme prokariotik

2. Banyak ahli biologi tidak menerima sistem Whittaker system, terutama disebabkan sistem tersebut tidak membedakan bakteri dan archaea
3. Beberapa sistem alternatif telah disarankan, seperti sistem enam kingdom dan dua kerajaan (*empire*), delapan kingdom

IV. Bergey's Manual of Systematic Bacteriology

A. Bergey's Manual of Systematic Bacteriology edisi pertama- terutama adalah fenetik (phenetic)
1. Terdiri dari 33 seksi (sections) dalam empat volume
2. Masing-masing seksi terdiri dari bakteri yang mempunyai kesamaan karakter yang secara mudah dapat ditentukan (contoh, morfologi, reaksi gram, hubungan oksigen) dan memuat judul yang menggambarkan sifat-sifat atau memberikan nama daerah bakteri

B. Bergey's Manual of Systematic Bacteriology edisi kedua
1. Lebih banyak filogenetik daripada fenetik
2. Terdiri dari lima volume

V. Survei filogenetik dan keragaman prokariot

A. **Volume 1** (of 2nd edition of Bergey's Manual): The Archaea, Genera bakteri fototropik dan dekat percabangan dengan archaea
1. **Archaea**-dibagi dua phyla
   a. **Crenarchaeota**- phylum yang beragam terdiri dari organisme termofilik dan hipertermofilik dan juga beberapa organisme yang tumbuh di laut pada suhu rendah sebagai picoplankton
   b. **Euryarchaeota**- terdiri dari terutama prokariot metanogenik dan halofilik dan uga prokariot termofilik, pereduksi sulfur
2. **Bakteri**
   a. **Aquificae** - phylum yang terdiri dari bakteri autotropik yang menggunakan hidrogen sebagai sumber energi; sebagian besar adalah bakteri termofilik
   b. **Thermatogae** - phylum yang terdiri dari bakteri gram negatip, fermentatif termofilik, anaerobik.; mempunyai asam lemak yang tidak umum
   c. **Deinococcus**-Thermus – phylum ini meliputi bakteri dengan resistensi luar biasa terhadap radiasi dan organisme termofilik
   d. **Chloroflexi** – phylum ini terdiri dari bakteri yang seringkali disebut bakteri nonsulfur hijau; beberapa melakukan fotosintesis anoksigenik (anoxygenic), sedangkan yang lain bakteri respiratori dan bergerak secara *gliding*; mempunyai peptidoglikan yang tidak biasa dan tidak mempunyai liposakarida dalam membran luarnya
   e. **Cyanobacteria**-phylum yang terdiri dari bakteri fotosintetik oksigenik
   f. **Chlorobi**- phylum ini terdiri dari bakteri fotosintetik anoksigenik yang dikenal sebagai bakteri sulfur hijau

B. **Volume 2**: **Proteobacteria** – hanya satu phylum disebut Proteobacteria, yang terdiri dari banyak ragam bakteri gram negatip.

C. **Volume 3**: **Bakteri gram positip dengan kandung G+C rendah** – hanya satu philum disebut **Firmicutes**; seluruhnya mempunyai kandungan G+C 50%; kecuali mycoplasma, yang tidak mempunyai dinding sel, seluruhnya adalah gram positip; meliputi genera yang menghasilkan endospora

D. **Volume 4**: **Bakteri gram positip dengan kandungan G+C tinggi** – mencakup phylum Actinobacteria; mempunyai kandungan G+C 50-55%; meliputi bakteri filamentous (actinomycetes) and bakteri dengan dinding sel yang tidak biasa (mycobacteria)

E. **Volume 5**: **Planctomycetes, Spriocheates, Fibrobacteres, Bacteroidetes, dan Fusobacteria**- campuran dari berbagai jenis kelompok filogenetik dengan percabangan dekat yang tidak harus berhubungan satu sama lain walaupun seluruhnya gram negatip.

   1. **Planctomycetes** - phylum terdiri dari bakteri dengan sifat tidak biasa, termasuk dinding sel yang tidak mempunyai peptidoglika dan sel dengan nukleoid yang diselimuti membran; membelah dengan bertunas dan membentuk tonjolan (appendages) yang disebut ***stalks***
   2. **Chlamydiae** - phylum terdiri dari patogen intraseluler obligat yang mempunyai siklus hidup unik; patogen ini tidak mempunyai peptidoglikan.
   3. **Spirochaetes**- phylum terdiri dari bakteri berbentuk heliks dengan morfologi dan motilitas unik
   4. **Bacteroides**- phylum yang terdiri dari sejumlah bakteri penting secara ekologis.

Situs Internet yang berkaitan

The Tree of Life
(http://phylogeny.arizona.edu/tree/phylogeny.html)
The Tree of Life is a multi-authored, Internet project containing information about the diversity of organisms on Earth, their history, and characteristics. The information is linked together in the form of the evolutionary tree that connects all organisms to each other.

Bergey's Manual of Determinative Bacteriology
(http://server.mph.msu.edu/bergeys/)

ARCHAEA

Chapter Overview

This chapter summarizes the properties of a diverse group of organisms known as the archaea. These organisms are very different from the eubacteria and from the eicaryotes. The chapter describes some of the major characteristics associates with each of the major groups of archaea.

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the morphological and physiological diversity of the archaea
2. discuss the difference between the cell walls of archaea and those of bacteria
3. describe the lipid composition of archaeal cell membranes
4. discuss the general genetic, molecular, and metabolic characteristics of the archaea
5. discuss the habitats that are typical for the archaea
6. discuss the classification scheme for the archaea that will be used in the 2nd edition of Bergey's Manual
7. discuss the unique cofactors used by methanogenic and sulfate-reducing archaea
8. describe the structural, chemical, and metabolic adaptations that allow the archaea to grow in extreme environments

These are the most important concepts you are learning in this chapter:

1. Archaea differ in many ways from both eubacteria and eucaryotes. These include differences in cell wall structure and chemistry, membrane lipid structure, molecular biology, and metabolism.
2. Archaea usually grow in a few restricted or specialized habitats: anaerobic, hypersaline, and high temperature.
3. Bergey's Manual currently divides the archaeobacteria into five major groups: methanogenic archaeobacteria, sulfate reducers, extreme halophiles, cell wall–less archaeobacteria, and extremely thermophilic S0-metabolizers.
4. The next edition of Bergey's Manual will divide the archaeobacteria into two kingdoms, the Crenarchaeota and Euryarchaeota, each with several orders.
5. Methanogenic and sulfate-reducing archaeobacteria have unique cofactors that participate in methanogenesis.
6. Archaea have special structural, chemical, and metabolic adaptations that enable them to grow in extreme environments.

Study Outline

I. Introduction to the Archaea
    A. The archaea are quite diverse, both in morphology and physiology
        1. They may stain gram positive or gram negative
        2. They may be spherical, rod-shaped, spiral, lobed, plate-shaped, irregularly shaped or pleomorphic
        3. They may exist as single cells, aggregates or filaments
        4. They may multiply by binary fission, budding, fragmentation, or other mechanisms
        5. They may be aerobic, facultatively anaerobic, or strictly anaerobic
        6. Nutritionally, they range from chemilithoautotrophs to organotrophs
        7. Some are mesophiles, while others are hyperthermophiles that can grow above 100°C
        8. They are often found in extreme aquatic and terrestrial habitats; recently, archaea have been found in cold environments and may constitute up to 34% of the procaryotic biomass in Antarctic surface waters; a few are symbionts in animal digestive systems
    B. Archaeal cell walls

1. Archaea can stain either gram positive or gram negative, but their cell wall structure differs significantly from that of bacteria
    a. Many archaea that stain gram positive have a cell wall made of a single homogeneous layer
    b. The archaea that stain gram negative lack the outer membrane and complex peptidoglycan network associated with gram-negative bacteria
2. Archaeal cell wall chemistry is different from that of bacteria
    a. Lacks muramic acid and D-amino acids and therefore is resistant to lysozyme and b-lactam antibiotics
    b. Some have pseudomurein, a peptidoglycan-like polymer that has L-amino acids in its cross-links and different monosaccharide subunits and linkage
    c. Others have different polysaccharides
3. The archaea that stain gram negative have a layer of protein or glycoprotein outside their plasma membrane

C. Archaeal lipids and membranes
1. Lipids have branched hydrocarbons attached to glycerol by ether links rather than straight-chain fatty acids attached to glycerol by ester links as seen in Bacteria and Eucarya
2. Other, more complex tetraether structures are also found
3. Membranes contain polar lipids such as phospholipids, sulfolipids, and glycolipids and also contain nonpolar lipids (7-30%), which are usually derivatives of squalene
4. Membranes of extreme thermophiles are almost completely tetraether monolayers

D. Genetics and molecular biology
1. The archaeal chromosomes that have been studied consist of a single, closed DNA circle like those of bacteria, except that some are considerably smaller; Archaea have few plasmids; genomic analysis suggests are as distinctive genotypically as they are in other respects
2. Archaeal mRNA is like that of bacteria (i.e., it may be polygenic, there is no evidence of intron-containing precursors, and its promoters are similar to those of bacteria)
3. There are many other differences between archaea and other organisms, including:
    a. The observation of modified bases in archaeal tRNA molecules that are not found in bacterial tRNA molecules
    b. Ribosomes with different morphological and physiological properties than bacterial and eucaryotic ribosomes
    c. Archaeal RNA polymerase enzymes that are more similar to eucaryotic enzymes than to bacterial enzymes

E. Metabolism
1. Carbohydrate metabolism is best understood
    a. Archaea do not use the Embden-Meyerhof pathway for glucose catabolism; however they frequently use a reversal of that pathway for gluconeogenesis
    b. Some (halophiles and extreme thermophiles) have a complete TCA cycle while others (methanogens) do not
2. Archaeal biosynthetic pathways appear to be similar to those of other organisms
3. Autotrophy is widespread; reductive TCA cycle and reductive Acetyl-CoA cycle are used for carbon fixation

F. Archaeal Taxonomy-the new edition of Bergey's Manual will divide the archaea into two phyla: Euryarchaeota and Crenarchaeota

II. Phylum Crenarchaeota

A. Many are extremely thermophilic, acidophilic, and sulfur-dependent
1. Sulfur may be used as an electron acceptor in anaerobic respiration, or as an electron source by lithotrophs
2. Almost all are strict anaerobes
3. They grow in geothermally heated water or soils (solfatara) that contain elemental sulfur (sulfur-rich hot springs, waters surrounding submarine volcanic activity); some (e.g., Pyrodictum spp.) can grow quite well above the boiling point of water (optimum @ 105oC)

4. Some are organotrophic; others are lithotrophic
5. There are 69 genera; two of the better-studied genera are Sulfolobus and Thermoproteus

B. Sulfolobus
   1. Stain gram negative; are aerobic, irregularly lobed, spherical bacteria
   2. Thermoacidophiles
   3. Cell walls lack peptidoglycan but contain lipoproteins and carbohydrates
   4. Oxidize sulfur to sulfuric acid; oxygen is the normal electron acceptor, but ferric iron can also be used
   5. Sugars and amino acids may serve as carbon and energy sources

C. Thermoproteus
   1. Long, thin, bent or branched rods
   2. Cell wall is composed of glycoprotein
   3. Strict anaerobes
   4. They have temperature optima from 70-97°C and pH optima from 2.5 to 6.5
   5. They grow in hot springs and other hot aquatic habitats that contain elemental sulfur
   6. They carry out anaerobic respiration using organic molecules as electron donors and elemental sulfur as the electron acceptor; they can also grow lithotrophically using H_2 and S0 as electron donors and CO or CO_2 as the sole carbon source

III. Phylum Euryarchaeota

A. The Methanogens
   1. Strict anaerobes that obtain energy by converting CO_2, H_2, formate, methanol, acetate, and other compounds to either methane or to methane and CO_2; there are at least five orders, which differ greatly in shape, 16S rRNA sequence, cell wall chemistry and structure, membrane lipids, and other features
   2. Methanogens belonging to the order Methanopyrales have been suggested to be among the earliest organisms to evolve on Earth
   3. Methanogenesis is an unusual metabolic process and methanogens contain several unique cofactors
   4. They thrive in anaerobic environments rich in organic matter, such as animal rumens and intestinal tracts, freshwater and marine sediments, swamps, marshes, hot springs, anaerobic sludge digesters, and even within anaerobic protozoa
   5. They are of great potential importance because methane is a clean-burning fuel and an excellent energy source
   6. They may be an ecological problem, however, because methane is a greenhouse gas that could contribute to global warming and also because methanogens can oxidize iron, which contributes significantly to the corrosion of iron pipes

B. The Halobacteria
   1. A group of extremely halophilic organisms divided into 15 genera
      a. They are aerobic chemoheterotrophs with respiratory metabolism; they require complex nutrients
      b. Motile or nonmotile by lophotrichous flagella
   2. They require at least 1.5 M NaCl and have growth optima near 3-4 M NaCl (if the NaCl concentration drops below 1.5 M the cell walls disintegrate; because of this they are found in high-salinity habitats and can cause spoilage of salted foods
   3. Halobacterium salinarum uses four different light-utilizing rhodopsin molecules
      a. Bacteriorhodopsin uses light energy to drive outward proton transport for ATP synthesis; thus they carry out a type of photosynthesis that does not involve chlorophyll
      b. Halorhodopsin uses light energy to transport chloride ions into the cell to maintain a 4-5 M intracellular KCl concentration
      c. Two other rhodopsins act as photoreceptors that control flagellar activity to position the bacterium in the water column at a location of high light intensity, but one in which the UV light is not sufficiently intense to be lethal

A. The Thermoplasms
   1. Thermoacidic organisms that lack cell walls; only two genera are know: Thermoplasma and Picrophilus
   2. Thermoplasma

a. Frequently found in coal mine refuse, in which chemolithotrophic bacteria oxidize iron pyrite to sulfuric acid and thereby produce a hot acidic environment
b. Optimum temperature for growth of 55-59°C and an optimal PH of 1 to 2
c. Cell membrane is strengthened by large quantities of diglycerol tetraethers, lipopolysaccharides, and glycoproteins
d. Histonelike proteins stabilize their DNA; DNA-protein complex forms particles resembling eucaryotic nucleosomes
e. At 59^oC Thermoplasma takes the form of an irregular filament; the cells may be flagellated and motile

3. Picrophilus
   a. Isolated from hot solfateric fields
   b. Has an S-layer outside the plasma membrane
   c. Irregularly shaped cocci with large cytoplasmic cavities that are not membrane bounded
   d. Aerobic and grows between 47°C and 65°C with an optimum of 60°C
   e. It grows only below pH 3.5, has an optimum of pH 0.7 and will even grow at or near pH 0

B. Extremely thermophilic S0 metabolizers
   1. Strictly anaerobic, reduce sulfur to sulfide
   2. Are motile by means of flagella
   3. Have optimum growth temperatures around 88-100°C

C. Sulfate-reducing archaea
   1. Gram-negative, irregular coccoid cells with walls of glycoprotein subunits
   2. Use a variety of electron donors (hydrogen, lactate, glucose) and reduce sulfite, sulfate, or thiosulfate to sulfide
   3. Are extremely thermophilic (optimum around 83°C); they are usually found near marine hydrothermal vents
   4. Contain two methanogen coenzymes

Chapter Web Links

Astrobiology Web
(http://www.astrobiology.com/extreme.html)
Life in Extreme Environments

Eukaryotes in extreme environments
(http://www.nhm.ac.uk/zoology/extreme.html)
Compiled by Dave Roberts, Department of Zoology, The Natural History Museum, London.

Archaea in Space
(http://www.accessexcellence.org/WN/SU/arch998.html)

BACTERIA

Chapter 21: Bacteria: The Deinococci and Nonproteobacteria Gram-Negatives

Chapter Overview

This chapter is devoted to nine of the more interesting and important eubacterial groups from volumes 1 and 5 of the 2nd edition of Bergey's Manual of Systematic Bacteriology. Though the organization and perspective of the 2nd edition is used, the description of each group in the current edition is summarized. Where appropriate the distinguishing characteristics, morphology, reproduction, physiology, metabolism, and ecology of each group is included. The taxonomy of each major group is summarized and representative species are mengetahuied.

