GEOBIOLOGY



Dawn Sumner
University of California, Davis



UCD: Geobiology (Sumner)

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (https://LibreTexts.org) and like the thousands of other texts available within this powerful platform, it is freely available for reading, printing, and "consuming."

The LibreTexts mission is to bring together students, faculty, and scholars in a collaborative effort to provide an accessible, and comprehensive platform that empowers our community to develop, curate, adapt, and adopt openly licensed resources and technologies; through these efforts we can reduce the financial burden born from traditional educational resource costs, ensuring education is more accessible for students and communities worldwide.

Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects. Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.



LibreTexts is the adaptable, user-friendly non-profit open education resource platform that educators trust for creating, customizing, and sharing accessible, interactive textbooks, adaptive homework, and ancillary materials. We collaborate with individuals and organizations to champion open education initiatives, support institutional publishing programs, drive curriculum development projects, and more.

The LibreTexts libraries are Powered by NICE CXone Expert and was supported by the Department of Education Open Textbook Pilot Project, the California Education Learning Lab, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptions contact info@LibreTexts.org or visit our main website at https://LibreTexts.org.

This text was compiled on 05/21/2026

TABLE OF CONTENTS

Licensing

1: Life and Earth

- 1.1: Daisyworld
- 1.2 Interactions Among Organisms

2: What is life?

- 1.1: What is life?

3: Genes to Enzymes

- DNA, RNA, Genes and Chromosomes
- DNA Replication
- How Asexual Prokaryotes Achieve Genetic Diversity
- Mutations
- Operon Theory
- Protein Synthesis (Translation)
- RNA Transcription
- What Are Genes?

4: Tracing the History of Evolution

- 4.1: Phylogenetic Trees
- 4.2: Limitations of Phylogenetic Trees
- 4.3: The Levels of Classification

5: Structure of life

- 3.1: Unique Characteristics of Prokaryotic Cells
- 3.2: Unique Characteristics of Eukaryotic Cells
- 3.3: Viruses
  - 3.3A: Viruses
  - 3.3B: The Viral Life Cycle

6: Microbial Metabolism

- 8.1: Energy, Matter, and Enzymes
- 8.2: Catabolism of Carbohydrates
- 8.3: Cellular Respiration
- 8.4: Fermentation
- 8.5: Catabolism of Lipids and Proteins
- 8.6: Photosynthesis and the Importance of Light
- 8.7: Biogeochemical Cycles

7: How Microbes Grow

- 5.1: How Microbes Grow

Index

Glossary

Detailed Licensing

Licensing

*A detailed breakdown of this resource's licensing can be found in **Back Matter/Detailed Licensing**.*

CHAPTER OVERVIEW

Front Matter

TitlePage

InfoPage

Table of Contents

Licensing

UCD: Geobiology (Sumner)

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (https://LibreTexts.org) and like the thousands of other texts available within this powerful platform, it is freely available for reading, printing, and "consuming."

The LibreTexts mission is to bring together students, faculty, and scholars in a collaborative effort to provide an accessible, and comprehensive platform that empowers our community to develop, curate, adapt, and adopt openly licensed resources and technologies; through these efforts we can reduce the financial burden born from traditional educational resource costs, ensuring education is more accessible for students and communities worldwide.

Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects. Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.



LibreTexts is the adaptable, user-friendly non-profit open education resource platform that educators trust for creating, customizing, and sharing accessible, interactive textbooks, adaptive homework, and ancillary materials. We collaborate with individuals and organizations to champion open education initiatives, support institutional publishing programs, drive curriculum development projects, and more.

The LibreTexts libraries are Powered by NICE CXone Expert and was supported by the Department of Education Open Textbook Pilot Project, the California Education Learning Lab, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptions contact info@LibreTexts.org or visit our main website at https://LibreTexts.org.

This text was compiled on 05/21/2026

TABLE OF CONTENTS

Licensing

1: Life and Earth

- 1.1: Daisyworld
- 1.2 Interactions Among Organisms

2: What is life?

- 1.1: What is life?

3: Genes to Enzymes

- DNA, RNA, Genes and Chromosomes
- DNA Replication
- How Asexual Prokaryotes Achieve Genetic Diversity
- Mutations
- Operon Theory
- Protein Synthesis (Translation)
- RNA Transcription
- What Are Genes?

4: Tracing the History of Evolution

- 4.1: Phylogenetic Trees
- 4.2: Limitations of Phylogenetic Trees
- 4.3: The Levels of Classification

5: Structure of life

- 3.1: Unique Characteristics of Prokaryotic Cells
- 3.2: Unique Characteristics of Eukaryotic Cells
- 3.3: Viruses
  - 3.3A: Viruses
  - 3.3B: The Viral Life Cycle

6: Microbial Metabolism

- 8.1: Energy, Matter, and Enzymes
- 8.2: Catabolism of Carbohydrates
- 8.3: Cellular Respiration
- 8.4: Fermentation
- 8.5: Catabolism of Lipids and Proteins
- 8.6: Photosynthesis and the Importance of Light
- 8.7: Biogeochemical Cycles

7: How Microbes Grow

- 5.1: How Microbes Grow

Index

Glossary

Detailed Licensing

Licensing

*A detailed breakdown of this resource's licensing can be found in **Back Matter/Detailed Licensing**.*

CHAPTER OVERVIEW

1: Life and Earth

Earth is the only known inhabited planet, and the geological record demonstrates that life and Earth have co-evolved for billions of years in a closely linked system. Life is sustained by energy and material exchanges among Earth's interior, Earth's surface, and the Sun. In turn, life has changed the surface chemistry of Earth. These changes have propagated into Earth's interior through subduction. Through time, the mantle, lithosphere, hydrosphere, atmosphere, and biosphere have slowly evolved, with intervals of rapid change due to historical events (e.g. impacts, evolution of land plants, etc.). Both incremental evolution and historical events are reflected in the co-evolution of Earth and life. This evolution is reflected in biogeochemical cycles that extend from the mantle to the top of the atmosphere, with ecosystems evolving in response to perturbations and inducing planetary-scale changes in Earth's surface processes.

The field of Geobiology focuses on understanding these changes using diverse fields of study. Geobiologists can study modern life through ecology, organismal processes, genetics, and biogeochemistry. They can study the history of these interactions through geological studies, paleontology, geochemical approaches, and modeling. They can study these processes on other planets by applying what we understand of interactions on Earth to our observations from missions and telescopes. The key aspect that makes a study part of Geobiology is that it provides insights into how life and Earth (or other planets or moons) interact through time.