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the deeply branching bacterial phyla Aquificae and Thermotogae
2. discuss the deinococci, focusing on their extraordinary resistance to desiccation and radiation
3. compare and contrast the phyla of photosynthetic bacteria
4. discuss the unique structural features of Planctomycetes
5. discuss the unique life style of the Chlamydiae
6. discuss the unique structural features and motility of the Spirochaetes
7. discuss the important metabolic and ecological characteristics of the Bacteroidetes
8. discuss gliding motility

These are the most important concepts you are learning in this chapter:

1. The first edition of Bergey's Manual takes a largely phenetic approach to classification and relates bacteria based on their overall similarity. The second edition will classify bacteria according to phylogenetic relationships with emphasis on 16S rRNA sequence comparisons.
2. Some eubacterial groups, such as those represented by the hyperthermophiles Aquifex and Thermotoga, are deeply branching and very old; other bacterial taxa have arisen more recently.
3. Because of its emphasis on phylogenetic relationships, the second edition of Bergey's Manual has substantially rearranged bacterial groups and taxonomic categories. For example, the second edition places the gram-positive deinococci in volume 1, which otherwise contains gram-negative bacteria. Bacteria such as the rickettsias and chlamydiae are separated into different sections despite their similar life-styles. The thermotogas and many other completely new groups have been added.
4. Although most of the photosynthetic bacteria are located in volume 1 of the second edition, the purple bacteria have been moved to the proteobacteria in volume 2. The cyanobacteria are separated from other photosynthetic bacteria because they resemble eucaryotic phototrophs in having photosystem II and carrying out oxygenic photosynthesis. Their rRNA sequences also indicate that they are different from other photosynthetic bacteria.
5. Bacteria such as the chlamydiae that are obligately intracellular parasites have relinquished some of their metabolic independence through loss of metabolic pathways. They use their host's energy supply and/or cell constituents.
6. Gliding motility is widely distributed among bacteria and is very useful to organisms that digest insoluble nutrients or move over the surfaces of moist, solid substrata.

Study Outline

1) Aquificae and Thermotogae
   a) Aquificae-thought to represent the deepest (oldest) branch of bacteria; two of its best studies genera are Aquifex and Hydrogenobacter
      i) Hyperthermophilic
      ii) Chemolithoautotrophic-generate energy by oxidizing electron donors such as hydrogen, thiosulfate, and sulfur with oxygen as the electron acceptor
   b) Thermotogae-second deepest branch of the bacteria; best studies are members of the genus Thermotoga

i) Hyperthermophiles with an optimum of 80°C and a maximum of 90°C
ii) Gram-negative rods with an outer sheath-like envelope (like a toga) that can balloon out from the ends of the cell
iii) Grow in active geothermal areas (e.g., marine hydrothermal vents and terrestrial solfataric springs)
iv) Chemoheterotrophs with a functional glycolytic pathway; can grow anaerobically on carbohydrates and protein digests

2) Deinococcus-Thermus
a) Consists of three genera; genus Deinococcus is the best studied
i) Spherical or rod-shaped; often associated in pairs or tetrads
ii) Aerobic, mesophilic, catalase positive, and usually able to produce acid from only a few sugars
iii) They stain gram-positive but have a layered cell wall and an outer membrane like gram-negative bacteria; have L-ornithine in their peptidoglycan and lack teichoic acid
iv) Have a plasma membrane with large amounts of palmitoleic acid rather than phosphatidylglycerol phospholipids
v) Extraordinarily resistant to desiccation and radiation
b) Relatively little is know about the biology of deinococci
i) Can be isolated from ground meat, feces, air, fresh water, and other sources but their natural habitat is not known
ii) Genome consists of two circular chromosomes, a mega plasmid, and a small plasmid
iii) Have an unusual ability to repair chromosomal damage (even fragmentation) and this probably accounts for their ability to resist desiccation and radiation; genomic analysis show they have many DNA repair genes and many repeat sequences

3) Photosynthetic Bacteria
a) Three groups: purple bacteria, green bacteria, and cyanobacteria
i) Cyanobacteria carry out oxygenic photosynthesis, using water as an electron source for the generation of NADH and NADPH
ii) Green and purple bacteria carry out anoxygenic photosynthesis, using reduced molecules other than water, as an electron source for the generation of NADH and NADPH
(1) Purple sulfur bacteria use reduced sulfur compounds as electron sources and accumulate sulfur granules within their cells
(2) Green sulfur bacteria use reduced sulfur compounds as electron sources and deposit sulfur granules outside their cells
(3) Purple nonsulfur bacteria use organics molecules as their electron sourcec
b) Type of photosynthetic pigments and oxygen relationships correlates with ecological distribution
i) Purple and green bacteria are anaerobes and use bacteriochlorophyll pigments
(1) Grow better in deeper, anaerobic zones of aquatic habitats
(2) Their bacteriochlorophylls absorb shorter wavelengths of light, which penetrate to these deeper zones
ii) Cyanobacteria have chlorophyll a, which absorbs longer wavelengths of light; these bacteria are found primarily at the surface of bodies of water
c) The 2nd edition of Bergey's Manual divides the photosynthetic bacteria into six groups:
i) Phylum Chloroflexi-green nonsulfur bacteria
ii) Phylum Chlorobi-green sulfur bacteria
iii) Phylum Cyanobacteria
iv) Phylum Proteobacteria-Purple sulfur bacteria (gammaproteobacteria) and purple nonsulfur bacteria (alphaproteobacteria and betaproteobacteria); these organisms are covered in chapter 22
(1) Phylum Chloroflexi-green nonsulfur bacteria
(a) Genus Chloroflexus-major representative of the photosynthetic green nonsulfur bacteria
1. Filamentous, gliding bacteria
2. Thermophilic, often isolated from neutral to alkaline hot springs where they grow in the form of orange-reddish mats
3. Ultrastructure and photosynthetic pigments are like green bacteria, but their metabolism is similar to that of the purple nonsulfur bacteria
4. Can carry out anoxygenic photosynthesis with organic compounds as carbon sources or can grow aerobically as a chemoheterotroph

(b) Genus Herpetosiphon-represents nonphotosynthetic members of phylum Chloroflexi; contains gliding, rod-shaped filamentous bacteria; aerobic chemoorganotrophs with respiratory metabolism; isolated from fresh water and soil

(2) Chlorobia-green sulfur bacteria

(i) Obligately anaerobic photolithoautotrophs that use hydrogen sulfide, elemental sulfur and hydrogen as electron sources; elemental sulfur produced by sulfide oxidation is deposited outside the cell

(ii) Photosynthetic pigments are located in ellipsoidal vesicles called chlorosomes, which are attached to the plasma membrane but not continuous with it; chlorosome membrane is not a normal lipid bilayer; chlorosomes have accessory bacteriochlorophylls but the reaction center bacteriochlorophyll is located in the plasma membrane

(iii) Lack flagella and are nonmotile; some species have gas vesicles to adjust their depth in water for adequate light and hydrogen sulfide; species without gas vesicles are found in sulfide-rich mud at the bottom of lakes and ponds.

(iv) Morphologically diverse (rods, cocci, or vibrios; grow singly, in chains, or in clusters); grass green or chocolate-brown in color

(3) Phylum Cyanobacteria

(a) Largest and most diverse group of photosynthetic bacteria (56 genera are described in the 2nd edition of Bergey's Manual)

(b) Photosynthetic system resembles that of eucaryotes, having chlorophyll a and photosystem II; carry out oxygenic photosynthesis

(c) Photosynthetic pigments are in thylakoid membranes lined with particles called phycobilisomes (contain phycobilin pigments), which transfer energy to photosystem II; some species are red-brown and contain the pigment phycoerythrin

(d) Fix carbon dioxide by the Calvin cycle

(e) Do not have functional TCA cycle; pentose phosphate pathway plays a central role in their metabolism

(f) Although they are oxygenic photolithoautotrophs, some can grow slowly in the dark as chemoheterotrophs, and some species can carry out anoxygenic photosynthesis if in an anaerobic environment

(g) Vary greatly in shape and appearance

(h) May be unicellular, exist as colonies of many shapes, or form filaments called trichomes (rows of bacterial cells that are in close contact with one another over a large area)

(i) Have typical procaryotic structures with a gram-negative cell wall

(j) Often use gas vesicles to move vertically in the water; many filamentous cyanobacteria have a gliding motility; although cyanobacteria lack flagella, some marine species are able to move by an unknown mechanism

(k) Reproduce by binary fission, budding, fragmentation, and multiple fission

- (i) Fragmentation generates small motile filaments called hormogonia
- (ii) Some species develop akinetes, which are thick-walled resting cells that are resistant to desiccation; these often germinate to form new filaments

(l) Many filamentous cyanobacteria fix atmospheric nitrogen in special cells (heterocysts), which protect the oxygen-sensitive nitrogenase; other cyanobacteria that lack heterocysts can also fix nitrogen

(m) Taxonomy of cyanobacteria is unsettled; the 2nd edition of Bergey's Manual divides them into five subsections

- (i) The prochlorophytes, which used to be categorized separately from other cyanobacteria, are now dispersed into subsections I and III
- (ii) Prochlorophytes differ from other cyanobacteria by having chlorophyll b as well as chlorophyll a and by lacking phycobilisomes
- (iii) The three recognized prochlorophyte genera are quite different from one another
- (iv) Prochloron-extracellular symbiont on the surface or within the cloacal cavity of marine colonial ascidan invertebrates
- (v) Prochlorothrix-free living
- (vi) Prochlorococcus-has a modified chlorophyll a and a-carotene rather than b-carotene
- (vii) The five subsections differ markedly in terms of morphology and reproduction

1. Subsection I-unicellular rods or cocci; most are nonmotile; reproduce by binary fission or budding
2. Subsection II-unicellular, though some may be held together in an aggregate by an outer wall; reproduce by multiple fission to form baeocytes
3. Subsections III, IV, and V-filamentous cyanobacteria

(viii) Tolerant of environmental extremes; thermophilic species can grow at temperatures up to 75°C

(ix) Successful at establishing symbiotic relationships (e.g., in lichens; symbionts with protozoa, fungi and plants)

(4) Phylum Planctomycetes

(a) Contains one class, one order, and four genera

(b) Spherical or oval, budding bacteria with distinctive crateriform structures (pits) in their walls

(c) In two genera, Gemmata and Pirullela, the nuclear body is membrane bounded, something that is not seen in other procaryotes

(d) The genus Planctomyces attaches to surfaces through a stalk and holdfast; other genera lack stalks

(e) Most have life cycles in which sessile cells bud to produce motile swarmer cells

(5) Phylum Chlamydiae

(a) This phylum has only 5 genera; Chlamydia is the most important and best-studied genus

(i) Nonmotile, coccoid, gram-negative bacteria

(ii) Reproduce within cytoplasmic vesicles of host cells by a unique developmental cycle involving elementary bodies (EBs) and reticulate bodies (RBs)

(iii) Gram-negative-like wall but lacks muramic acid and peptidoglycan; EBs use cross-linking of outer membrane proteins, and possibly, periplasmic proteins to achieve osmotic stability

(iv) Obligately intracellular parasites; found mostly in mammals and birds but have been recently isolated from spiders, clams, and freshwater invertebrates

(v) Have one of the smallest procaryotic genomes

(b) Chlamydial reproduction

(i) Begins with attachment of an EB to host cell

(ii) Host cell phagocytizes the EB, but fusion of lysosome with the phagosome is prevented by the EB

(iii) EB reorganizes itself into a reticulate body (RB), which is specialized for reproduction

(iv) RB reproduces repeatedly, giving rise to many RBs, all within a vacuole

(v) RBs change back into EBs, and these are released when the host lyses

(c) Chlamydial metabolism

(i) Usually thought of as being completely dependent on host for ATP; however, recent genomic analysis indicates that some genes for ATP synthesis are present in the genome

(ii) RBs have a number of biosynthetic capabilities (e.g., DNA, RNA, glycogen, lipid, protein, some amino acids and coenzymes)

(iii) EBs have very little metabolic activity; seem to be dormant forms concerned exclusively with transmission and infection

(d) Three recognized human pathogens

(i) C. trachomatis-trachoma, nongonococcal urethritis, and other diseases in humans and mice

(ii) C. psittaci-causes psittacosis in humans and infects many other mammals as well; invades the respiratory and genital tracts, the placenta, developing fetuses, the eye, and synovial fluid of the joints

(iii) C. pneumoniae-a causative agent of human pneumonia and possibly atherosclerosis and heart disease

(6) Phylum Spirochaetes

(a) Gram-negative, chemoheterotrophic, flexibly helical bacteria that exhibit a creeping (crawling) motility due to a structure called an axial filament

(b) The axial filament (a complex of periplasmic flagella) lies in a flexible outer sheath (outer membrane) outside the protoplasmic cylinder, which houses the nucleoid and cytoplasm; function of the sheath is essential (spirochetes will die if it is removed) but unknown

(c) Flagellar rotation is responsible for motility by an unknown mechanism, presumably by rotating the outer sheath or flexing the cell for a crawling motion.
(d) Can be anaerobic, facultatively anaerobic, or aerobic and can use a diverse array of organic molecules as carbon and energy sources
(e) Ecologically diverse
  (i) Spirochaeta-free-living and often found in anaerobic, sulfide-rich aquatic environments
  (ii) Leptospira-aerobic water and moist soils
  (iii) Many, including Criptispira and Treponema form symbiotic associations with other organisms
  (iv) Some members of Treponema, Borrelia, and Leptospira cause disease (e.g., T. pallidum is the causative agent of syphilis, and B. burgdorferi is the causative agent of Lyme disease)

(7) Phylum Bacteroidetes

(a) Consists of 50 genera divided into 3 classes (Bacteroides, Flavobacteria, and Shpingobacteria)
(b) Class Bacteroides
  (i) Obligate anaerobes, nonsporing, chemoheterotrophic, fermentative, rods
  (ii) Found in oral cavity and intestinal tract of humans and other animals and the rumen of ruminants where they often benefit the host by degrading cellulose, pectins, and other complex carbohydrates, thereby providing extra nutrition for the host
  (iii) Some species can be associated with disease
(c) Class Sphingobacteria
  (i) Often have sphinolipids in their cell walls
  (ii) Contains several genera including Flexibacter, Cytophaga and Sporocytophaga; differ in morphology, life cycle and physiology
    1. Cytophaga-slender rods with pointed ends
    2. Sporocytophaga-similar to Cytophaga but form spherical resting cells called microcysts
    3. Flexibacter-form long threads; unlike the other two genera, they are unable to degrade complex carbohydrates
  (iii) Physiology (as seen in the genera Cytophaga and Sporocytophaga)
    1. Aerobes that actively degrade complex carbohydrates (e.g., cellulose, chitin, keratin)
    2. Play a major role in the mineralization of organic matter and can damage exposed wooden structures
    3. Contribute significantly to wastewater treatment
  (iv) Most cytophagas are free-living, but some pathogenic species are known (e.g., C. columnaris causes disease in freshwater and marine fish)
  (v) Are nonmotile when in suspension, but exhibit gliding motility when in contact with a surface; leaves a slime trail;
  (vi) Gliding motility has advantages
    1. Enables them to find and digest insoluble material encountered as they move
    2. Allows motility in drier habitats
    3. Enables them to position themselves for optimal environmental conditions

Chapter 22: Bacteria: The Proteobacteria

Chapter Overview

This chapter presents the diverse group of eubacteria known as the proteobacteria. The distinguishing characteristics of these gram-negative bacteria: morphology, physiology, metabolism, and ecology are presented. The phylogenetic relationships are mengetahuied and representative species are examined

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the importance of this diverse group of organisms
2. describe the diverse life styles and metabolism of members of this group of organisms
3. discuss the complex structures (prosthecae, stalks, buds, sheaths, or complex fruiting bodies produced by some members of this group
4. discuss the ecological impact by chemolithotrophic bacteria
5. discuss the dependence of parasitic bacteria, such as Bdellovibrio and the rickettsia, on their hosts for energy and/or cell constituents

These are the most important concepts you are learning in this chapter:

1. The proteobacteria of the second edition of Bergey's Manual come from volumes 1 and 3 of the first edition. In the first edition bacteria are placed in a particular section based on a few major phenotypic properties such as general shape, nutritional type, motility, oxygen relationships, and so forth. The second edition uses nucleic acid sequences, particularly 16S rRNA sequence comparisons, to place bacteria in phylogenetic groupings.
2. Many of these gram-negative bacteria are of considerable importance, either as disease agents or because of their effects on the habitat. Others, such as E. coli, are major experimental organisms studied in many laboratories.
3. Although many of these bacteria do not vary drastically in general appearance, they often are very diverse in their metabolism and life-styles, which range from obligately intracellular parasitism to a free-living existence in soil and aquatic habitats.
4. Bacteria do not always have simple, unsophisticated morphology but may produce prosthecae, stalks, buds, sheaths, or complex fruiting bodies.
5. Chemolithotrophic bacteria obtain energy and electrons by oxidizing inorganic compounds rather than the organic nutrients employed by most bacteria. They often have substantial ecological impact because of their ability to oxidize many forms of inorganic nitrogen and sulfur.
6. Many bacteria that specialize in predatory or parasitic modes of existence, such as Bdellovibrio and the rickettsias, have relinquished some of their metabolic independence through the loss of metabolic pathways. They depend on the prey's or host's energy supply and/or cell constituents.