Sometimes it helps to look at a simplified system to understand a more complex one. The first part of this chapter introduces a very simple biosphere on a very simple world: Daisyworld (Watson and Lovelock, 1983). Black and white daisies on a planet receive energy from a star and influence the planet's temperature. We ignore all the biological aspects of daisies except their preferred temperature for sprouting and growth, plus their need for somewhere to grow. Even though Daisyworld represents a very simple ecosystem, it is still an interesting planet!

The second part of this chapter discusses some of the interactions among organisms that create complexity in ecosystems. In all cases, these interactions occur in the context of our planet and the resources it provides. While reading about interactions types, think about the interactions among the daisies in Daisyworld. How many different types of interactions are there? Can they be classified into the interaction types described in the second part of the chapter? If this was a real ecosystem, what other organisms would be needed to allow the daisies to grow? How would any of these needs affect the simple Daisyworld model?

Thumbnail: An artist's impression of ice age Earth at glacial maximum. CC-BY-SA 3.0 Unported; Ittiz via wikipedia).

1.1: Daisyworld

1.2 Interactions Among Organisms

References

Watson, Andrew J. & James E. Lovelock (1983) Biological homeostasis of the global environment: the parable of Daisyworld, Tellus B: Chemical and Physical Meteorology, 35:4, 284-289, DOI: 10.3402/tellusb.v35i4.14616)

This page titled 1: Life and Earth is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Dawn Sumner.

1.1: Daisyworld

(Content based on: Andrew J. Watson & James E. Lovelock (1983) Biological homeostasis of the global environment: the parable of Daisyworld, Tellus B: Chemical and Physical Meteorology, 35:4, 284-289, DOI: 10.3402/tellusb.v35i4.14616)

Summary

Life and Earth have interacted over billions of years, with life profoundly changing environments on Earth. In turn, Earth provides the boundary conditions for life. Lovelock (1983) and Watson and Lovelock (1983) proposed that life and Earth be considered as two parts of a coupled system. This system is too complex to fully model, but some of the behaviors of the interactions can be explored with a very simple system proposed by Watson and Lovelock (1983): Daisyworld. Daisyworld is a biosphere consisting of two species of daisy with different colors. “The growth rate of the daisies depends on only one environmental variable, temperature, which the daisies in turn modify because they absorb different amounts of radiation.” These relationships produce feedbacks that can stabilize or destabilize the temperature, depending on the temperature growth preferences for the two daisy species. Temperature is stabilized when the growth-temperature curve is peaked with darker (more heat absorbing) daisies growing at lower temperatures than white (more heat reflecting) daisies. Watson and Lovelock (1983) propose that these sorts of feedbacks stabilize temperature on Earth.

Introduction

Environments on Earth are modified by living things at scales from individual chemicals to the oxidation state of Earth’s surface. Even the formation of granite has been proposed as due to biological carbon cycling (e.g. ref). “In turn, geophysical and geochemical constraints have shaped the evolution of life and continue to dictate what type of life, and how much of it, can colonize” environments on Earth (Watson and Lovelock, 1983). Watson and Lovelock (1983) created a coupled system with two components: life and Earth. In their model, perturbations of life affect Earth and of Earth reflect life, leading to feedbacks between the two components. The coupling between the components may amplify a perturbation in a positive feedback or dampen it in a negative feedback.

Studying these feedbacks is difficult as demonstrated by the challenges of modeling climate change (e.g. refs). Non-linear feedbacks produce chaotic systems; for example the dynamics of the atmosphere led to the Lorenz Equations, which are a classic example of systematic behaviors but unpredictable results in detail. Consider a model that includes all of life and Earth processes over geological time; it is too complex to model in full. However, Watson and Lovelock (1983) proposed “an artificial world, having a very simple biota which is specifically designed to display the characteristic in which [they] are interested-namely, close-coupling of the biota and the global environment.” They proposed a few equations to capture this world and illustrate the importance of life-Earth interactions. The equations can be found in the original reference and are not reproduced here (yet) (Watson and Lovelock, 1983).

Daisyworld Model

Daisyworld is a planet colonized only by two species of daisy of different colors. One species is dark (called “black” here), and one species is light (called “white” here). Black daisies absorb more heat than white daisies do, so the parts of Earth covered by black daisies tends to warm up through time, whereas the parts covered by white daisies tend to cool down relative to bare ground. Watson and Lovelock (1983) propose a set of coupled differential equations to rigorously model the changes in temperature and to calculate the proportion of the planet covered with bare ground and each type of daisy. This model is fun to play with. However, it is also more complicated than we need to understand the feedbacks. Even a system as simple at the GEL 53 Geobiology Daisyworld Game produces interesting dynamics.

The key to understanding the feedbacks is to explore how the rules of the system either dampen or enhance perturbations. If black daisies grow better at lower temperatures than white daisies, cooler temperatures will lead to more black daisies, which will in turn increase the amount of heat absorbed. The absorption of more heat leads to warmer temperatures. As temperatures increase, more white daisies will grow, leading to less heat absorption and cooler temperatures. In this scenario, perturbations in temperature are dampened by the growth of the daisies, which is a negative (dampening) feedback. In the full Watson and Lovelock (1983) model:

> *The "environmental feedback" in the model as described so far is strongly limiting on both species of daisy. Black daisies are warmer than white, and tend therefore to be favoured by cooler mean temperatures, yet an increase in the numbers of black daisies tends to warm the planet. The same goes in reverse for the white daisies. Under these circumstances it is perhaps not surprising that the system exhibits a stable point around which the daisies can successfully homeostat the temperature over a wide range of luminosities.*

In contrast, if black daisies grow better at higher temperatures than white daisies, an increase in temperature will lead to more black daisies, which absorb more heat, which increases temperature even more. In this scenario, perturbations in temperature are amplified by the growth of the daisies, which is a positive (amplifying) feedback. Watson and Lovelock (1983) show how this positive feedback can be countered by adding another negative (dampening) feedback process to the system:

> *Owing to a subtle change of climate, clouds appear on daisyworld. The clouds are light in colour. We will assume that the clouds form only over stands of black daisies because of the rising air generated over these warm spots. Now, therefore, black daisies no longer tend to increase the temperature. Instead, more black daisies mean more white clouds and a colder planet.*

However, this change in dynamics has a huge impact on white daisies. They end up going extinct in the Watson and Lovelock (1983) model:

> *White daisies were not deliberately suppressed, but became extinct of their own accord. White daisies fail because, in the battle for survival of the fittest, they are now distinctly less fit than the black daisies. An increase in either species now tends to cool the planet, but black daisies, being warmer than the mean, thrive better at low temperatures.*

The conditions for daisy growth in their model are slightly different than that in the Daisyworld Game; it is not clear to me that white daisies can go extinct in our game without significant rule changes.

Relevance to Earth

The behaviors in Daisyworld are relevant to Earth even though the system is exceptionally simplified. Nearly a century of work developing numerical climate models has demonstrated that feedbacks among the biosphere, hydrosphere, and atmosphere are complexly interrelated (see Pinho, 2020 for a brief explanation). In particular, life has a substantial influence on Earth's temperature through both the heat absorbed and the cycling of greenhouse gases. It is very interesting to read Watson and Lovelock's original section on the relevance of Daisyworld to Earth in the context of our relatively poor understanding of greenhouse processes at that time. Here it is in its entirety:

> ***5. Relevance to the earth***
>
> *Extrapolation from daisyworld to the earth is, to say the least, rather tenuous at this stage. However, a peaked growth versus temperature curve is a universal property of living things. Furthermore, the biota may have a substantial influence oh the earth's temperature via the abundance of green- house gases in the atmosphere. Recently, Owen et al. (1979) and Walker et al. (1981) have speculated that the abundance of atmospheric CO_2 may have been dominant in determining the mean temper- ature of the earth through geological time, in which case the biota as a whole would appear to be depressing the mean temperature below that of the "sterile earth" by tending to reduce atmospheric CO_2*

> *pressures (Lovelock and Watson, 1982). In the present context, neither the direction nor the mechanism whereby life affects the temperature are of themselves important---only the assumption that the biota influence the temperature is required. For the sake of illustration, however, let us suppose that the net effect of life on Earth is to reduce atmospheric carbon dioxide, and that the biota are temperature limited. Thus a decrease in temper- ature would lead to an extension of the barren polar regions and would decrease the average level of biological activity over the earth as a whole, while a temperature increase would have the opposite effect. But a decrease in biological activity as a whole would presumably also decrease those activities which tend to reduce atmospheric CO_2. Thus carbon dioxide would increase to oppose the original change. We then have the rudiments of a temperature stabilization system for the earth analogous to that on daisyworld. We can speculate that some such mechanisms may have played a part in regulating the temperature and other environmental variables over the long history of the earth.*

References

Lovelock, J. E. 1983. Gaia as seen through the atmosphere. In *Biomineralization and biological metal accumulation* (eds. P. Westbroek and E. W. de Jong). The Netherlands: D. Reidel Publishing Co., Dordrecht, 15-25.

Lovelock, J. E. and Watson, A. J. 1982. The regulation of carbon dioxide and climate. Gaia or geochemistry? *Planet. Space Sci.* 30,193-802.

Owen, T., Cess, R. D. and Ramanathan, V., 1919. Enhanced CO2**,** greenhouse to compensate for reduced solar luminosity on the early earth. *Nature 2 7 7* , 640-642.

Pihno, Bárbara, 2020, How do climate models predict global warming? *Discovery* (online), accessed December 31, 2020 https://www.discovermagazine.com/env...global-warming

Walker, J. C. G., Hays, P. and Kasting, J. F. 1981. A negative feedback mechanism for the long-term stabilization of earth's surface temperature. *J. Geo-* phys. *Res.* 86,9116-9182.

Watson, A. J. and Lovelock, J. E., 1983. Biological homeostasis of the global environment: the parable of Daisyworld, Tellus B: Chemical and Physical Meteorology, 35:4, 284-289, DOI: 10.3402/tellusb.v35i4.14616

This page titled 1.1: Daisyworld is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Dawn Sumner.

1.2 Interactions Among Organisms

Introduction

In the previous section on Daisyworld, the interactions among daisies appear very simple. Yet Daisyworld has some very interesting behaviors due to feedbacks among black and white daisies and temperature . In real ecosystems, the interactions are more varied and complex. These interactions commonly produce feedbacks in the respective populations of various species. Competition for resources and predation can limit populations of organisms. Mutually beneficial relationships can increase the populations of both species interacting. And the organisms influence their environment, shaping Earth's surface and the resources available to ecosystems. Thus, interactions among species are a major component of how like on Earth persists and evolves through time.

Some Interaction Types

Most interactions between species have produce harms and benefits for the organisms involved, but sometimes the results are closer to neutral. There are typically 6 types of interactions when considering the harms and benefits to each species (Figure), but there are also other ways to frame interactions (see this Khan Academy video for example).