Study Outline

I. Introduction
    A. The phylum Firmicutes contains cell wall-less bacteria (mycoplasmas) and the low G+C gram-positive bacteria
    B. Firmicutes is divided into three classes: Mollicutes, Clostridia, and Bacilli
II. Class Mollicutes (The Mycoplasmas)
    A. Has five orders and six families having the following characteristics:
        1. Lack cell walls and cannot synthesize peptidoglycan precursors; therefore are penicillin resistant and susceptible to lysis by osmotic shock and detergent treatment
        2. Are smallest bacteria capable of self-reproduction
        3. Most are nonmotile but some can glide along liquid-covered surfaces
        4. Most species require sterols (unusual for bacteria)
        5. Usually facultative anaerobes but a few are strict anaerobes
        6. Have some of the smallest genomes observed in procaryotes; G + C content ranges from 23 to 41%
        7. Can be saprophytes, commensals or parasites
    B. Metabolism is not particularly unusual
        1. Are deficient in several biosynthetic pathways
        2. Some produce ATP by the Embden-Meyerhoff pathway and lactic acid fermentation; others catabolize arginine to urea
        3. Pentose phosphate pathway functions in some; none have a complete TCA cycle
    C. Widespread
        1. Can be isolated from plants, animals, soil, and compost piles
        2. Serious contaminants of mammalian cell cultures; difficult to detect; difficult to eliminate

3. In animals, they colonize mucous membranes and joints and are often associated with diseases of the respiratory and urogenital tracts
4. Pathogenic species include:
    a. M. mycoides-bovine pleuropneumonia in cattle
    b. M. gallisepticum-chronic respiratory disease in chickens
    c. M. pneumoniae-primary atypical pneumonia in humans
    d. M hominis and Ureaplasma urealyticum-pathogenic in humans
    e. Spiroplasmas-pathogenic in insects, ticks, and a variety of plants

III. Low G + C Gram-Positive Bacteria in Bergey?s Manual
  A. First edition treats low G + C gram positives phenotypically
    1. Classified on the basis of cell shape, clustering and arrangement of cells, presence or absence of endospores, oxygen relationships, fermentation patterns, peptidoglycan chemistry, etc.
    2. Peptidoglycan structure varies considerably
        a. Some contain meso-diaminopimelic acid cross-linked through its free amino group to the carboxyl group of the terminal D-alanine of the adjacent chain
        b. Others contain lysine cross-linked by interpeptide bridges
        c. Others contain L,L-diaminopimelic acid and have one glycine as the interpeptide bridge
        d. Others use ornithine to cross-link between positions 2 and 4 of the peptide chains rather than positions 3 and 4 as used by the other forms
        e. Other cross-links and differences in cross-link frequency also contribute to variation in structure
        f. These variations are characteristic of particular groups and are therefore taxonomically useful
    3. Bacterial endospores are complex structures that allow survival under adverse conditions; sporeformers are distributed widely but found mainly in soil
  B. Second edition takes a phylogenetic approach dividing the low G + C gram positives into two classes: Clostridia and Bacilli; endospore-formers are found in both groups

IV. Class Clostridia
  A. Contains three orders and 11 families
  B. The largest genus is Clostridium
    1. Obligate anaerobes, sporeformers, do not carry out dissimilatory sulfate reduction
    2. Over 100 species in distinct phylogenetic clusters
    3. Practical impact
        a. Responsible for many cases of food spoilage, even in canned foods (e.g., C. botulinum)
        b. C. perfringens-gas gangrene
        c. C. tetani-tetanus
        d. Some are of industrial value (e.g., C. acetobutylicum-used to manufacture butanol)
  C. Genus Desulfotomaculum
    1. Anaerobic, endospore-forming bacteria that reduce sulfate and sulfite to hydrogen sulfide during anaerobic respiration
    2. Stains gram-negative but actually has a gram-positive type cell wall with a lower than normal peptidoglycan content
  D. Genera Heliobacterium and Heliophilum
    1. Are anaerobic, photosynthetic bacteria that use bacteriochlorophyll g; have a photosystem like the green sulfur bacteria, but lack intracytoplasmic photosynthetic membranes (pigments are in the plasma membrane)
    2. Stain gram negative but have gram-positive type cell wall with lower than normal peptidoglycan content
  E. Genus Veillonella (family Veillonellaceae)
    1. Anaerobic, chemoheterotrophic cocci
    2. Usually diplococci
    3. Have complex nutritional requirements; ferment carbohydrates, lactate and other organic acids, and amino acids; produce gas and a mixture of volatile fatty acids
    4. Parasites of homeothermic animals; part of the normal microflora of the mouth, the gastrointestinal tract, and urogenital tract of humans and other animals

V. Class Bacilli

A. Order Bacilliales

1. Genus Bacillus
   a. Largest genus in the order
   b. Gram-positive, endospore-forming, chemoheterotrophic rods that are usually motile with peritrichous flagella
   c. Usually aerobic, sometimes facultative, and catalase positive
   d. Many species are of considerable importance: some produce antibiotics, some cause disease (e.g., B. cereus-causes food poisoning and B. anthracis-causes anthrax), and some are used as insecticides (e.g., B. thuringiensis and B. sphaericus)
2. Genus Thermoactinomyces
   a. Thermophilic; form single spores on both aerial and substrate mycelia
   b. Commonly found in damp haystacks, compost piles, and other high-temperature habitats
   c. The spores are very heat-resistant and thus are true bacterial endospores-can survive 90oC for 30 minutes
   d. T. vulgaris-causative agent for farmer's lung disease, an allergic respiratory disease in agricultural workers
3. Genus Caryophanon-strict aerobe, catalase positive, motile by peritrichous flagella; lives in cow dung; disk-shaped cells that join together to form rods
4. Genus Staphylococcus (family Staphylococcaceae)
   a. Facultatively anaerobic, nonmotile cocci that form irregular clusters
   b. Catalase positive, oxidase negative; ferment glucose anaerobically
   c. Normally associated with skin, skin glands, and mucous membranes of warm-blooded animals
   d. Cause many human diseases (e.g., endocarditis, wound infections, surgical infections, urinary tract infections, various skin infections, pneumonia, toxic shock syndrome, and food poisoning
5. Genus Listeria (family Listeriaceae)-short rods that are peritrichously flagellated; aerobic or facultative, catalase positive; L. monocytogenes is a human pathogen that causes listeriosis, an important food infection

B. Order Lactobacilliales

1. Lactic acid bacteria-nonsporing, nonmotile, fermentative (lactic acid fermentation), nutritionally fastidious, facultative or aerotolerant anaerobes;
2. Largest genus is Lactobacillus with nearly 80 species
   a. Can be rods and sometimes coccobacilli; lack catalase
   b. Can carry out heterolactic or homolactic acid fermentation
   c. Grow optimally between pH 4.5 and pH 6.4
   d. Found on plant surfaces and in dairy products, meat, water, sewage, beer, fruits, and many other materials
   e. Normal microflora of mouth, intestinal tract, and vagina; usually not pathogenic
   f. Used in the production of fermented vegetable foods, beverages, sour dough, hard cheeses, yogurt, and sausages
   g. Responsible for spoilage of beer, milk, and meat
3. Genus Leuconostoc (family Leuconostocaceae)
   a. Facultatively cocci that may be elongated or elliptical shape; clustered in pairs or chains
   b. Lack catalase; carry out heterolactic fermentation
   c. Isolated from plants, silage, and milk
   d. Important in wine production, fermentation of vegetables such as cabbage and cucumbers, manufacture of buttermilk, butter, cheese, and dextrans; involved in food spoilage
4. Genus Streptococcus (family Streptococcaceae)
   a. Most are facultative anaerobes; catalase negative; a few are obligate anaerobes
   b. Form pairs or chains in liquid media; do not form endospores; nonmotile
   c. Homolactic fermentation; produces lactic acid but no gas

d. The many species of this genus are distinguished by hemolysis reactions (b-hemolysis-incomplete with greenish zone or b-hemolysis-complete with clear zone but no greening), serologically, and by a variety of biochemical and physiological tests

5. Members of the genera Enterococcus, Streptococcus, and Lactococcus have great practical importance:
   a. S. pyogenes-causes streptococcal sore throat, acute glomerulonephritis and rheumatic fever
   b. S. pneumonia-causes lobar pneumonia
   c. S. mutans-associated with dental caries
   d. E. faecalis-opportunistic pathogen that can cause urinary tract infections and endocarditis
   e. L. lactis-used in the production of buttermilk and cheese

Chapter 23. Bacteria: The Low G+C Gram Positives

Chapter Overview

This chapter describes the different approaches to gram-positive organisms taken by the 1st and 2nd editions of Bergey's Manual and then focuses on the mycoplasmas, Clostridium and its relatives, and the bacilli and lactobacilli.

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the difference in classification of gram-positives that is used in the 1st and 2nd editions of Bergey's Manual
2. discuss the variation in peptidoglycan structure that is useful in identifying specific types of gram-positive bacteria
3. discuss the various roles of these organisms

These are the most important concepts you are learning in this chapter:

1. Volume 2 of the first edition of Bergey's Manual contains six sections covering all gram-positive bacteria except the actinomycetes. Bacteria are distributed among these sections on the basis of their shape, the ability to form endospores, acid fastness, oxygen relationships, the ability to temporarily form mycelia, and other properties.
2. The second edition of Bergey's Manual will group the gram-positive bacteria phylogenetically into two major groups: the low G+C gram positives and the high G +C gram positives. The new classification will be based primarily on nucleic acid sequences rather than phenotypic similarity.
3. The low G+C gram positives will contain (1) clostridia and relatives and (2) the bacilli and lactobacilli. Endospore formers, cocci, and rods are found in both groups rather being placed in separate sections as in the first edition. Thus common possession of a complex structure such as an endospore does not necessarily indicate close relatedness between the genera.
4. Peptidoglycan structure varies among different groups in ways that are often useful in identifying specific groups.
5. Although most gram-positive bacteria are harmless free-living saprophytes, some species from most major groups are pathogens of humans, other animals, and plants. Other gram-positive bacteria are very important in the food and dairy industries.

I. Introduction
   A. The phylum Firmicutes contains cell wall-less bacteria (mycoplasmas) and the low G+C gram-positive bacteria
   B. Firmicutes is divided into three classes: Mollicutes, Clostridia, and Bacilli
II. Class Mollicutes (The Mycoplasmas)
   B. Has five orders and six families having the following characteristics:
      1. Lack cell walls and cannot synthesize peptidoglycan precursors; therefore are penicillin resistant and susceptible to lysis by osmotic shock and detergent treatment
      2. Are smallest bacteria capable of self-reproduction
      3. Most are nonmotile but some can glide along liquid-covered surfaces
      4. Most species require sterols (unusual for bacteria)
      5. Usually facultative anaerobes but a few are strict anaerobes
      6. Have some of the smallest genomes observed in procaryotes; G + C content ranges from 23 to 41%
      7. Can be saprophytes, commensals or parasites
   C. Metabolism is not particularly unusual
      7. Are deficient in several biosynthetic pathways
      8. Some produce ATP by the Embden-Meyerhoff pathway and lactic acid fermentation; others catabolize arginine to urea
      9. Pentose phosphate pathway functions in some; none have a complete TCA cycle
   D. Widespread
      9. Can be isolated from plants, animals, soil, and compost piles
      10. Serious contaminants of mammalian cell cultures; difficult to detect; difficult to eliminate
      11. In animals, they colonize mucous membranes and joints and are often associated with diseases of the respiratory and urogenital tracts
      12. Pathogenic species include:
         a. M. mycoides-bovine pleuropneumonia in cattle
         b. M. gallisepticum-chronic respiratory disease in chickens
         c. M. pneumoniae-primary atypical pneumonia in humans
         d. M hominis and Ureaplasma urealyticum-pathogenic in humans
         e. Spiroplasmas-pathogenic in insects, ticks, and a variety of plants
III. Low G + C Gram-Positive Bacteria in Bergey?s Manual
   A. First edition treats low G + C gram positives phenotypically
      1. Classified on the basis of cell shape, clustering and arrangement of cells, presence or absence of endospores, oxygen relationships, fermentation patterns, peptidoglycan chemistry, etc.
      2. Peptidoglycan structure varies considerably
         a. Some contain meso-diaminopimelic acid cross-linked through its free amino group to the carboxyl group of the terminal D-alanine of the adjacent chain
         b. Others contain lysine cross-linked by interpeptide bridges
         c. Others contain L,L-diaminopimelic acid and have one glycine as the interpeptide bridge
         d. Others use ornithine to cross-link between positions 2 and 4 of the peptide chains rather than positions 3 and 4 as used by the other forms
         e. Other cross-links and differences in cross-link frequency also contribute to variation in structure
         f. These variations are characteristic of particular groups and are therefore taxonomically useful
      3. Bacterial endospores are complex structures that allow survival under adverse conditions; sporeformers are distributed widely but found mainly in soil
   B. Second edition takes a phylogenetic approach dividing the low G + C gram positives into two classes: Clostridia and Bacilli; endospore-formers are found in both groups
IV. Class Clostridia
   B. Contains three orders and 11 families
   C. The largest genus is Clostridium
      11. Obligate anaerobes, sporeformers, do not carry out dissimilatory sulfate reduction
      12. Over 100 species in distinct phylogenetic clusters

13. Practical impact
    e. Responsible for many cases of food spoilage, even in canned foods (e.g., C. botulinum)
    f. C. perfringens-gas gangrene
    g. C. tetani-tetanus
    h. Some are of industrial value (e.g., C. acetobutylicum-used to manufacture butanol)

D. Genus Desulfotomaculum
12. Anaerobic, endospore-forming bacteria that reduce sulfate and sulfite to hydrogen sulfide during anaerobic respiration
13. Stains gram-negative but actually has a gram-positive type cell wall with a lower than normal peptidoglycan content

E. Genera Heliobacterium and Heliophilum
13. Are anaerobic, photosynthetic bacteria that use bacteriochlorophyll g; have a photosystem like the green sulfur bacteria, but lack intracytoplasmic photosynthetic membranes (pigments are in the plasma membrane)
14. Stain gram negative but have gram-positive type cell wall with lower than normal peptidoglycan content