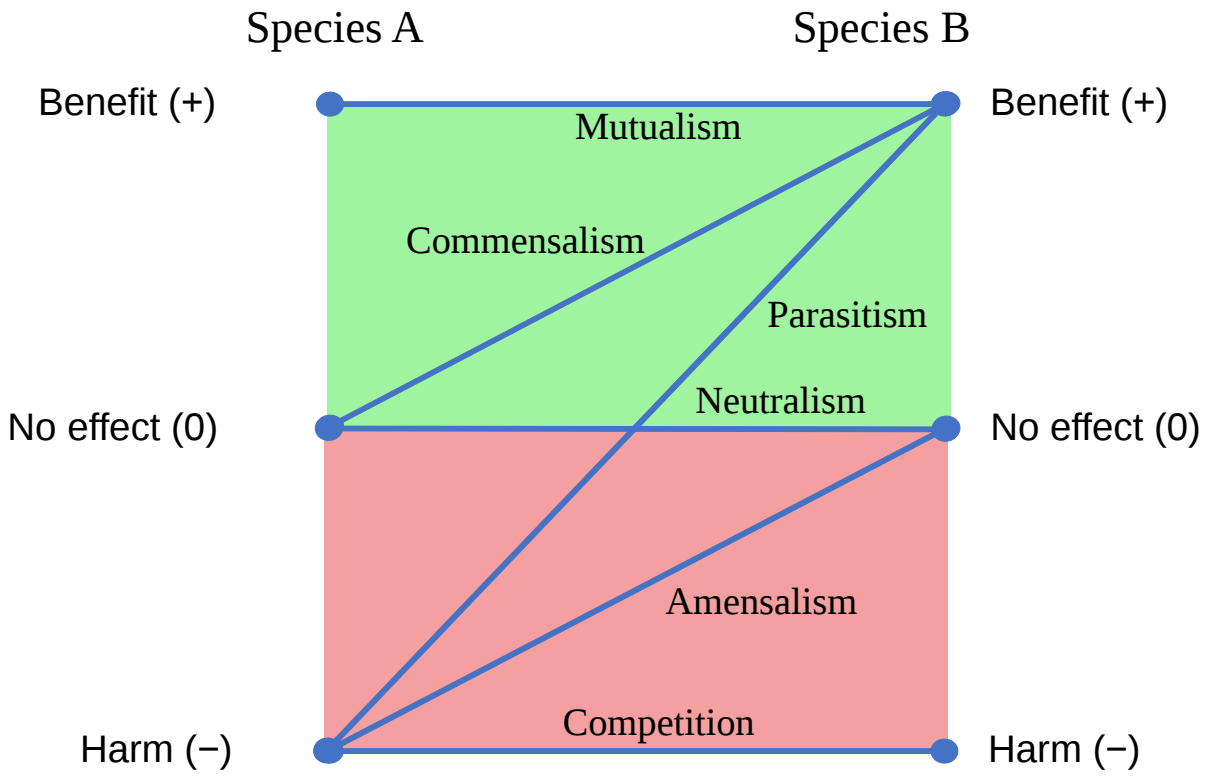


Figure: The benefits and harms to organisms with different types of interactions. Predation has the equivalent effects as parasitism in this diagram. (Diagram by Ian Alexander, Wikipedia, CC BY-SA 4.0)

The following sections include these interactions types, with examples. For the first three interactions types, mutualism, neutralism, and competition, the effects of the interaction are similar on both of the species. For the next three, the effects are asymmetric, with one species benefiting more than the other from the interaction. Note that these categories are neither the only interaction types nor

are they able to capture the intricacies of actual interactions among organisms. For example, how does an opossum pushing a skunk into the water fit within this classification? (Confession: I just wanted to include a link to the video.)

Mutualism

Many interactions result in benefits to both organisms, and for a relationship to be mutually beneficial, both species need to do better when interacting with the other. These relationships include organisms providing resources and protection for each other. Ecosystems are commonly built around these relationships, and mutualistic relationships allow large amounts of biomass to accumulate, say in a rainforest. Organisms helping each other increases the amount and diversity of life that can be supported.

> **Examples:** Insects pollinate flowers, which provide the insects with nectar and pollen as food. Fungi obtain their energy from breaking down dead wood to release nutrients for the living trees. Bacteria in our guts help us digest our food, and we provide them with a stable environment with plenty of food for themselves. The examples are limitless.

Neutralism

Some species exist in the same environment without directly affecting each other. If they use different resources in the environment and do not prey on each other, their direct interactions are neutral - neither good nor bad for either species. Even if their interactions are neutral, they are part of the same ecosystem, so changes in the ecosystem can affect both species similarly or differently.

> **Example**: California ground squirrels and mule deer both live in many California ecosystems. The squirrels generally eat seeds, barley, oats, and acorns with some insects and bird eggs. In contrast, mule deer largely browse on bushes and trees, with acorns being an important part of their diet in summer and fall (Sommer et al., 2007). These two species might compete for acorns when other resources are sparse, but they mostly exist in neutral proximity to each other. However, both are hunted by coyotes, bobcats, and pumas, so their populations are linked through other species. For example, if the population of squirrels declines, say from predation by red tailed hawks, there might be more predator pressure on deer from their common predators, e.g. coyotes, bobcats, and pumas. Thus, a large population of squirrels might reduce predation on deer, indirectly benefiting them, while also increasing competition for acorns if other food resources are low.

Competition

Competition for resources and space is very common among species that occupy similar roles in an ecosystem. When species compete with each other, both pay a price for that competition because they are sharing resources. When interactions are predominantly competitive, either species would do better if the other was not present. Competition tends to drive selection of the organisms that are best suited for a particular ecosystem role, with the population of the better adapted species increasing relative to that of the less well adapted species. As the population of the more successful species increases, it is less affected by the competition because each organism experiences fewer interactions with its competitors. In contrast, each individual of the less successful species experiences relatively more competitive interactions, making the harm experiences greater.

> **Example:** California grasslands have been invaded by new species of grass introduced by humans. These new species out competed the native species due to their greater ability to reproduce in many of the environments (see for example, Corbin and D'Antonio, 2010). The new species are taking up the space and nutrients previously used by the native grasses. In this case, the native species experienced a significantly greater harm during the competition than the invasive species.

> **Example:** Virginia opossums and striped skunks actually do compete with each other to some degree. Both are opportunistic feeders, eating almost anything that is available, with opossums eating more small vertebrates and plants and skunks focusing more on insects. They are also about the same size. Thus, they play a similar role in the ecosystem and can compete for both food and dens, although opossums can also den in trees. In contrast to the example of the grasses, opossums and skunks commonly co-exist, with the competition less intense and their abilities to reproduce more equal in many ecosystems.

Commensalism

Sometimes interactions benefit one organism while being of neither benefit nor harm to the other organism. These types of relationships are also very common and help promote diverse ecosystems.

> **Examples:** A tree frog in a rainforest benefits from the habitat created by the tree it lives in without harming or benefiting the tree. A cattle egret can catch half again as much food while expending two thirds of the energy if it searches for insects near grazing animals who disturb the insects. This activity does not directly benefit the grazing animals, nor does it harm them.

Amensalism

Interactions can have no effect on one species while harming another. These interactions are usually incidental to a behavior of the species that does not experience harm or benefit. They can include interactions such as a change in the environment, incidental killing of organisms, and other influences.

> **Examples:** Hippos consume a significant amount of undigestible organic matter, and they create a very large volume of poop. They often poop in ponds, and these ponds can become anoxic, killing the aquatic organisms that require oxygen to live (Pennisi, 2018). Most animals have stepped on insects, killing them.

Parasitism and Predation

Parasitism and predation both have a strong benefit for one species and a significant harm to the other. In both cases, one organism takes resources from another. Parasitism involves one organism living off the resources of another for an extended period of time without causing their death. Parasites benefit from the survival of their host organism. In contrast, predation usually involves killing the prey organism and consuming it. Often, parasites are small relative to their hosts, whereas predators are frequently about the same size as or larger than their prey. This difference in size is related to the energy needs of an organism relative to its size: in general, larger organisms need more energy to accumulate their biomass and to maintain their activity. A small parasite can take energy from a larger host for an extended period of time without killing it. In contrast, a larger organism generally needs more energy, so it is difficult to maintain itself without killing the organism it is preying on. Similarly, it is easier to kill an organism that is of similar size or smaller, so predators tend to prey on smaller organisms. In contrast, parasites typically kill by causing systemic problems for their hosts, such as diseases, extracting too many resources, or taking over cellular processes in the case of viruses.

> **Parasitism Examples:** Parasites include organisms like ticks that live by sucking the blood of mammals. Other parasites include mistletoe living in trees; mistletoe has evolved to plant its "roots" into the circulation system of the trees, extracting nutrients and water from the host. This can cause significant damage to the tree.

Predation Examples: Obvious examples include animals that prey on other animals. (see https://necsi.edu/predator-prey-relationships for some examples.)

Extra:

There are a lot of questions as to how herbivory (eating of plants) fits into this relationship scheme. If an herbivore kills the plant, the interaction is similar to predation. However, many plants survive and some have even evolved to do better when fed on by other species. For example, fruits often attract other species to help distribute the seeds for the plant. Thus, the relationships between plants and the things that eat them can be evaluated in terms of harms and benefits much like those involving other species interactions.

Summary

Relationships among organisms can be more complicated than who benefits or loses from the direct interactions. Both direct and indirect interactions have been driving forces for evolution, leading to deeply interconnected communities within ecosystems. The relationships often become more intricate and interdependent through time as species help and harm each other, responding to the organisms around them. These interactions often lead to stabilizing feedbacks and persistent ecosystems. Sometimes, however, a geological event, evolution of a revolutionary process, or the introduction of a new species can disrupt the established relationships and lead to ecological change that triggers an amplifying feedback.

Return to Daisyworld

In the introduction to this chapter, I posed some questions about the interactions among daisies in Daisyworld:

> *How many different types of interactions are there? Can they be classified into the interaction types described in the second part of the chapter? If this was a real ecosystem, what other organisms would be needed to allow the daisies to grow? How would any of these needs affect the simple Daisyworld model?*

How would you answer these questions after reading about different interaction types? What would you like to add to a Daisyworld model?

References

https://animaldiversity.org

Sommer, M. L., R. L. Barboza, R. A. Botta, E. B. Kleinfelter,
M. E. Schauss and J. R. Thompson. 2007. Habitat Guidelines for Mule Deer: California Woodland Chaparral Ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies. PDF

Pennisi, 2018 https://www.sciencemag.org/news/2018...-across-africa

Corbin and D'Antonio, 2010 https://link.springer.com/article/10...258-010-9722-0

1.2 Interactions Among Organisms is shared under a not declared license and was authored, remixed, and/or curated by LibreTexts.

CHAPTER OVERVIEW

2: What is life?

We only know life from Earth, which makes it difficult to define objectively. As scientists, we use what we know as a model, e.g. life on Earth. These readings help us understand what life is and how we classify it in the context of the evolution of life on Earth - with an understanding that it could be different elsewhere in the Universe.

1.1: What is life?

Thumbnail: Several types of photosynthetic bacteria (Cyanobacteria) that grow in Antarctic lakes and form pinnacles.

2: What is life? is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

1.1: What is life?

LEARNING OBJECTIVES

- Understand essential properties of life
- Distinguish between living and non-living systems

If we are going to talk about biology, and organisms and cells and such, we have to define what we mean by life. This raises a problem peculiar to biology as a science. We cannot define life generically because we know of only one type of life. We do not know whether this type of life is the only type of life possible or whether radically different forms of life exist elsewhere in the Universe or even on Earth, in as yet to be recognized forms.

While you might think that we know of many different types of life, from mushrooms to whales, from humans to the bacterial communities growing on the surfaces of our teeth (that is what dental plaque is, after all), the closer we look the more these different "types of life" are in fact all versions of a common underlying motif: they represent versions of a single type of life. Based on their common chemistry, molecular composition, cellular structure, and the way that they encode hereditary information in the form of molecules of deoxyribonucleic acid (DNA), all topics we will consider later on, there is no reasonable doubt that all organisms are related; they are descended from a common ancestor. We will have to deal with viruses, too. Are they life and do they share an common ancestor with the rest of life?

Astrobiology

We cannot currently answer the question of whether the origin of life is a simple, likely, and predictable event given the conditions that existed on the Earth when life first arose, or whether it is an extremely rare and unlikely event. In the absence of empirical data for life elsewhere, it is challenging for astrobiologists to rigorously use scientific methods to search for something - life - that might not exist. However, asking questions that are seemingly impossible to answer, provided that empirically-based interpretations can be generated, has often been a significant driver of scientific progress.

The techniques scientists use to detect and characterize life depend on our current understanding of life. Essentially all of the methods are based on what we already know about life. When we search life in extreme environments on Earth, for example, we often rely on the fact that all known organisms use DNA to encode their genetic information; we use methods to detect and characterize that DNA. However, these methods would not detect organisms that used a non-DNA method to encode genetic information; DNA-based methods would not be expected to recognize dramatically different types of life. Alternatively, we can look for evidence of metabolism - chemical reactions catalyzed by life. However, if metabolism occurs on a different time scale than our observations, we will not recognize it as a product of life.

One challenge with developing alternative methods for detecting dramatically different types of life is that we do not know what to look for. We need models of water alternative life might look like to be able to recognize it. If we could generate living systems de novo in the laboratory or if we better characterize organics on other planets or moons, we would have a better understanding of what functions are necessary for life and how to look for possible "non-standard" organisms using better methods. The research might even lead to the discovery of alternative forms of life on Earth, if they exist.[28] We can also work to develop realistic models for alternative forms of life; even though scientists have studied alternative chemical and organic systems, no one has yet been able to construct a model that predicts life-like behavior for any system significantly different from life as we know it on Earth. In the absence of a model for non-standard forms of life, even a theoretical one, the reasonable scientific approach is to concentrate on the characteristics of life as we know them from Earth, while keeping in mind that we may be excluding other types of life in the Universe.

Properties of life

So, let us try to produce a good definition for life, or given the fact that we know only of one version of life, a useful description of what we mean by life. First, the core units of life are organisms, which are individual living objects. From a structural and thermodynamic perspective, each organism is a **bounded, non-equilibrium system that persists over time.** From a practical point of view, an organism needs to be able to produce one or more copies of itself, and it consumes energy to do so. Even though organisms are composed of one or more cells, the organism that is the basic unit of life because it is the organism that reproduces.

Reproduction

Why do we include reproduction in our definition of life? This is basically a pragmatic criterion: organisms have to be able to reproduce to persist through time. Assume that a non-reproducing form of life was possible. A system that could not reproduce runs the risk of death (or perhaps better put, extinction) by accident. Over time, the probability of death for a single individual will approach one – that is, certainty. In contrast, a system that can reproduce makes multiple copies of itself and so minimizes, although by no means eliminates, the chance of accidental extinction, the death of all of its descendants. We see the value of this strategy when we consider the history of life. Even though there have been a number of mass extinction events over the course of life's history,[31] organisms descended from a common ancestor that appeared billions of years ago, and they continue to survive and flourish - and reproduce.