F. Genus Veillonella (family Veillonellaceae)
14. Anaerobic, chemoheterotrophic cocci
15. Usually diplococci
16. Have complex nutritional requirements; ferment carbohydrates, lactate and other organic acids, and amino acids; produce gas and a mixture of volatile fatty acids
17. Parasites of homeothermic animals; part of the normal microflora of the mouth, the gastrointestinal tract, and urogenital tract of humans and other animals

V. Class Bacilli

B. Order Bacilliales
17. Genus Bacillus
    h. Largest genus in the order
    i. Gram-positive, endospore-forming, chemoheterotrophic rods that are usually motile with peritrichous flagella
    j. Usually aerobic, sometimes facultative, and catalase positive
    k. Many species are of considerable importance: some produce antibiotics, some cause disease (e.g., B. cereus-causes food poisoning and B. anthracis-causes anthrax), and some are used as insecticides (e.g., B. thuringiensis and B. sphaericus)
18. Genus Thermoactinomyces
    k. Thermophilic; form single spores on both aerial and substrate mycelia
    l. Commonly found in damp haystacks, compost piles, and other high-temperature habitats
    m. The spores are very heat-resistant and thus are true bacterial endospores-can survive 90oC for 30 minutes
    n. T. vulgaris-causative agent for farmer's lung disease, an allergic respiratory disease in agricultural workers
19. Genus Caryophanon-strict aerobe, catalase positive, motile by peritrichous flagella; lives in cow dung; disk-shaped cells that join together to form rods
20. Genus Staphylococcus (family Staphylococcaceae)
    h. Facultatively anaerobic, nonmotile cocci that form irregular clusters
    i. Catalase positive, oxidase negative; ferment glucose anaerobically
    j. Normally associated with skin, skin glands, and mucous membranes of warm-blooded animals
    k. Cause many human diseases (e.g., endocarditis, wound infections, surgical infections, urinary tract infections, various skin infections, pneumonia, toxic shock syndrome, and food poisoning
21. Genus Listeria (family Listeriaceae)-short rods that are peritrichously flagellated; aerobic or facultative, catalase positive; L. monocytogenes is a human pathogen that causes listeriosis, an important food infection

C. Order Lactobacilliales
21. Lactic acid bacteria-nonsporing, nonmotile, fermentative (lactic acid fermentation), nutritionally fastidious, facultative or aerotolerant anaerobes;

22. Largest genus is Lactobacillus with nearly 80 species
    h. Can be rods and sometimes coccobacilli; lack catalase
    i. Can carry out heterolactic or homolactic acid fermentation
    j. Grow optimally between pH 4.5 and pH 6.4
    k. Found on plant surfaces and in dairy products, meat, water, sewage, beer, fruits, and many other materials
    l. Normal microflora of mouth, intestinal tract, and vagina; usually not pathogenic
    m. Used in the production of fermented vegetable foods, beverages, sour dough, hard cheeses, yogurt, and sausages
    n. Responsible for spoilage of beer, milk, and meat
23. Genus Leuconostoc (family Leuconostocaceae)
    n. Facultatively cocci that may be elongated or elliptical shape; clustered in pairs or chains
    o. Lack catalase; carry out heterolactic fermentation
    p. Isolated from plants, silage, and milk
    q. Important in wine production, fermentation of vegetables such as cabbage and cucumbers, manufacture of buttermilk, butter, cheese, and dextrans; involved in food spoilage
24. Genus Streptococcus (family Streptococcaceae)
    q. Most are facultative anaerobes; catalase negative; a few are obligate anaerobes
    r. Form pairs or chains in liquid media; do not form endospores; nonmotile
    s. Homolactic fermentation; produces lactic acid but no gas
    t. The many species of this genus are distinguished by hemolysis reactions (b-hemolysis-incomplete with greenish zone or b-hemolysis-complete with clear zone but no greening), serologically, and by a variety of biochemical and physiological tests
25. Members of the genera Enterococcus, Streptococcus, and Lactococcus have great practical importance:
    t. S. pyogenes-causes streptococcal sore throat, acute glomerulonephritis and rheumatic fever
    u. S. pneumonia-causes lobar pneumonia
    v. S. mutans-associated with dental caries
    w. E. faecalis-opportunistic pathogen that can cause urinary tract infections and endocarditis
    x. L. lactis-used in the production of buttermilk and cheese

VI. Introduction
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  C. Firmicutes is divided into three classes: Mollicutes, Clostridia, and Bacilli

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    2. Are smallest bacteria capable of self-reproduction
    3. Most are nonmotile but some can glide along liquid-covered surfaces
    4. Most species require sterols (unusual for bacteria)
    5. Usually facultative anaerobes but a few are strict anaerobes
    6. Have some of the smallest genomes observed in procaryotes; G + C content ranges from 23 to 41%
    7. Can be saprophytes, commensals or parasites
  D. Metabolism is not particularly unusual
    7. Are deficient in several biosynthetic pathways
    8. Some produce ATP by the Embden-Meyerhoff pathway and lactic acid fermentation; others catabolize arginine to urea
    9. Pentose phosphate pathway functions in some; none have a complete TCA cycle
  E. Widespread
    9. Can be isolated from plants, animals, soil, and compost piles

10. Serious contaminants of mammalian cell cultures; difficult to detect; difficult to eliminate
11. In animals, they colonize mucous membranes and joints and are often associated with diseases of the respiratory and urogenital tracts
12. Pathogenic species include:
    a. M. mycoides-bovine pleuropneumonia in cattle
    b. M. gallisepticum-chronic respiratory disease in chickens
    c. M. pneumoniae-primary atypical pneumonia in humans
    d. M hominis and Ureaplasma urealyticum-pathogenic in humans
    e. Spiroplasmas-pathogenic in insects, ticks, and a variety of plants

VIII. Low G + C Gram-Positive Bacteria in Bergey?s Manual
  A. First edition treats low G + C gram positives phenotypically
    1. Classified on the basis of cell shape, clustering and arrangement of cells, presence or absence of endospores, oxygen relationships, fermentation patterns, peptidoglycan chemistry, etc.
    2. Peptidoglycan structure varies considerably
      a. Some contain meso-diaminopimelic acid cross-linked through its free amino group to the carboxyl group of the terminal D-alanine of the adjacent chain
      b. Others contain lysine cross-linked by interpeptide bridges
      c. Others contain L,L-diaminopimelic acid and have one glycine as the interpeptide bridge
      d. Others use ornithine to cross-link between positions 2 and 4 of the peptide chains rather than positions 3 and 4 as used by the other forms
      e. Other cross-links and differences in cross-link frequency also contribute to variation in structure
      f. These variations are characteristic of particular groups and are therefore taxonomically useful
    3. Bacterial endospores are complex structures that allow survival under adverse conditions; sporeformers are distributed widely but found mainly in soil
  B. Second edition takes a phylogenetic approach dividing the low G + C gram positives into two classes: Clostridia and Bacilli; endospore-formers are found in both groups

IX. Class Clostridia
  B. Contains three orders and 11 families
  C. The largest genus is Clostridium
    11. Obligate anaerobes, sporeformers, do not carry out dissimilatory sulfate reduction
    12. Over 100 species in distinct phylogenetic clusters
    13. Practical impact
      e. Responsible for many cases of food spoilage, even in canned foods (e.g., C. botulinum)
      f. C. perfringens-gas gangrene
      g. C. tetani-tetanus
      h. Some are of industrial value (e.g., C. acetobutylicum-used to manufacture butanol)
  D. Genus Desulfotomaculum
    12. Anaerobic, endospore-forming bacteria that reduce sulfate and sulfite to hydrogen sulfide during anaerobic respiration
    13. Stains gram-negative but actually has a gram-positive type cell wall with a lower than normal peptidoglycan content
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    13. Are anaerobic, photosynthetic bacteria that use bacteriochlorophyll g; have a photosystem like the green sulfur bacteria, but lack intracytoplasmic photosynthetic membranes (pigments are in the plasma membrane)
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  F. Genus Veillonella (family Veillonellaceae)
    14. Anaerobic, chemoheterotrophic cocci
    15. Usually diplococci
    16. Have complex nutritional requirements; ferment carbohydrates, lactate and other organic acids, and amino acids; produce gas and a mixture of volatile fatty acids

17. Parasites of homeothermic animals; part of the normal microflora of the mouth, the gastrointestinal tract, and urogenital tract of humans and other animals

X. Class Bacilli

B. Order Bacilliales

17. Genus Bacillus
    h. Largest genus in the order
    i. Gram-positive, endospore-forming, chemoheterotrophic rods that are usually motile with peritrichous flagella
    j. Usually aerobic, sometimes facultative, and catalase positive
    k. Many species are of considerable importance: some produce antibiotics, some cause disease (e.g., B. cereus-causes food poisoning and B. anthracis-causes anthrax), and some are used as insecticides (e.g., B. thuringiensis and B. sphaericus)
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22. Largest genus is Lactobacillus with nearly 80 species
    h. Can be rods and sometimes coccobacilli; lack catalase
    i. Can carry out heterolactic or homolactic acid fermentation
    j. Grow optimally between pH 4.5 and pH 6.4
    k. Found on plant surfaces and in dairy products, meat, water, sewage, beer, fruits, and many other materials
    l. Normal microflora of mouth, intestinal tract, and vagina; usually not pathogenic
    m. Used in the production of fermented vegetable foods, beverages, sour dough, hard cheeses, yogurt, and sausages
    n. Responsible for spoilage of beer, milk, and meat
23. Genus Leuconostoc (family Leuconostocaceae)
    n. Facultatively cocci that may be elongated or elliptical shape; clustered in pairs or chains
    o. Lack catalase; carry out heterolactic fermentation
    p. Isolated from plants, silage, and milk
    q. Important in wine production, fermentation of vegetables such as cabbage and cucumbers, manufacture of buttermilk, butter, cheese, and dextrans; involved in food spoilage
24. Genus Streptococcus (family Streptococcaceae)
    q. Most are facultative anaerobes; catalase negative; a few are obligate anaerobes
    r. Form pairs or chains in liquid media; do not form endospores; nonmotile

s. Homolactic fermentation; produces lactic acid but no gas
t. The many species of this genus are distinguished by hemolysis reactions (b-hemolysis-incomplete with greenish zone or b-hemolysis-complete with clear zone but no greening), serologically, and by a variety of biochemical and physiological tests

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v. S. mutans-associated with dental caries
w. E. faecalis-opportunistic pathogen that can cause urinary tract infections and endocarditis
x. L. lactis-used in the production of buttermilk and cheese

Chapter 24. Bacteria: The High G+C Gram Positives

Chapter Overview

This chapter surveys the general characteristics of the actinomycetes and other organisms that are classified as high G + C gram-positives in the 2nd edition of Bergey's Manual. The actinomycetes are filamentous bacteria that form branching hyphae and asexual spores.

Chapter Objectives

After reading this chapter you should be able to:

- describe the filamentous actinomycetes
- describe the morphology and arrangement of spores, cell wall chemistry, and the types of sugars present in cell extracts within the actinomycetes
- discuss the roles of actinomycetes in the mineralization of organic compounds and in the production of antibiotics
- describe the important human pathogens contained in the genera Corynebacterium and Mycobacterium

These are the most important concepts you are learning in this chapter:

1. Volume 4 of the first edition of Bergey's Manual contains aerobic, gram-positive bacteria — the actinomycetes — that form branching hyphae and asexual spores.
2. The morphology and arrangement of spores, cell wall chemistry, and the types of sugars present in cell extracts are particularly important in actinomycete taxonomy and are used to divide these bacteria into different groups.
3. The second edition of Bergey's Manual will classify high G+C gram-positive bacteria using 16S rRNA data. They will be placed in the class Actinobacteria, which will contain the actinomycetes in volume 4 of the first edition plus gram-positive bacteria from sections 12, 15, 16, and 17 of volume 2.
4. Actinomycetes have considerable practical impact because they play a major role in the mineralization of organic matter in the soil and are the primary source of most naturally synthesized antibiotics. The genera Corynebacterium and Mycobacterium contain important human pathogens.

Study Outline

I. General Properties of the Actinomycetes
A. Exhibit filamentous growth
1. Form substrate mycelia
2. 2 Septa divide the mycelia into long cells (20 um and longer), each containing several nucleoids
3. Some form a tissue-like mass called a thallus

4. They may have aerial mycelia that form conidospores at the ends of filaments or that form sporangiospores within a sporangium; spores are not heat resistant but withstand desiccation

B. Actinomycetes are generally nonmotile, but spores may be flagellated

C. Cell wall types vary and can be distinguished by the amino acid in position 3 of the tetrapeptide, the presence of glycine in the interpeptide bridge, and the sugar content; four types are known

D. Cell wall type, sugars in extracts, morphology and color of mycelia and sporangia, G + C content, membrane phospholipid composition, and heat resistance of the spores are all important in classifying these organisms, as is comparison of 16S rRNA sequences and pulse-field electrophoresis of large DNA fragments produced by restriction endonuclease digestion

E. Are of considerable practical importance

1. Those in soil degrade a number of organic compounds and are important in the mineralization processes; also produce most of the medically important, naturally synthesized antibiotics
2. A few species are pathogenic in humans, other animals, and plants

II. High G + C Gram-Positive Bacteria in Bergey?s Manual

A. The 1st edition of Bergey?s Manual divides the actinomycetes into 7 sections, primarily based on cell wall type, conidia arrangement, and the presence or absence of a sporangium

B. The 2nd edition uses 16S rRNA sequences to create a large phylum, Actinobacteria, containing one class Actinobacteria, five subclasses, six orders, 14 suborders and 40 families

C. This chapter focuses on the subclass Actinobacteridae and the order Actinomycetales; the order Bfidobacteriales is also briefly described

III. Suborder Actinomycineae

A. Most genera are irregularly shaped, nonsporing rods with aerobic or facultative metabolism

B. Genus Actinomyces

1. Straight or slightly curved rods and slender filaments with true branching
2. Facultative or obligate anaerobes; require CO2 for best growth
3. Cell walls contain lysine but not diaminopimelic acid
4. Normal inhabitants of mucosal surfaces of warm-blooded animals; some cause disease in their hosts

IV. Suborder Micrococcineae

A. Contains 10 families and many genera

B. Genus Micrococcus

1. Aerobic, catalase-positive cocci that occur in pairs, tetrads or irregular clusters; usually nonmotile
2. Often, yellow, red, or orange pigmented
3. Widespread in soil, water, and on mammalian skin; usually not pathogenic

C. Genus Arthrobacter

1. Aerobic, catalase-positive rods with respiratory metabolism and lysine in peptidoglycan
2. Exhibit a rod-coccus growth cycle
   a. When growing in exponential phase they are rods that reproduce by a snapping division
   b. In stationary phase they change to a coccoid form
   c. Upon transfer to fresh medium, coccoid cells produce outgrowths and resume active reproduction as rods
3. Most important habitat is soil
   a. Resistant to desiccation and nutrient deprivation
   b. Very flexible nutritionally; able to degrade some herbicides and pesticides

D. Genus Dermatophilus

1. Forms packets of motile spores with tufts of flagella
2. Facultative anaerobe
3. Mammalian parasite responsible for a skin infection called streptothrichosis

V. Suborder Corynebacterineae

A. Contains seven families with several important genera

B. Genus Corynebacterium (family Corynebacteriaceae)

1. Aerobic and facultative species; catalase-positive; straight to slightly curved rods, often with tapered ends
    a. Remain partially attached after snapping division resulting in angular arrangements
    b. Form metachromatic granules
    c. Cell walls contain meso-diaminopimelic acid
2. Some species are harmless soil and water saprophytes; many are animal and human pathogens (e.g., C. diphtheriae-causative agent of diphtheria in humans)

C. Genus Mycobacterium (family Mycobacteriaceae)
1. Straight or slightly curved rods that sometimes branch or form filaments
2. Aerobic and catalase-positive; grow very slowly
3. Cell walls contain waxes with 60-90 carbon mycolic acids-make them acid-fast (i.e. basic fuchsin dye cannot be removed with acid-alcohol treatment)
4. Some are free-living saprophytes; but they are best known as human and animal pathogens
    a. M. bovis-tuberculosis in cattle and other ruminants
    b. M. tuberculosis-tuberculosis in humans
    c. M. leprae-causes leprosy in humans