Metabolism and structure

Metabolism consists of the chemical reactions that occur within organisms that allow them to persist. These reactions are essential to life because they provide energy and raw materials to make the cell structure, control the exchange of materials with the environment, and allow reproduction. Metabolism is the foundation of how life works. Much of an organism's structure is related to facilitating metabolism. Organisms confine their metabolic reactions to within cells, but they also exchange resources with their environment. Organisms are able to import, in a controlled manner, energy and matter from their environment and to export waste products into their environment. To control these fluxes, a distinct boundary between the organism and the rest of the world is required. The basic barrier for all organisms (except viruses - if they are organisms) is a cell membrane, and it appears to be a homologous structure across all organisms – that is, cell membranes were present in and inherited from the common ancestor to all life. The cell membrane modulates the transport of chemicals into and out of cells, and is thus critical to metabolism. The importation of chemicals to produce energy, specifically energy that can be used to drive various cellular processes, is what enables the organism to maintain its non-equilibrium state and its dynamic structure. The boundary with the environment must be able to retain the valuable molecules generated, while at the same time allow waste products to leave. This ability to import matter and export waste enables the organism to grow and to reproduce.

Metabolism allows organisms to persist in disequilibrium with their environment. We see evidence of the non-equilibrium nature of organisms in their activities, including their ability to move, to change their environmental chemistry, and to grow. It is important for all aspects of the living state. In particular, organisms use thermodynamically favorable reaction to capture energy from their environment. They use this energy to drive a wide range of thermodynamically unfavorable chemical reactions, creating disequilibrium with their environment. An organism that reaches thermodynamic equilibrium is a dead organism because it no longer has energy to live.

Non-living structures

It is often useful to think of systems that have some of the properties of life, but are not alive. There are examples of non-living, non-equilibrium systems that can "self-organize" or appear *de novo*. Hurricanes and tornados form spontaneously and then dissipate. They use energy from their environment, which is then dispersed back into the environment, a process associated with increased entropy. These non-living systems differ from organisms in that they cannot produce offspring - they are the result of specific environmental conditions. They are individual entities, unrelated to one another, which do not and cannot evolve through inheritance. Tornados and hurricanes that formed billions or millions of years ago would (if we could observe them) be similar to those that form today because they emerge from the same processes. Since we understand (more or less) the conditions that produce tornados and hurricanes, we can predict, fairly reliably, the conditions that will lead to their appearance and how they will behave once they form. In contrast, organisms that lived in the past were different from those that are alive today. The further into

the past we go, the more different they appear. Some ancient organisms became extinct, some gave rise to the ancestors of current organisms. In contrast, modern tornados and hurricanes originate anew, they are not derived from parental storms.

Question to ponder:

- Speculate on how you might look for evidence of life on another planet or moon. What are characteristics might be universal to all life and what might be specific to life on Earth?
- Are viruses alive? You might not know much about them now, so feel free to speculate. How would you look for evidence of something like a virus on another planet or moon?
- Make a model of what properties a biological boundary with its environment needs to possess. Using your current knowledge, how would you build such a boundary layer?
- Ponder the non-equilibrium nature of a specific form of life, maybe your pet or something from your favorite natural area. What about it tells you it is alive? What happens to it when it dies? How does that relate to thermodynamics and equilibrium?
- Ponder a non-living structure that has a pattern. How can you tell that it is not living? For example, how might you be able to demonstrate that the great red spot on Jupiter is not a life form?
- What do you think about considering Earth and all the life on it as a single organism, similar to the Gaia concept? What aspects of the Earth-life system fit a traditional definition of life and which do not?

Additional Reading

- How astrobiologist Chris McKay thinks about "What is life?"
- Dozens of answers to the Question of the Month "What is life?" on Philosophy Now

References

28 The possibility of alternative microbial life on Earth: http://www.ncbi.nlm.nih.gov/pubmed/18053938 Signatures of a shadow biosphere: http://www.ncbi.nlm.nih.gov/pubmed/19292603; Life on Earth but not as we know it (with the caveat that this is a relatively old article; we now know that most of life in desert varnish is related to the rest of know life; however, this article is still an interesting example of the arguments that scientists have on what is actually present on Earth): https://www.theguardian.com/science/2013/apr/14/shadow-biosphere-alien-life-on-earth

Contributors

- Template:ContribKlymkowsky
- ◦ Dawn Sumner (Department of Earth and Planetary Sciences, UC Davis)

1.1: What is life? is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

CHAPTER OVERVIEW

3: Genes to Enzymes

- DNA, RNA, Genes and Chromosomes
- DNA Replication
- How Asexual Prokaryotes Achieve Genetic Diversity
- Mutations
- Operon Theory
- Protein Synthesis (Translation)
- RNA Transcription
- What Are Genes?

Thumbnail: DNA Double Helix. Image used with permission (Public Domain; Apers0n).

This page titled 3: Genes to Enzymes is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Dawn Sumner.

DNA, RNA, Genes and Chromosomes

skills to develop

- Explain the differences between RNA and DNA in terms of function
- Recognize the structure of DNA
- Explain the two functions of the genome
- Explain how DNA and genes are converted into proteins (the "central dogma")
- Differentiate between genotype and phenotype and explain how environmental factors influence phenotype
- Describe why DNA is packaged into chromosomes

Nucleic Acids

Nucleic acids are macromolecules that all life on Earth uses to hold its evolutionary memory. They carry the genetic blueprint of a cell in the form of deoxyribonucleic acid (DNA) and the instructions for the function of the cell in the form of ribonucleic acid (RNA). Chromosomes are composed of DNA arranged into genes and other non-coding areas. The genes are the blueprints for making various molecules that cells need to function, including enzymes. The non-coding areas are critical for influencing when genes are activated or expressed and play diverse other roles in cell function, some of which are not yet understood. DNA is a relatively stable molecule that is tightly controlled by the host cell. RNA is much more reactive than DNA. It plays diverse, reactive functions in cells. When most genes are expressed, they are translated into messenger RNA (mRNA) molecules, which are then transcribed into proteins. Some genes produce RNA molecules that play critical functions in cells, such as transcribing mRNA into proteins (ribosomal RNA or rRNA), transporting amino acids (transfer RNA or tRNA), and influencing gene expression (microRNA). RNA is so fundamental to basic cell functions that some scientists think that life originated in a “RNA world” with the transition from abiotic organic chemistry to life requiring the catalytic properties of RNA molecules (See https://www.khanacademy.org/science/ap-biology/natural-selection/origins-of-life-on-earth/a/rna-world for more information).

Although RNA is critical to cell function, it is a reactive molecule and does not provide a reliable memory system for inheritance in organisms. In contrast, the structure of DNA molecules makes them much less reactive, and they can be packaged into nested spirals that protect them from damage. Thus, DNA is a more reliable memory system for inheritance. It is used by all organisms (except some viruses – if they are organisms) to encode critical cell functions. Most of the DNA in cells is packaged into chromosomes that are copied when cells reproduce. However, some DNA is present in plasmids (small circular DNA molecules outside of chromosomes) and Eukaryotic organelles (e.g. plastids and mitochondria). The entire genetic content of a cell is known as its genome.

What are DNA and RNA?

Nucleic acids are made up of nucleotides composed of a nitrogenous base, a pentose sugar, and a phosphate group. The nitrogenous bases have 5 different structures and are the letters that compose the codes in DNA and RNA molecules. These bases include: adenine (A), guanine (G) cytosine (C), thymine (T) in DNA, and uracil (U) in RNA (figure showing the structure of the bases). DNA and RNA molecules consist of chains of nitrogenous bases bound together by their attached phosphate groups.

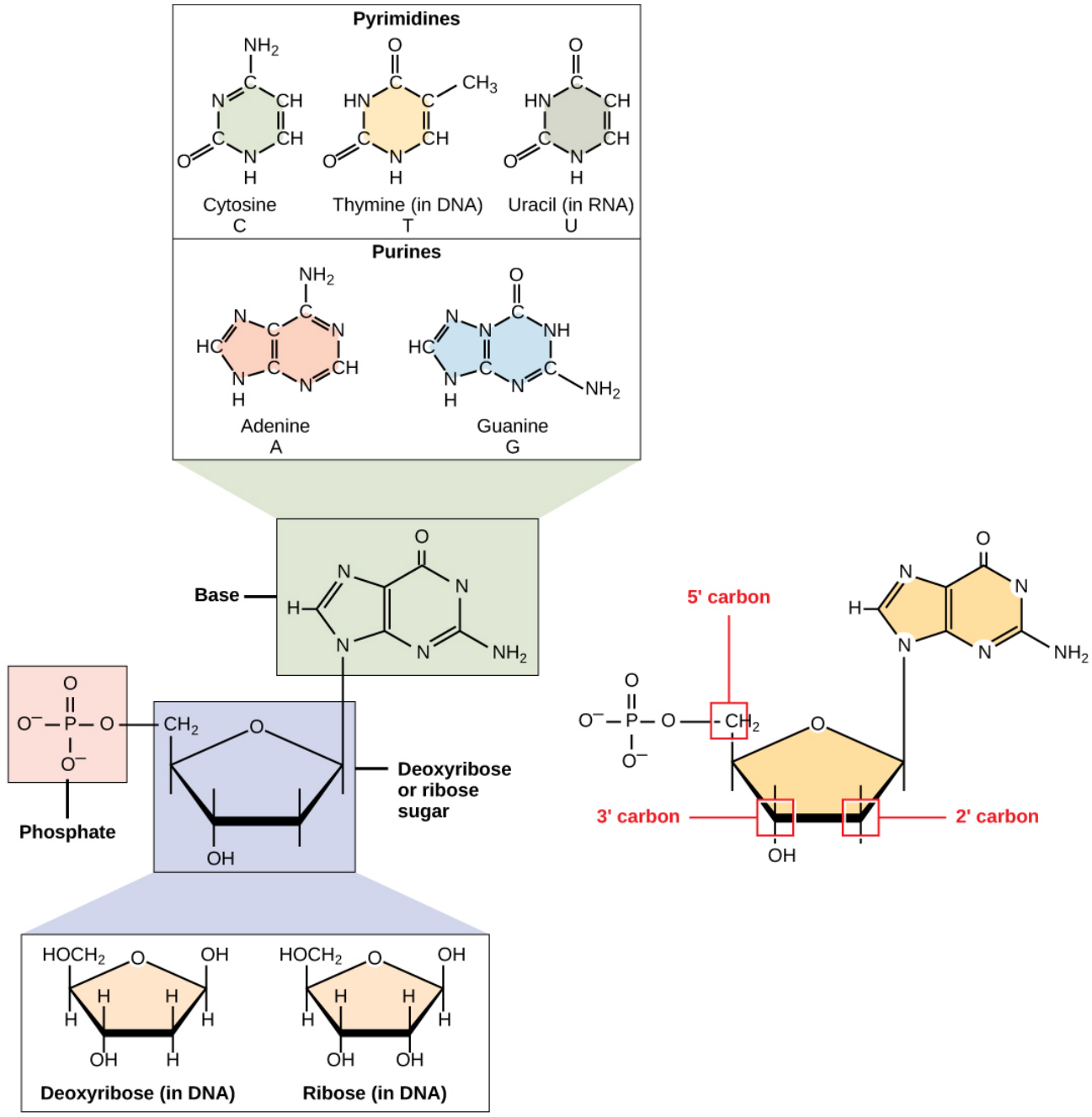


Figure Nucleotides: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime ′ notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a nucleotide is added to a DNA or RNA molecule, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring. Variations in the structures of these molecules affect their function, differentiating DNA from RNA and the reactivity of the molecules.

In DNA, two strands of nucleotides are paired together by hydrogen bonds between their bases in a very systematic way. A can bond with T, and G can bond with C when the two strands are oriented in opposite directions. The two strands only pair if their sequences of bases are complementary. For example, if the sequence of one strand is AATTGGCC, the complementary strand

would have the sequence TTAACCGG. When each base is matched to its complement on the other strand, the two strands spiral around each other, creating a very stable (and famous) double-helical structure.