D. Genera Nocardia and Rhodococcus (family Nocardiaceae)
1. These and related species are collectively called nocardioforms
2. Develop a substrate mycelium that readily breaks into rods and coccoid elements; some develop aerial mycelia
3. Most are strict aerobes
4. They are found in soil and aquatic habitats
    a. Nocardia degrade hydrocarbons and waxes and are involved in biodegradation of rubber joints in water and sewage pipes; most are free-living saprophytes, but some species (e.g., N. asteroides) are opportunistic pathogens causing nocardiosis
    b. Rhodococcus can degrade a wide variety of molecules, including those found in toxic wastes

VI. Suborder Micromonosporineae

A. Contains many genera that are often referred to as Actinoplanetes
1. Extensive substrate mycelia; aerial mycelia are absent or rudimentary
2. Form conidiospores within a sporangium that extends above the surface of the substratum; spores can be motile or nonmotile
3. Genera vary in arrangement and development of spores

B. Found in soil and freshwater habitats and occasionally in the ocean
1. Soil dwellers play an important role in plant and animal decomposition
2. Some produce antibiotics such as gentamicin

VII. Suborder Propionibacterineae

A. Contains two families and 10 genera

B. Genus Propionibacterium
1. Pleomorphic, nonmotile rods that are often club shaped; cells may also be coccoid or even branched; single cells, short chains, or in clumps
2. Facultatively anaerobic or aerotolerant; ferment sugars to produce propionic acid
3. Found on skin and in the digestive tract of animals; also in dairy products such as cheese; contribute to the production of Swiss cheese; P. acne is involved in the development of body odor and acne vulgaris

C. Suborder Streptomycineae

D. Only one family, Streptomycetaceae and three genera
1. Have aerial mycelia that divide in a single plane to form chains of nonmotile conidiospores
2. Commonly called streptomycetes

E. Genus Streptomyces
1. An enormous genus with around 500 species 2 Strict aerobes
2. Form nonmotile spores within a thin sheath

F. Streptomycetes are ecologically and medically important
1. Natural habitat is soil where they represent from 1-20% of the organisms present (impart the characteristic odor of moist earth by producing volatile substances such as geosmin)

2. Metabolically flexible; major contributors to mineralization
3. Best known for the synthesis of a vast array of antibiotics useful in medicine and research
4. Only S. somaliensis is known to be pathogenic in humans; it causes actinomycetoma, an infection of subcutaneous tissues that produces swelling, abscesses and bone destruction

G. Genus Streptoverticillium-has aerial hyphae in a whorl of three to six short branches

VIII. Suborder Streptosporangineae

A. Contains 3 families and 14 genera
B. Many referred to as maduromycetes because the sugar madurose (3-O-methyl-D-galactose) is found in their cell extracts; have aerial mycelia that produce pairs or short chains of spores; substrate mycelia are branched; some genera form sporangia
C. Genus Thermomonospora-produce single spores on the aerial mycelium or on both the aerial and the substrate mycelium; isolated from high temperature habitats such as compost piles and hay

IX. Suborder Frankineae

A. Genera Frankia and Geodermatophilus
   1. Form clusters of spores
   2. The genus Geodermatophilus has motile spores and is an aerobic soil organism
   3. The genus Frankia
      a. Forms nonmotile sporangiospores in a sporogenous body
      b. Grows in symbiotic relationship with at least 8 families of higher nonleguminous plants
      c. Microaerophilic and able to fix atmospheric nitrogen
B. Genus Sporichthya-lack a substrate mycelium but use holdfasts to anchor to the substratum; grow upward to form aerial mycelia that release motile, flagellated conidia in the presence of water

X. Order Bfidobacteriales

A. Contains one true family and 8 genera
B. Genera Falcivibrio and Gardnerella are found in the human genitourinary tract; Gardnerella may be a major cause of vaginitis
C. Genus Bfidobacterium is best studied
   1. Nonmotile, nonsporing, gram-positive rods of varied shapes that are slightly curved and clubbed; often they are branched; rods can be single cells, in clusters or in V-shaped pairs
   2. Anaerobic and ferment carbohydrates to produce acetic and lactic acids but no carbon dioxide
   3. Found in the mouth and intestinal tract of warm-blooded animals, in sewage, and in insects
      a. B.bfidus is a pioneer colonizer of the human intestinal tract, particularly when babies are breast-fed
      b. Some infections of humans have been reported but does not appear to be a major cause of disease

THE FUNGI

Chapter Overview

This chapter discusses the characteristics of the members of the kingdom Fungi. The diversity of these organisms is described, and their ecological and economic impact is discussed. In addition, certain protists-the slime molds and water molds, which resemble fungi-are also presented in this chapter.

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the distribution of fungi and their roles in the environment
2. discuss the morphological characteristics of fungi
3. describe the external digestion of organic matter by fungi
4. explain the formation of both asexual and sexual spores for reproduction
5. discuss the five major types of true fungi: zygomycetes, ascomycetes, basidiomycetes, deuteromycetes, and chytrids
6. discuss the criteria upon which fungi are categorized
7. discuss the slime molds and water molds and their resemblance to fungi

These are the most important concepts you are learning in this chapter:

1. Fungi are widely distributed and are found wherever moisture is present. They are of great importance to humans in both beneficial and harmful ways.
2. Fungi exist primarily as filamentous hyphae. A mass of hyphae is called a mycelium.
3. Like some bacteria, fungi digest insoluble organic matter by secreting exoenzymes, then absorbing the solubilized nutrients.
4. Two reproductive structures occur in the fungi: (1) sporangia form asexual spores, and (2) gametangia form sexual gametes.
5. The zygomycetes are characterized by resting structures called zygospores—cells in which zygotes are formed.
6. The ascomycetes form zygotes within a characteristic saclike structure, the ascus. The ascus contains two or more ascospores.
7. Yeasts are unicellular fungi—mainly ascomycetes.
8. Basidiomycetes possess dikaryotic hyphae with two nuclei, one of each mating type. The hyphae divide uniquely, forming basidiocarps within which club-shaped basidia can be found. The basidia bear two or more basidiospores.
9. The deuteromycetes (Fungi Imperfecti) have either lost the capacity for sexual reproduction, or it has never been observed.

Study Outline

I. Introduction
   A. Fungi-eucaryotic, spore-bearing organisms with absorptive metabolism and no chlorophyll; reproduce sexually and asexually
   B. Mycologists-scientists who study fungi
   C. Mycology-the study of fungi
   D. Mycotoxicology-the study of fungal toxins and their effects on various organisms
   E. Mycoses-diseases in animals caused by fungi
   F. Belong to the kingdom Fungi within the domain Eucarya; is a monophyletic group known as the eumycota (true fungi)

II. Distribution
   F. Primarily terrestrial with a few freshwater and marine organisms
   G. Many are pathogenic in plants or animals
   H. Form beneficial associations with plant roots (mycorrhizae) or with algae or cyanobacteria (lichens)

III. Importance
   H. Decomposers-break down organic material and return it to environment
   I. Major cause of plant disease; also cause disease in animals, including humans
   J. Industrial fermentation-bread, wine, beer, cheese, tofu, soy sauce, steroid manufacture, antibiotic production, and the production of the immunosuppressive drug cyclosporine
   K. Research-fundamental biological processes can be studied in these simple eucaryotic organisms

IV. Structure
   K. Thallus-body or vegetative structure of a fungus; fungal cell walls are usually composed of chitin, a nitrogen-containing polysaccharide consisting of N-acetyl glucosamine residues
   L. Yeast-unicellular fungus with single nucleus; reproduces asexually by budding, or sexually by spore formation; daughter cells may separate after budding or may aggregate to form colonies
   M. Mold-a fungus with long, branched, threadlike filaments
      1. Hyphae-the filaments of a mold; may be coenocytic (i.e., have no cross walls within the hyphae) or septate (i.e., have cross walls)
      2. Mycelia-bundles or tangled masses of hyphae
   N. Dimorphism-a property of some fungi, which change from the yeast (Y) form (within an animal host) to the mold (M) form (in the environment); this is referred to as the YM shift; the reverse relationship exists in plant-associated fungi

V. Nutrition and Metabolism
   N. Most fungi are saprophytes, securing nutrients from dead organic material (chemoorganoheterotrophs); fungi secrete hydrolytic enzymes that promote external digestion
   O. Glycogen is the primary storage polysaccharide
   P. Most are aerobic (some yeasts are facultatively anaerobic); obligate anaerobic fungi are found in the rumen of cattle

VI. Reproduction
   P. Asexual reproduction-occurs by several mechanisms
      1. Transverse fission
      2. Budding
      3. Direct spore production
         a. Hyphal fragmentation-component cells behave as arthrospores or chlamydiospores (if enveloped in thick cell wall before separation)
         b. Sporangiospores are produced in sporangium (sac) at the end of an aerial hypha (sporangiophore)
         c. Conidiospores are unenclosed spores produced at the tip or on the sides of aerial hypha
         d. Blastospores are produced when a vegetative cell buds off
   Q. Sexual reproduction
      2. Involves the union of compatible nuclei
      3. Some fungi are self-fertilizing (male and female gametes produced on the same mycelium (homothallic), while others require outcrossing between different but sexually compatible mycelia (heterothallic)
      4. Zygote formation proceeds by one of several mechanisms
         d. Fusion of gametes
         e. Fusion of gamete-producing bodies (gametangia)
         f. Fusion of hyphae
         g. Sometimes there is immediate fusion of nuclei and cytoplasm; however, more common is a delayed fusion of nuclei, resulting in the formation of a cell with two haploid nuclei (dikaryotic stage)
      5. Zygotes can develop into spores (zygospores, ascospores, or basidiospores); spores are used for identification purposes and also aid fungal dissemination

VII. Characteristics of the Fungal Divisions
   A. Division Zygomycota-zygomycetes
      1. Most are saprophytes; a few are plant and animal parasites
      2. Coenocytic hyphae (no crosswalls), with many haploid nuclei
      3. Asexual reproduction leads to the formation of sporangiospores

4. Sexual reproduction leads to the formation of zygospores; these are tough, thick-walled zygotes that can remain dormant when the environment is too harsh for growth
5. Representative member: Rhizopus stolonifer (commonly known as bread mold, but also grows on fruits and vegetables)
    a. Normally reproduces asexually
    b. Reproduces sexually by fusion of gametangia if food is scarce or environment is unfavorable
    c. Zygospores (diploid) are produced and remain dormant until conditions are favorable
    d. Meiosis often occurs at time of germination
6. Zygomycetes are used in the production of foods, anesthetics, coloring agents, and other useful products

B. Division Ascomycota-ascomycetes
    6. Members of this division cause food spoilage, a number of plant diseases (e.g., powdery mildew, chestnut blight, ergot,and Dutch elm disease)
    7. Include many types of yeast, edible morels, and truffles, as well as the pink bread mold Neurospora crassa
    8. Mycelia are septate
    9. Produce conidiospores when reproducing asexually
    10. Ascospores (haploid spores located in a sac called an ascus) are formed when reproducing sexually
    11. Thousands of asci may be packed together in a cup-shaped ascocarp

C. Division Basidiomycota-basidiomycetes (club fungi)
    11. Includes smuts, jelly fungi, rusts, shelf fungi, stinkhorns, puffballs, toadstools, mushrooms, and bird's nest fungi
    12. Basidia are produced at the tips of the hyphae, in which the basidiospores will develop
    13. Basidiospores are held in fruiting bodies called basidiocarps
    14. Usefulness-many basidomycetes are decomposers; some mushrooms serve as food (some are poisonous); one is the causative agent of cryptococcosis; and some are plant pathogens

D. Division Deuteromycota-deuteromycetes (commonly called Fungi Imperfecti)
    14. This is a classical division grouping together fungi that lack a sexual reproductive phase or fungi for which a sexual reproductive phase has not been observed; more recently molecular systematics places the Deuteromycota among their closest relatives in the Eumycota and eliminates the Deuteromycota as a separate division
    15. Most are terrestrial; a few are freshwater or marine organisms; most are saprophytes or plant parasites; some are parasitic on other fungi
    16. Human impact
        a. Some are human parasites (e.g., causing ringworm, athlete's foot, histoplasmosis)
        b. Some are used industrially to produce antibiotics, cheese, soy sauce, and other products
        c. Some produce substances that are highly toxic and carcinogenic to animals (e.g., aflatoxin and trichothecenes)

E. Division Chytridiomycota-chytrids (simplest of true fungi)
    15. Terrestrial and aquatic fungi that reproduce asexually by forming motile zoospores
    16. Microscopic in size; may consist of single cells, a small multinucleate mass, or a true mycelium
    17. Reproduce asexually or sexually
    18. Some saprophytic; others are parasites of algae, other true fungi, and plants

VIII. Slime Molds and Water Molds

A. Resemble fungi in appearance and life-style, but their cellular organization, reproduction, and life cycles are more closely related to protists

B. Division Myxomycota-plasmodial (acellular) slime molds
    18. The multinucleated protoplasm (plasmodium) moves by amoeboid movement as it phagocytizes organic matter

19. Form ornate fruiting bodies when food and/or moisture are in short supply; fruiting bodies form spores with cellulose cell walls that are resistant to environmental extremes
    c. Spores germinate to produce myxamoeba or flagellated swarm cells
    d. Myxamoeba and swarm cells are initially haploid, but eventually fuse to form a diploid zygote
    e. Zygote feeds, grows and carries out multiple nuclear divisions, giving rise to a plasmodium

C. Division Acrasiomycota-cellular slime molds
    18. During the vegetative stage, amoeboid cells called myxamoeba feed phagocytically on bacteria and yeasts
    19. When food is scarce, myxamoeba form pseudoplasmodia by aggregating and secreting a slimy sheath around themselves
    20. Become sedentary and differentiate into prestalk and prespore cells
    21. Form sorocarps that mature to sporangia; sporangia produce spores
    22. Released spores will later germinate to form haploid amoebae to begin the cycle again

D. Division Oomycota-oomycetes (water molds)
    22. Resemble fungi, but cell walls are composed of cellulose, not chitin
    23. Produce a relatively large egg cell that is fertilized by a small sperm cell or an even smaller antheridium; zygote germinates forming asexual, flagellated zoospores
    24. Usually saprophytic in freshwater environments; some parasitic in fish and plants

Chapter 26: The Algae

Chapter Overview

This chapter discusses the characteristics of the diverse polyphyletic group of organisms known as the algae. They range from single cells to multicellular organisms over 75 meters in length. They are found in oceans and freshwater environments and are the major producers of oxygen and organic material. A few algae live in moist soil and other terrestrial environments. They do not constitute a unique kingdom. An overview of their characteristics is presented, followed by discussion of each of the major groups of algae.

Chapter Objectives

After reading this chapter you should be able to:

1. discuss the various habitats in which algae are found
2. discuss the various morphological characteristics of algae
3. discuss the taxonomic relationships of this diverse polyphyletic group of organisms
4. discuss asexual and sexual reproduction of algae
5. discuss the various classical divisions of algae and the characteristics used to establish the divisions

These are the most important concepts you are learning in this chapter:

1. Most algae are found in freshwater and marine environments; a few grow in terrestrial habitats.
2. The algae are not a single, closely related taxonomic group but, instead, are a diverse, polyphyletic assemblage of unicellular, colonial, and multicellular eucaryotic organisms.
3. Although algae can be autotrophic or heterotrophic, most are photoautotrophs. They store carbon in a variety of forms, including starch, oils, and various sugars.
4. The body of an alga is called the thallus. Algal thalli range from small solitary cells to large, complex multicellular structures.
5. Algae reproduce asexually and sexually.
6. The following classical divisions of the algae are discussed: Chlorophyta (green algae), Charophyta (stoneworts/brittleworts), Euglenophyta (euglenoids), Chrysophyta (golden-brown and yellow-green algae; diatoms), Phaeophyta (brown algae), Rhodophyta (red algae), and Pyrrhophyta (dinoflagellates).

Study Outline

I. Introduction
   A. Algae-not a monophyletic group; instead the term is used to describe a group of organisms that lack roots, stems, and leaves, but that have chlorophyll and other pigments for carrying out oxygenic photosynthesis
   B. Phycologists (algologists)-scientists who study algae
   C. Phycology (algology)-the study of algae
II. Distribution of Algae
   C. Primarily aquatic
      1. Planktonic-suspended in the aqueous environment
         a. Phytoplankton-algae and other small aquatic plants
         b. Zooplankton-animals and other nonphotosynthetic protists
      2. Benthic-attached and living on the bottom of a body of water
      3. Neustonic-living at the air-water interface
   D. Moist rocks, wood, trees, and soil
   E. Some are endosymbionts in protozoa, mollusks, worms, corals, and plants
   F. Some associate with fungi to form lichens
   G. Some are parasitic
III. Classification of Algae
   G. In the Whittaker system
      1. Divided into seven divisions within two different kingdoms
      2. Primary classification is based on cellular properties
         a. Cell wall (if present) chemistry and morphology
         b. Storage food and photosynthetic products
         c. Types of chlorophyll and accessory pigments
         d. Number of flagella and their insertion location
         e. Morphology of cells and/or thallus (body)
         f. Habitat
         g. Reproductive structures
         h. Life history patterns
   D. Molecular systems have reclassified the algae as polyphyletic; they fall into five different lineages
      1. Plants
      2. Red algae
      3. Stramenopiles (this lineage also includes some protozoa)
      4. Alveolates (this lineage also includes some protozoa)
      5. Amoeboflagellates (this lineage also includes some protozoa)
IV. Ultrastructure of the Algal Cell
   A. Surrounded by a thin, rigid cell wall (some also have an outer matrix)
   B. Some are motile by flagella
   C. The nucleus has a typical nuclear envelope with pores
   D. Chloroplasts have thylakoids (sacs) that are the site of photosynthetic light reactions; may also have a dense proteinaceous pyrenoid that is associated with the synthesis and storage of starch
   E. Mitochondria can have discoid cristae, lamellar cristae, or tubular cristae
V. Algal Nutrition
   E. Most are autotrophic-require only light and inorganic compounds for energy; use CO2 as carbon source
   F. Some are heterotrophic-use external organic materials as source of energy and carbon
VI. Structure of the Algal Thallus (Vegetative Form)
   F. Thallus-vegetative body of algae; can be unicellular or multicellular
   G. Algae can be unicellular, colonial, filamentous, membranous, or tubular
VII. Algal Reproduction
   G. Asexual-occurs only with unicellular algae
      1. Fragmentation-thallus breaks up and each fragment forms a new thallus
      2. Spores formed in ordinary vegetative cell or in sporangium
         a. Zoospores are flagellated motile spores
         b. Aplanospores are nonmotile spores
      3. Binary fission-nuclear division followed by cytoplasmic division
   H. Sexual-occurs in multicellular and unicellular algae
      3. Oogonia-relatively unmodified vegetative cells in which eggs are formed

4. Antheridia-specialized structures in which sperm are formed
5. Zygote-product of fusion of sperm and egg

VIII. Characteristics of the Algal Divisions

A. Chlorophyta (green algae)-molecular classification places these with plants
   1. Are extremely varied
      a. Contain chlorophylls a and b and carotenoids; store carbohydrate as starch; cell walls are made of cellulose
      b. Live in fresh and salt water, soil, and associated with other organisms
      c. Can be unicellular, colonial, filamentous, membranous, or tubular
      d. Exhibit both asexual and sexual reproduction
   2. Genus Chlamydomonas-Members of this genus are microscopic, rounded, with two flagella at anterior end; have single haploid nucleus, a large chloroplast with conspicuous pyrenoid for starch production and storage, a stigma (phototactic eyespot), and contractile vacuole (acts as osmoregulator); exhibit asexual reproduction (zoospores) and sexual reproduction
   3. Genus Chlorella-members of this genus are nonmotile, unicellular algae; are widespread in aquatic habitats and in soil; only reproduce asexually; lack flagella; have eyespots, contractile vacuoles, and a very small nucleus
   4. Genus Volvox-members of the genus exist as hollow spheres made up of a single layer of 500-60,000 flagellated cells; flagella beat in a coordinated fashion; some cells are specialized for reproduction
   5. Prototheca moriformis, which is common in soil, causes the disease protothecosis in humans and other animals

B. Charophyta (stoneworts/brittleworts)
   5. Abundant in fresh and brackish waters; worldwide distribution
   6. Some species precipitate calcium and magnesium carbonate from water to form a limestone covering (helps preserve them as fossils)

C. Euglenophyta (euglenoids)-molecular classification places these with amoeboflagellates
   6. Same chlorophylls (a and b) as Chlorophyta and Charophyta; found in fresh and brackish waters and in moist soils
   7. Genus Euglena-members of this genus:
      a. Have elongated cells bounded by a plasma membrane; inside the plasma membrane is a pellicle (articulated proteinaceous strips lying side-by-side), which is elastic enough to enable turning and flexing of the cell, yet rigid enough to prevent excessive alterations in cell shape
      b. Have a stigma located near an anterior reservoir
      c. Have a large contractile vacuole, which collects water and empties it into the reservoir for osmotic regulation
      d. Have paired flagella at anterior end that arise from reservoir base; only one beats to move the cell
      e. Reproduce by longitudinal mitotic cell division

D. Chrysophyta (golden-brown and yellow-green algae and diatoms)-molecular classification places these with the stramenopiles
   6. Divided into three classes: golden-brown algae, yellow-green algae, and diatoms
   7. Contain chlorophylls a and c1/c2, and the carotenoid fucoxanthin
   8. Major carbohydrate reserve is chrysolaminarin
   9. Some lack cell walls; some have intricately patterned scales on the plasma membrane; diatoms have a distinctive two-piece wall of silica called a frustule; have zero, one, or two flagella (of equal or unequal length)
   10. Most are unicellular or colonial; reproduction is usually asexual, but occasionally sexual
   11. Diatoms are photosynthetic, circular or oblong cells with overlapping silica shells (epitheca-larger half and hypotheca-smaller half)
      e. Grow in aquatic habitats and moist soil
      f. Some are faculatative heterotrophs
      g. Vegetative cells are diploid and reproduce asexually with each daughter getting one old theca and constructing one new theca; this type of reproduction results in diatoms getting progressively smaller with each reproductive cycle; when diminished to 30% of original size, sexual reproduction occurs

E. Phaeophyta (brown algae)-molecular classification places these with stramenopiles
    10. Multicellular seaweeds; some species have the largest linear dimensions known in the eucaryotic world
    11. Simplest species have branched filaments; more complex species (kelps) are differentiated into flattened blades, stalks, and holdfast organs that anchor them to rocks
    12. Contain chlorophylls a and c; carotenoids include fucoxanthin, violaxanthin, and b-carotene

F. Rhodophyta (red algae)-molecular classification gives these a separate lineage
    12. Some are unicellular, but most are multicellular, filamentous seaweeds; comprise most of the seaweeds
    13. Carbohydrate reserve is floridean starch
    14. Contain phycoerythrin (red pigment) and phycocyanin (blue pigment), and can therefore live in deeper waters
    15. Their cell walls include a rigid inner part composed of microfibrils and a mucilaginous matrix consisting of sulfated polymers of galactose (agar); many also deposit calcium carbonate in their cell walls and contribute to coral reef formation

G. Pyrrhophyta (dinoflagellates)-molecular classification places these with the alveolates
    15. Unicellular, photosynthetic protists
    16. Most are marine organisms but a few are freshwater dwellers; some are responsible for phosphorescence in ocean waters and for toxic red tides
    17. Their flagella and protective coats are distinctive
        g. Are clad in stiff, patterned, cellulose plates (thecae)
        h. Most have two perpendicular flagella that function in a manner that causes organism to spin
    18. Contain chlorophylls a and c, carotenoids, and xanthophylls
    19. Some can ingest other cells; some are heterotrophic; some are endosymbiotic, living within host cells where they lose their cellulose plates and flagella (zooxanthellae)

THE PROTOZOA

Chapter Overview

This chapter discusses the characteristics of those protists that are commonly referred to as the protozoa. Protozoa exhibit different types of locomotion and this has been traditionally important in their classification. Using molecular methods, the protozoa have been shown to be polyphyletic. In addition to a discussion of their general features and the vast array of their niches and habitats, individual coverage of some representative protozoa is given.

Chapter Objectives

After reading this chapter you should be able to:

1. describe the various habitats, types of locomotion, and specialized organelles of protozoa
2. discuss the characteristics of the seven phyla of protozoa
3. describe the reproductive strategies employed by protozoa
4. discuss the various types of nuclei that are found in protozoa
5. describe the various feeding mechanisms used by protozoa

These are the most important concepts you are learning in this chapter:

1. Protozoa are protists exhibiting heterotrophic nutrition and various types oflocomotion. They occupy a vast array of habitats and niches and have organelles similar to those found in other eucaryotic cells, and also specialized organelles.
2. Current protozoan taxonomy divides the protozoa into seven phyla: Sarcomastigophora, Labyrinthomorpha, Apicomplexa, Microspora, Ascetospora,Myxozoa, and Ciliophora. These phyla represent four major groups: flagellates, amoebae, ciliates, and sporozoa. In molecular classification schemes, the protozoa are polyphyletic eucaryotes.
3. Protozoa usually reproduce asexually by binary fission. Some have sexual cycles,involving meiosis and the fusion of gametes or gametic nuclei resulting in a diploid zygote. The zygote is often a thick-walled, resistant, and resting cell called a cyst.
4. Some protozoa undergo conjugation in which nuclei are exchanged between cells.
5. All protozoa have one or more nuclei; some have a macro- and micronucleus.
6. Various protozoa feed by holophytic, holozoic, or saprozoic means; some are predatory or parasitic.

Study Outline

I. Introduction
   A. Protozoa are a polyphyletic group of organisms
   B. Protozoa are unicellular, eucaryotic protists that are usually motile
   C. Protozoology is the study of protozoa
II. Distribution
   C. Primarily in moist habitats, including freshwater, marine, and moist terrestrial environments
   D. Most are free living, but some are parasitic in plants and animals
III. Importance
   D. Serve as an important link in food chains and food webs (zooplankton)
      1. Food chain-series of organisms, each feeding on the preceding one
      2. Food web-complex interlocking series of food chains
   E. Important in the study of biochemistry and molecular biology because they use the same metabolic pathways as multicellular eucaryotes
   F. Causative agents of some important diseases in humans and other animals
IV. Morphology
   F. Many aspects of their morphology are the same as those of cells of multicellular animals; however, protozoa have some unique features
      1. Ectoplasm is the gelatinous cytoplasm just inside the plasma membrane; it provides some rigidity and shape
      2. Pellicle consists of the plasma membrane and the structures immediately beneath it

3. Endoplasm is the more fluid cytoplasm in the interior of the cell
4. Some have one nucleus, some have two or more identical nuclei, and some have two distinct types of nuclei
   a. The macronucleus is associated with trophic activities and regenerative processes
   b. The micronucleus controls reproductive activities by sequestering genetic material for exchange during reproduction

G. Vacuoles are usually present
   3. Contractile vacuoles are osmoregulatory
   4. Phagocytic vacuoles are sites of food digestion
   5. Secretory vacuoles usually contain enzymes for specific functions, such as excystation

H. Some protozoa are anaerobic (e.g., Trichonympha lives in the gut of termites)
   5. Most anaerobic protozoa do not have mitochondria or cytochromes, and have an incomplete TCA cycle
   6. Some anaerobic protozoa contain hydrogenosomes-small membrane-delimited organelles containing a unique electron transfer system that uses protons as terminal electron acceptors to form molecular hydrogen

IX. Nutrition
   A. In holozoic nutrition, nutrients are acquired by phagocytosis; some ciliates have a specialized structure, called a cytosome, for phagocytosis
   B. In saprozoic nutrition, nutrients are acquired by pinocytosis, diffusion, or carrier-mediated transport (facilitated diffusion or active transport)

VI. Encystment and Excystment
   B. Encystation is the development of a resting stage structure called a cyst
      1. The cyst is a dormant form that has a wall and greatly reduced metabolic activity
      2. Functions of cysts
         a. Protect against adverse changes in the environment
         b. Function as sites for nuclear reorganization and cell division
         c. Serve as a means of transfer from one host to another for parasitic species
   C. Excystation is the escape of vegetative forms, called trophozoites, from the cyst; it is usually triggered by a return to a favorable environment (e.g., such as entry into a new host for parasitic species)

VII. Locomotory Organelles
   C. A few protozoa are nonmotile
   D. Most use one of three major types of locomotory organelles
      6. Pseudopodia-cytoplasmic extensions
      7. Cilia-filamentous extensions (short)
      8. Flagella-filamentous extensions (long)

VIII. Reproduction
   C. The most common method of asexual reproduction is binary fission, which involves mitosis followed by cytokinesis
   D. The most common type of sexual reproduction is conjugation, an exchange of gametic nuclei between paired protozoa of complementary mating types

IX. Classification
   D. The most accepted scheme classifies protozoa as a subkingdom of protists, containing seven phyla; classification is based primarily on types of nuclei, mode of reproduction, and mechanism of locomotion
   E. Recently, other schemes have been suggested
      8. Cavalier-Smith has proposed elevating the protozoa to the status of a kingdom with 18 phyla
      9. Molecular classification schemes suggest that the protozoa do not exist as an evolutionary taxon, but rather that the protozoa are polyphyletic

X. Representative Types
   D. Phylum Sarcomastigophora
      1. This phylum includes protists with a single type of nucleus and flagella or pseudopodia; they reproduce asexually and sexually
      2. Subphylum Mastigophora contains both phytoflagellates (chloroplast-bearing flagellates) and zooflagellates; zooflagellates have the following characteristics:
         a. Do not have chlorophyll; are holozoic or saprozoic

b. Asexual reproduction occurs by longitudinal binary fission; sexual reproduction is known for a few species, and encystment is common
c. One group, the kinetoplastids, has mitochondrial DNA in a special region called the kinetoplast
d. Some are free living; some are endosymbiotic (e.g., Trichonympha species in the intestines of termites
e. Many are important human parasites (e.g., Trichomonas vaginalis, Giardia lamblia, and Trypanosoma brucei)

3. Subphylum Sarcodina-contains amoeboid organisms
   e. Found in aquatic and terrestrial habitats, where they take up nutrients by phagocytosis and pinocytosis
   f. Reproduction is usually by simple asexual binary fission; some form cysts
   g. Some have a loose-fitting shell called a test (e.g., foraminiferans and radiolarians, which are primarily marine amoebae; a few occur in fresh or brackish water)
   h. Some are endosymbionts and can be either commensals or parasites; some are free-living, disease-causing amoebae

E. Phylum Labyrinthomorpha
   1. Protists with spindle-shaped or spherical, nonamoeboid, vegetative cells; some move by gliding motion on mucous tracks
   2. Most members are marine organisms and are either saprozoic or parasitic on algae

A. Phylum Apicomplexa
   2. Often called sporozoans because they have a spore-forming stage in their life cycle; lack locomotory organelles, except the male gametes and the zygotes (ookinetes); are either intra- or intercellular parasites having a characteristic structure called the apical complex
   3. Apical complex-a unique arrangement of fibrils, tubules, vacuoles, and other organelles at one end of the cell
      h. One or two polar rings at the apical end
      i. Conoid-spirally arranged fibers adjacent to the polar rings
      j. Subpellicular microtubules radiate from the polar rings and probably serve as support elements
      k. Rhoptries extend to the plasma membrane and secrete their contents at the cell surface (probably aids in host cell penetration)
      l. Micropores take in nutrients
   4. Have complex life cycles involving two different hosts (usually mammal and often a mosquito)
      l. Life cycle has both asexual and sexual phases and is characterized by an alternation of haploid and diploid generations
      m. At some point in the life cycle, they undergo schizogony, a rapid series of mitotic events producing a large number of small infective organisms through the formation of uninuclear buds
      n. Sexual reproduction involves the formation of a thick-walled oocyst after fertilization; meiosis within this structure then produces haploid infective spores
   5. This group includes some very important pathogens
      n. Plasmodium-malaria
      o. Cryptosporidium-cryptosporidiosis
      p. Toxoplasma-toxoplasmosis
      q. Eimeria-coccidiosis

G. Phylum Microspora
   2. Obligately intracellular parasites lacking mitochondria and transmitted by a resistant spore
   3. Several economically important pathogens of insects
   4. There has been increased interest in their use as biological pest control
   5. Recently, five genera have been implicated in human diseases in immunosuppressed patients (e.g., AIDS patients)

H. Phylum Acetospora-parasitic protists with spores that lack polar caps or polar filaments, parasitic in mollusks

I. Phylum Myxozoa-parasitic protists with resistant spores having one to six coiled polar filaments; parasitic on freshwater and marine fish; can cause a major economic problem in cultured salmon

J. Phylum Ciliophora

9. The largest of the seven phyla; these organisms are distinguished by the use of cilia as locomotory organelles
    b. Cilia arranged in longitudinal rows or spirals
    c. Oblique stroke of cilia causes ciliates to rotate as they swim
    d. Can move forward or backward

10. Numerous interesting morphological characteristics are observed: slipper-shaped cells, stalked cells, tentacles, and threadlike darts called toxicysts

11. Feeding behavior
    b. Food is captured by action of cilia around the buccal cavity; food enters the cytostome and passes to phagocytic vacuoles that fuse with lysosomes, where digestion occurs
    c. After digestion the vacuoles fuse with a special region of the pellicle, called the cytoproct, which empties the cell's waste material to the outside

12. Most have two types of nuclei
    c. Micronucleus-diploid; functions in mitosis and meiosis
    d. Macronucleus-polyploid for some genes; maintains routine cellular functions

13. Asexual reproduction is by transverse binary fission; sexual reproduction usually is by conjugation

14. Most are free-living; some are harmless commensals; others are disease-causing parasites

VIRUS

Chapter 16. The Viruses: Introduction and General Characteristics

Chapter Overview

Viruses are generally small, acellular entities that usually possess only a single type of nucleic acid and that must use the metabolic machinery of a living host in order to reproduce. Viruses have been and continue to be of tremendous importance for a variety of reasons: many human diseases have a viral etiology; the study of viruses has contributed greatly to our knowledge of molecular biology; and the blossoming field of genetic engineering is based on discoveries in the field of virology. This chapter focuses on the general properties of viruses, the development of the science of virology, and the methodology used to study viruses.

Chapter Objectives

After reading this chapter you should be able to:

1. define viruses and discuss the implications of the concepts embodied in the definition
2. discuss the various requirements for culturing viruses
3. discuss the methodology employed for virus purification and enumeration
4. discuss the composition and arrangement(s) of viral capsids
5. discuss the variety found in viral genomes (DNA or RNA, single or double stranded, linear or circular, etc.)
6. describe the way in which viruses are classified

These are the most important concepts you are learning in this chapter:

1. Viruses are simple, acellular entities consisting of one or more molecules of either DNA or RNA enclosed in a coat of protein.
2. Viruses can reproduce only within living cells and are obligately intracellular parasites.
3. All viruses have a nucleocapsid composed of a nucleic acid surrounded by a protein capsid that may be icosahedral, helical or complex in structure.
4. More variety is found in the genomes of viruses than in those of procaryotes and eucaryotes.
5. Viruses genomes may be either single-stranded or double-stranded DNA or RNA. The nucleic acid strands can be linear, closed circle, or able to assume either shape.
6. Viruses are classified on the basis of their nucleic acid's characteristic, capsid symmetry, the presence or absence of an envelope,their host, and the diseases caused by animal and plant viruses.

Study Outline

I. Early Development of Virology
   A. Many epidemics of viral diseases occurred before anyone understood the nature of the causative agents of those diseases
   B. Edward Jenner (1798) published case reports of successful attempts to prevent disease (smallpox) by vaccination; these attempts were made even though Jenner did not know that the etiological agent of the disease was a virus
   C. The word virus, which is Latin for poison, was used to describe diseases of unknown origin; filtering devices, which trapped bacteria but not viruses, were used by several scientists (Ivanowski, Beijerinck, Loeffler, Frosch, and Reed) to study a number of infectious agents; their recognition of an entity that was filterable (i.e., passed through a filter) led to the modern use of the term virus
   D. The role of viruses in causing malignancies was established by Ellerman and Bang (1908), who showed that leukemia in chickens was caused by a filterable virus, and Peyton Rous (1911), who showed that muscle tumors in chickens were caused by a filterable virus
   E. The existence of bacterial viruses was established by the work of Frederick Twort (1915), who first isolated bacterial viruses, and Felix díHerelle (1917), who devised a method for enumerating them and demonstrated that they could reproduce only in live bacteria

F. W.M. Stanley (1935) helped demonstrate the chemical nature of viruses when he crystallized the tobacco mosaic virus and showed that it was mostly composed of protein; subsequently, F. C. Bawden and N. W. Pirie (1935) separated tobacco mosaic virus particles into protein and nucleic acid components

II. General Properties of Viruses
   F. They have a simple, acellular organization, consisting of one or more molecules of DNA or RNA enclosed in a coat of protein, and sometimes in more complex layers
   G. With one known exception, virions contain either DNA or RNA, but not both
   H. They are obligate intracellular parasites

III. The Cultivation of Viruses
   H. Cultivation requires a suitable host B. Hosts for animal viruses
      1. Suitable host animals
      2. Embryonated eggs 3. Tissue (cell) cultures-monolayers of animal cells
         a. Cell destruction can be localized if infected cells are covered with a layer of agar; the areas of localized cell destruction are called plaques
         b. Viral growth does not always result in cell lysis to form a plaque; microscopic (or macroscopic) degenerative effects can sometimes be seen; these are referred to as cytopathic effects
   I. Bacteriophages (viruses that infect bacteria) are usually cultivated in broth or agar cultures of suitable, young, actively growing host cells; broth cultures usually clear, while plaques form in agar cultures
   J. Plant viruses can be cultivated in
      1. Plant tissue cultures
      2. Cultures of separated plant cells
      3. Whole plants-may cause localized necrotic lesions or generalized symptoms of infection
      4. Plant protoplast cultures
   K. Virus Purification and Assays
   L. Virus purification
      4. Centrifugation of virus particles
         a. Differential centrifugation separates according to size
         b. Gradient centrifugation separates according to density or to sedimentation rate (size and density), and is more sensitive to small differences between various viruses
      5. Differential precipitation with ammonium sulfate or polyethylene glycol separates viruses from other components of the mixture
      6. Denaturation and precipitation of contaminants with heat, pH, or even organic solvents can sometimes be used
      7. Enzymatic degradation of cellular proteins and/or nucleic acids can sometimes be used because viruses tend to be more resistant to these types of treatment
   M. Virus assays
      7. Particle count
         a. Direct counts can be made with an electron microscope
         b. Indirect counts can be made using methods such as hemagglutination (virus particles can cause red blood cells to clump together or agglutinate)
      8. Measures of infectivity
         b. Plaque assays involve plating dilutions of virus particles on a lawn of host cells; clear zones result from viral damage to the cells; results are expressed as plaque-forming units (PFU)
         c. Infectious dose assays are an end point method for determining the smallest amount of virus needed to cause a measurable effect, usually on 50% of the exposed target units; results are expressed as infectious dose (ID_{50}) or lethal dose (LD_{50})

IV. The Structure of Viruses
   I. Virion size-ranges from 10 nm to 400 nm
   J. General Structural Properties
      7. Nucleocapsid-the nucleic acid plus the surrounding capsid (protein coat that surrounds the genome); for some viruses this may be the whole virion; other viruses may possess additional structures

8. Four morphological types of capsids and virions
    c. Icosahedral
    d. Helical
    e. Enveloped-having an outer membranous layer surrounding the nucleocapsid
    f. Complex-having capsid symmetry that is neither purely icosahedral or helical
9. Viral capsids are constructed from many copies of one or a few types of proteins (protomers), which are assembled, together with the viral genome, by a process called self-assembly

K. Helical capsids-hollow tube with a protein wall shaped as a helix or spiral; may be either rigid or flexible;

L. Icosahedral capsids-regular polyhedron with 20 equilateral triangular faces and 12 vertices; appears spherical; constructed of capsomeres (ring or knob-shaped units), each usually made of five or six protomers

M. Nucleic acids
7. Viral genome may be either RNA or DNA, single- or double-stranded, linear or circular
8. DNA viruses
    c. Most use double stranded DNA as genome
    d. Many have one or more unusual bases (e.g., hydroxymethylcytosine instead of cytosine)
9. RNA Viruses-most have single-stranded RNA (ssRNA) as their genome
10. Plus strand viruses have a genomic RNA with the same sequence as the viral mRNA; the genomic RNA molecules may have other features (5¢ cap, poly-A tail, etc.) common to mRNA and may direct the synthesis of proteins immediately after entering the cell
11. Negative strand viruses have a genomic RNA complementary to the viral mRNA
12. Segmented genomes are those in which the virion contains more than one RNA molecule; each segment is unique and frequently encodes a single protein

N. Viral envelopes and enzymes
12. Envelopes are membrane structures surrounding some (but not all) viruses
    c. Lipids and carbohydrates are usually derived from the host membranes
    d. Proteins are virus specific
    e. Many have protruding glycoprotein spikes (peplomeres)
13. Enzymes-some viruses have capsid-associated enzymes; many are involved in viral nucleic acid replication

O. Viruses with capsids of complex symmetry
13. Poxviruses are large (200 to 400 nm) with an ovoid exterior shape
14. Some bacteriophages have complex, elaborate shapes composed of heads (icosahedral symmetry) coupled to tails (helical symmetry); the structure of the tail regions are particularly variable; such viruses are said to have binal symmetry

V. Principles of Virus Taxonomy

L. In 1971, the International Committee for Taxonomy of Viruses developed a uniform classification system, which places the greatest weight on these properties:
14. Nucleic acid type
15. Nucleic acid strandedness (double or single stranded)
16. The sense of ssRNA genomes
17. The presence or absence of an envelope
18. The host

M. In addition, other characteristics (capsid symmetry, diameter of capsid or nucleocapsid, number of capsomeres in icosahedral viruses, immunological properties, gene number and genomic map, intracellular location of virus replication, presence or absence of a DNA intermediate in the replication of ssRNA viruses, type of virus release, and disease caused by the virus) can be considered

Chapter Web Links

<u>All the Virology on the WWW</u>
(http://www.tulane.edu/~dmsander/garryfavweb.html)

All the Virology on the WWW "seeks to be the best single site for Virology information on the Internet. We have collected all the virology related Web sites that might be of interest to our fellow virologists, and others interested in learning more about viruses".

The Big Picture Book of Viruses
(http://www.tulane.edu/~dmsander/Big_Virology/BVFamilyGenome.html)
The Big Picture Book of Viruses is "intended to serve as both a catalog of virus pictures on the WWW and as an educational resource to those seeking more information about viruses".

Electron microsopic images of Human Viruses
(http://www.uct.ac.za/depts/mmi/stannard/linda.html)
Electron microsopic images of Human Viruses - Linda Stannard's "illustrated tutorial on the morphology of most of the clinically significant viruses. The section on Hepatitis B virus is especially recommended".

Visualizations of Viruses at the University of Wisconsin - Madison
(http://www.bocklabs.wisc.edu/virusviztop.html)

The Index Virum
(http://life.anu.edu.au/viruses/Ictv/index.html)
The Index Virum presents lists of virus taxa that reflect the currently approved classification of the International Committee on Taxonomy of Viruses (ICTV).

The Viruses: Bacteriophages

Chapter Overview

This chapter focuses on the characteristics of the bacterial viruses (bacteriophages). It begins with their classification and then details the infectious cycle of those DNA viruses that cause destruction (lysis) of host cells. RNA phages are discussed briefly, and the chapter concludes with information about phages that can set up a stable residence within the host cell. These phages are called temperate phages, and the process is referred to as lysogeny.

Chapter Objectives

After reading this chapter you should be able to:

1. describe the four phases of the viral life cycle
2. discuss the differences between DNA phages and RNA phages in terms of their life cycles and their interactions with their hosts
3. discuss the establishment and maintenance of lysogeny by temperate phages

These are the most important concepts you are learning in this chapter:

1. Since a bacteriophage cannot independently reproduce itself, the phage takes over its host cell and forces the host to reproduce it.
2. The lytic bacteriophage life cycle is composed of four phases: adsorption of the phage to the host and penetration of virus genetic material, synthesis of virus nucleic acid and capsid proteins, assembly of complete virions, and the release of phage particles from the host.
3. Temperate virus genetic material is able to remain within host cells and reproduce in synchrony with the host for long periods in a relationship known as lysogeny. Usually the virus genome is found integrated into the host genetic material as a prophage. A repressor protein keeps the prophage dormant and prevents virus reproduction.

Study Outline

I. Classification of Bacteriophages
  A. The most important criteria used for classification are phage morphology and nucleic acid properties
  B. Most bacteriophages have double-stranded DNA (dsDNA), although single-stranded DNA (ssDNA) and RNA viruses are known
  C. Most can be placed in one of a few morphological groups: tailless icosahedral, viruses with contractile tails, viruses with noncontractile tails, and filamentous viruses

II. Reproduction of Double-Stranded DNA Phages
  C. Lytic cycle-culminates with the host cell bursting and releasing virions
  D. The one-step growth experiment
    1. Reproduction is synchronized so that events during replication can be observed
      a. Bacteria are infected and then diluted so that the released phages will not immediately find new cells to infect
      b. The released phages are then enumerated
    2. Several distinct phases are observed in the viral replication cycle
      b. Latent period-no release of virions detected; represents the shortest time required for virus reproduction and release; the early part of this period is called the eclipse period, and during this period no infective virions can be found even inside infected cells
      c. Rise period (burst)-rapid lysis of host cells and release of infective phages; burst size is the number of infective virions released per infected cellc. Plateau period-no further release of infective virions
  E. Adsorption to the host cell and penetration
    1. Viruses attach to specific receptor sites (proteins, lipopolysaccharides, teichoic acids, etc.) on the host cell
    2. Many viruses inject DNA into the host cell, leaving an empty capsid outside
  F. Synthesis of phage nucleic acids and proteins
    2. mRNA molecules transcribed early in the infection (early mRNA) are synthesized using host RNA polymerase; early proteins, made at the direction of these mRNA molecules, direct the synthesis of protein factors and enzymes required to take over the host cell
    3. Transcription of viral genes then follows an orderly sequence due to the modification of the host RNA polymerase and changes in sigma factors
    4. Later in the infection viral DNA is replicated
      c. Synthesis of viral DNA sometimes requires the initial synthesis of alternate bases; these are sometimes used to protect the phage DNA from host enzymes (restriction endonucleases) that would otherwise degrade the viral DNA and thereby protect the host
      d. For some bacteriophages, concatemers of the DNA genome are formed; these are later cleaved during assembly
  G. The assembly of phage particles
    3. Late mRNA molecules (those made after viral nucleic acid replication) direct the synthesis of capsid proteins and other proteins involved in assembly (e.g., scaffolding proteins) and release of the virus
    4. Assembly proceeds sequentially by subassembly lines, which assemble different structural units (e.g., baseplate, tail tube); these are then put together to make the complete virion 3. DNA packaging is still not well understood
  H. Release of phage particles
    4. Many phages lyse their host by damaging the cell wall or the cytoplasmic membrane
    5. A few phages (e.g., filamentous fd phages) are released without lysing the host cell; instead the phages are released through a secretory process

III. Reproduction of Single-Stranded DNA phages
  D. fX174 (+stand DNA virus-virus DNA that has the same sequence as the viral mRNA)
    1. ssDNA is converted to double-stranded replicative form (RF) by host DNA polymerase
    2. RF directs synthesis of more RF, RNA and +strand DNA genome
  E. Filamentous phages (e.g., fd)
    2. DNA enters via sex pilus
    3. Replicative form is synthesized

    4. Replicative form directs mRNA synthesis
    5. Protein encoded by mRNA then directs phage DNA replication via rolling circle method

IV. Reproduction of RNA Phages
  A. Single-stranded RNA phages
    1. RNA replicase-the virus must provide an enzyme for replicating the RNA genome because the host does not produce an enzyme with this capability
      a. The RNA genome is usually plus stranded (+) and can act as mRNA to direct the synthesis of the replicase during an initial step after penetration
      b. +strand RNA is then converted to dsRNA, the replicative form
      c. Replicative form is then used as a template for production of multiple copies of the genomic (and messenger) +strand RNA
    2. Capsid proteins are made, and +strand RNA is packaged into new virions
    3. One or more lysis proteins then function to release the phage
  B. Only one dsRNA phage has so far been discovered (f6); it infects Pseudomonas phaseolicola and possesses a membranous envelope

V. Temperate Bacteriophages and Lysogeny
  B. Temperate phages are capable of lysogeny, a nonlytic relationship with their hosts (virulent phages lyse their hosts)
    1. In lysogeny, the viral genome (called a prophage) remains in the host (usually integrated into the host chromosome) but does not kill (lyse) the host cell; the cells are said to be lysogenic (or are called lysogens)
    2. It may switch to the lytic cycle at some later time; this process is called induction
  C. Most bacteriophages are temperate; it is thought that being able to lysogenize bacteria is advantageous; supporting this is the observation that certain conditions favor the establishment of lysogeny
  D. Lysogenic conversion is a change that is induced in the host phenotype by the presence of a prophage and that is not directly related to the completion of the viral life cycle; examples include:
    5. Modification of lipopolysaccharide structure in infected Salmonella
    6. Production of diphtheria toxin only by lysogenized strains of Corynebacterium diphtheriae
  E. Establishment of lysogeny (bacteriophage lambda)
    6. Two sets of promoters are available to host RNA polymerase
    7. A repressor protein may be made from genes adjacent to one of these promoters
    8. If this repressor binds to its target operator before the other promoter is used, then that promoter is blocked and lysogeny is established
    9. If genes associated with that second promoter are expressed before the repressor can bind to the operator, then the lytic cycle is established
    10. Induction (the termination of lysogeny and entry into the lytic cycle) will occur if the level of the repressor protein decreases; this is usually in response to environmental damage to the host DNA
  F. For lambda and most temperate phages, if lysogeny is established, the viral genome integrates into the host chromosome; however, some temperate phages can establish lysogeny without integration

Chapter Web Links

<u>The Bacteriophage Ecology Group</u>
(http://www.phage.org/)
Home of Phage Ecology and Evolutionary Biology

<u>Bacteriophage Home Page</u>
(http://www.evergreen.edu/user/T4/home.html)

<u>The Life Cycle Of Bacteriophage Lambda - graphic</u>
(http://www.accessexcellence.com/AB/GG/bact_Lambda.html)

THE VIRUSES: VIRUSES OF EUCARYOTES

Chapter Overview

This chapter focuses on the characteristics of viruses that infect eucaryotes. Animal (mammalian) viruses are emphasized because they are causative agents of many human diseases. Other viruses, such as plant viruses and insect viruses, are also mengetahuied. The chapter concludes with a mengetahuiion of infectious agents that are even simpler than viruses, the viroids and prions.

Chapter Objectives

After reading this chapter you should be able to:

1. compare and contrast viruses that infect eucaryotes with those that infect procaryotes
2. describe the various ways that viruses of eucaryotes can harm their host organisms
3. discuss the establishment of persistent virus infections
4. discuss the mechanisms by which viruses may contribute to the development of certain cancers
5. discuss the importance of plant viruses and the technical difficulties that have hindered rapid progress in understanding them
6. discuss fungal and algal viruses
7. discuss the potential use of insect viruses for pest control
8. discuss the nature and significance of viroids and prions

These are the most important concepts you are learning in this chapter:

1. Although the details differ, animal virus reproduction is similar to that of the bacteriophages in having the same series of phases: adsorption, penetration and uncoating, replication of virus nucleic acids, synthesis and assembly of capsids, and virus release.
2. Viruses may harm their host cells in a variety of ways, ranging from direct inhibition of DNA, RNA, and protein synthesis to the alteration of plasma membranes and formation of inclusion bodies.
3. Not all animal virus infections have a rapid onset and relatively short duration. Some viruses establish long-term chronic infections; others are dormant for a while and then become active again. Slow virus infections may take years to develop.
4. Cancer can be caused by a number of factors, including viruses. Viruses may bring oncogenes into a cell, carry promoters that stimulate a cellular oncogene, or in other ways transform cells into tumor cells.
5. Plant viruses are responsible for many important diseases but have not been intensely studied due to technical difficulties. Most are RNA viruses. Insects are the most important transmission agents, and some plant viruses can even multiply in insect tissues before being inoculated into another plant.
6. Members of at least seven virus families infect insects; the most important belonging to the Baculoviridae Reoviridae, or Iridoviridae. Many insect infections are accompanied by the formation of characteristic inclusion bodies. A number of these viruses show promise as biological control agents for insect pests.

Study Outline

I. Classification of Animal Viruses
   A. Morphology-most important characteristic for classification
   B. Physical and chemical nature of virion, especially nucleic acids, are also important for classification
   C. Genetic relatedness-can be estimated by nucleic acid hybridization and sequencing

II. Reproduction of Animal Viruses
   C. Adsorption of virions
      1. Attach to specific receptor sites; usually cell surface glycoproteins that are required by the cell for normal cell functioning (e.g., hormone receptors, chemokine receptors)
      2. Viral surface glycoproteins and/or enzymes may mediate virus attachment to the cellular receptor molecules
   D. Penetration and uncoating

2. Little is known about precise mechanisms, but there appear to be three different modes of entry
    a. Changes in capsid structure leads to entry of nucleic acid into host
    b. Fusion of viral envelope with the host cytoplasmic membrane results in deposition of the nucleocapsid core within the cell
    c. Engulfment of virus within coated vesicles (endocytosis); lysosomal enzymes and low endosomal pH often trigger the uncoating process
3. Once in the cytoplasm the nucleic acid may function while still attached to capsid components or may only after completion of uncoating

E. Replication and transcription in DNA viruses
3. Expression of early viral genes (usually catalyzed by host enzymes) is devoted to taking over host cell; this may involve halting synthesis of host DNA, RNA, and protein or in some cases these processes may be stimulated
4. Later, viral DNA replication occurs, usually in the nucleus
5. Some examples
    a. Parvoviruses (ssDNA)-have a very small genome with overlapping genes; use host enzymes for all biosynthetic process
    b. Herpesviruses (dsDNA)-host RNA polymerase is used to transcribe early genes; DNA replication is catalyzed by viral DNA polymerase
    c. Poxviruses (dsDNA)-viral RNA polymerase synthesizes early mRNA; one of the early gene products is viral DNA polymerase, which replicates the viral genome
    d. Hepadnaviruses (circular dsDNA)-use reverse transcriptase to replicate its DNA genome via an RNA intermediate

F. Replication and transcription in RNA viruses
4. Transcription in RNA viruses (except retroviruses)
    a. +strand RNA viruses use their genome as mRNA
    b. -strand RNA viruses use viral RNA-dependent RNA polymerase (transcriptase) to synthesize mRNA, using the genome as the template
    c. dsRNA viruses use viral RNA-dependent RNA polymerase to synthesize mRNA
5. Replication in RNA viruses (except retroviruses)
    c. ssRNA viruses use viral replicase (an RNA-dependent RNA polymerase) to convert ssRNA into dsRNA (replicative form); replicative form serves as template for genome synthesis
    d. dsRNA viruses-viral mRNA molecules associate with special proteins to form a large complex; replicase then uses these mRNA molecules as templates for synthesis of dsRNA genome
6. For dsRNA viruses and -strand RNA viruses, the viral RNA-dependent RNA polymerase functions both as the transcriptase and the replicase; the mode of action depends on associated proteins and other factors
7. Retroviruses make a dsDNA copy (called proviral DNA) using the enzyme reverse transcriptase
    d. The proviral DNA is integrated into the host chromosome
    e. The integrated proviral DNA can then direct the synthesis of mRNA
    f. Sometimes these viruses can change the host cells into tumor cells

G. Synthesis and assembly of virus capsids
6. Capsid proteins are synthesized by host cell ribosomes under the direction of viral late genes
7. Empty procapsids are produced
8. Nucleic acid is inserted
9. Enveloped virus nucleocapsids are assembled similarly (except for poxvirus nucleocapsids, which are assembled by a complex process that begins with enclosure of some of the cytoplasmic matrix by construction of a membrane, followed by movement of viral DNA into the center of the immature virus)

H. Virion release
9. Naked viruses are usually released when host cell lyses
10. Enveloped viruses are usually released by the following mechanisms:

f. Virus-encoded proteins are incorporated into plasma membrane (some viruses use nuclear membrane, endoplasmic reticulum, Golgi apparatus, or other membranes)
g. Nucleocapsid buds outward, forming the envelope during release
11. Actin cytoskeleton microfilaments can aid virion release (e.g., poxviruses) without destroying the host cell

III. Cytocidal Infections and Cell Damage
A. Viruses often damage their host cells, in some cases causing cell death; if death occurs the infection is cytocidal
B. Seven mechanisms for causing cell damage have been identified
11. Inhibition of host DNA, RNA, and protein synthesis
12. Lysosome damage, leading to release of hydrolytic enzymes into the cell
13. Plasma membrane alteration, leading to host immune system attack on the cell or to cell fusion
14. Toxicity from high viral protein concentrations
15. Formation of inclusion bodies that may cause direct physical disruption of cell structure
16. Chromosomal disruptions
17. Malignant transformation to a tumor cell

IV. Persistent, Latent, and Slow Virus Infections
A. Persistent infections-long lasting infections
1. Chronic infection-virus is usually detectable, but clinical symptoms are mild or absent for long periods
2. Latent infections-virus stops reproducing and remains dormant for a period before becoming active again; during latency, no symptoms, antibodies or viruses are detectable
B. Causes of persistence and latency are probably multiple
2. Viral genome integrates into host chromosome
3. Virus becomes less antigenic
4. Virus mutates to less virulent and slower reproducing form
5. Deletion mutation produces defective interfering (DI) particles, which cannot reproduce but slow normal virus reproduction and thereby reduce host damage and establish a chronic infection
C. Slow virus infections are those that cause progressive, degenerative diseases with symptoms that increase slowly over a period of years

V. Viruses and Cancer
C. Cancer-a disease where there is abnormal cell growth (neoplasia) and the spread of the abnormal cells throughout the body (metastasis)
1. Tumor-a growth or lump of tissue; can be benign (nonspreading) or malignant (cancerous)
2. Carcinogenesis is a complex, multistep process that involves a triggering event and the activity of oncogenes
D. Viral etiology of human cancers is difficult to establish because Kochís postulates can only be satisfied for these diseases by experimenting on humans
E. Viruses and human cancers
17. Epstein-Barr virus (EBV)-a herpesvirus that may cause:
f. Burkittís lymphoma; found mostly in central and western Africa
g. Nasopharyngeal carcinoma; found in Southeast Asia
h. Infectious mononucleosis; found in the rest of the world
i. Evidence suggests that host infection with malaria is necessary for EBV to cause Burkittís lymphoma; this is supported by the low incidence of Burkittís lymphoma in the U.S. where there is almost no malaria
18. Hepatitis B virus may be associated with one form of liver cancer
19. Human papillomavirus has been linked to cervical cancer
20. Human T-cell lymphotropic viruses (the retroviruses HTLV-1 and HTLV-2) are associated with adult T-cell leukemia and hairy-cell leukemia, respectively
F. Viruses may cause cancer by a variety of mechanisms
20. Virus may carry one or more cancer-causing genes (oncogenes)
21. Viruses may produce a regulatory protein, which activates cell division

22. Viruses may insert a promoter or enhancer next to a cellular oncogene (an unexpressed cellular gene that regulates cell growth and reproduction), causing an abnormal expression of this gene and thereby deregulating cell growth

VI. Plant Viruses
  D. Have not been well studied, primarily because they are difficult to cultivate and purify
  E. Virion morphology does not differ significantly from that of animal viruses or bacteriophages; most are RNA viruses
  F. Plant virus taxonomy-classified on the basis of nucleic acid type, strandedness, capsid symmetry, size, and the presence or absence of an envelope
  G. Plant virus reproduction (using tobacco mosaic virus as an example)
    22. The virus uses either a cellular or a virus-specific RNA-dependent RNA polymerase
    23. The virus produces proteins, which then spontaneously assemble
    24. Viral spread is through the plant vascular system
    25. The virus causes many cytological changes, such as the formation of inclusion bodies and the degeneration of chloroplasts
  H. Transmission of plant viruses-process is complicated by the tough walls that cover plant cells
    25. Some may enter only cells that have been mechanically damaged
    26. Some are transmitted through contaminated seeds, tubers, or pollen
    27. Soil nematodes can transmit viruses while feeding on roots
    28. Some may be transmitted by parasitic fungi
    29. Most important agents of transmission are insects such as aphids or leafhoppers that feed on plants

VII. Viruses of Fungi and Algae
  F. Most viruses of higher fungi (mycoviruses) are dsRNA viruses that cause latent infections
  G. Viruses of lower fungi are dsRNA or dsDNA viruses that cause lysis of infected cells
  H. Algal viruses have been detected in electron micrographs, but have not been well studied

VIII. Insect Viruses
  H. Members of at least seven virus families are known to infect insects
  I. Infection is often accompanied by formation of granular or polyhedral inclusion bodies
  J. May persist as latent infections
  K. Current interest in most insect viruses focuses on their use for biological pest control; they have several advantages over chemical toxins:
    29. They are invertebrate-specific and, therefore, should be safe
    30. They have a long shelf life and high environmental stability
    31. They are well suited for commercial production because they reach high concentrations in infected insects

IX. Viroids and Prions
  J. Viroids
    1. Circular ssRNA molecules
    2. No capsids
    3. Cause diseases in plants
    4. Do not act as mRNAs
    5. Mechanism that produces symptoms of disease is unknown
    6. May give rise to latent infections
  K. Prions
    6. Proteinaceous infectious particles (PrP) that are not associated with a nucleic acid
    7. Genes have been identified in normal animal tissue that encode PrP

    It is hypothesized that abnormal PrP causes prion diseases by inducing a change from the normal conformation of the cellular PrP to the abnormal form b. This new abnormal PrP then causes other normal cellular PrP molecules to change to the abnormal form

    8. Cause progressive, degenerative central nervous system disorders
      a. Scrapie in sheep and goats
      b. Bovine spongiform encephalopathy (mad cow disease)
      c. Kuru (found only in the Fore, an eastern New Guinea tribe that practice ritual cannibalism)

d. Creutzfeldt-Jakob, fatal familial insomnia and Gerstmann-Strassler-Scheinker Syndrome are all human diseases caused by prions

Chapter Web Links

Common Cold web site
(http://www.commoncold.org/)

All the Virology on the WWW
(http://www.tulane.edu/~dmsander/garryfavweb.html)

The Big Picture Book of Viruses
(http://www.tulane.edu/~dmsander/Big_Virology/BVHomePage.html)

Electron microsopic images of Human Viruses
(http://www.uct.ac.za/depts/mmi/stannard/linda.html)
Linda Stannard's "illustrated tutorial on the morphology of most of the clinically significant viruses".

Visualizations of Viruses at the University of Wisconsin - Madison
(http://www.bocklabs.wisc.edu/virusviztop.html)