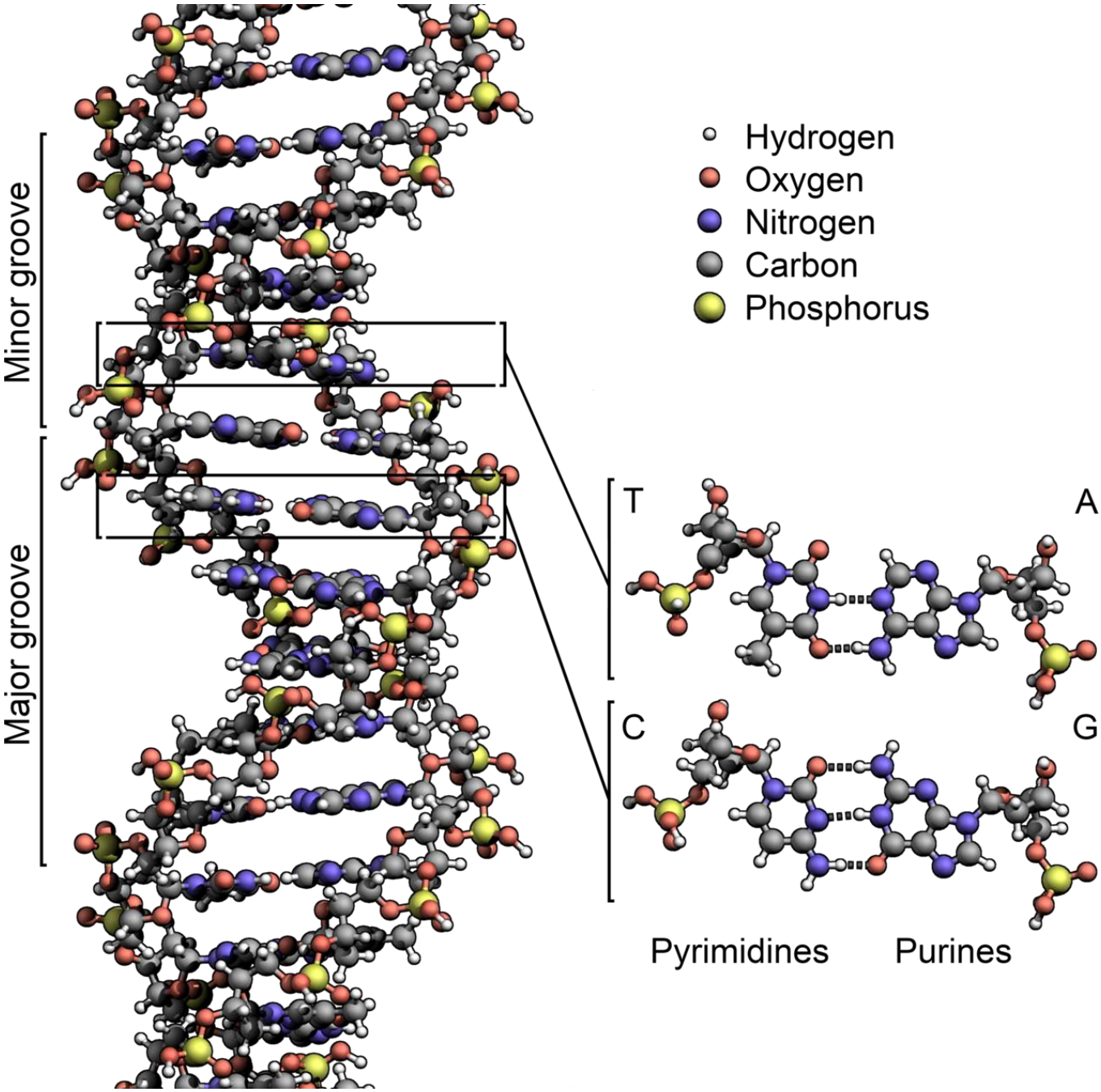


Figure DNA: The structure of DNA showing the details of hydrogen bonds (dashed lines) between complementary base pairs. Note that the yellow phosphate groups point upward on the right side and downward on the left side. The grooves are due to asymmetry in the spiral. (Figure credit: Zephyris (Richard Wheeler))

In contrast to DNA, RNA is single-stranded, and the nitrogenous bases are not necessarily paired with their complements. (U takes the place of T in RNA, bonding with A.) The bases are, however, reactive. If there are stretches of complementary base pairs elsewhere on the RNA molecule or on another RNA molecule, those segments will form hydrogen bonds, tying the two complementary parts together. When sections of RNA bind with each other, the RNA strand(s) folds into specific shapes, which affect how they catalyze reactions. The patterns of RNA base pairs determine how the strands fold, allowing them to perform different functions for the cells.

Management of DNA and RNA is critical for organisms to live and reproduce.

Genes

DNA is the genetic material responsible for inheritance and is passed from parent to offspring for all life on Earth. To preserve the integrity of this genetic information, DNA must be replicated with great accuracy, with minimal errors that introduce changes to the DNA sequence. A genome contains the full complement of DNA within a cell and is organized into smaller, discrete units called genes that are arranged on chromosomes and plasmids.

A gene is composed of DNA that is "read" or transcribed to produce an RNA molecule during the process of transcription. One major type of RNA molecule, called messenger RNA (mRNA), provides the information for the ribosome to catalyze protein synthesis in a process called translation. The processes of transcription and translation are collectively referred to as gene expression. Gene expression is the synthesis of a specific protein with a sequence of amino acids that is encoded in the gene. The flow of genetic information from DNA to RNA to protein is described by the central dogma (Figure 11.1.111.1.1). Each of the processes of replication, transcription, and translation includes the stages of 1) initiation, 2) elongation (polymerization), and 3) termination. These stages will be described in more detail in this chapter.



Figure 11.1.111.1.1: The central dogma states that DNA encodes messenger RNA, which, in turn, encodes protein.

A cell's genotype is the full collection of genes it contains, whereas its phenotype is the set of observable characteristics that result from those genes. The phenotype is the product of the array of proteins being produced by the cell at a given time, which is influenced by the cell's genotype as well as interactions with the cell's environment. Genes code for proteins that have functions in the cell. Although a cell's genotype remains constant, not all genes are used to direct the production of their proteins simultaneously. Cells carefully regulate expression of their genes, only using genes to make specific proteins when those proteins are needed (Figure 11.1.211.1.2). Thus, their phenotype changes through time.

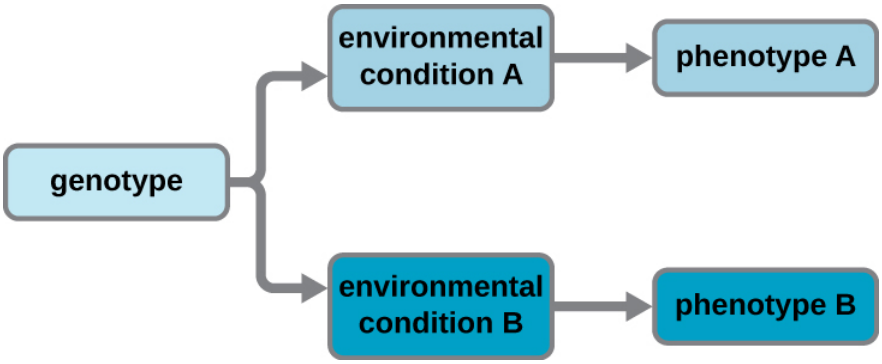


Figure 11.1.211.1.2: Phenotype is determined by the specific genes within a genotype that are expressed under specific conditions. Although multiple cells may have the same genotype, they may exhibit a wide range of phenotypes resulting from differences in patterns of gene expression in response to different environmental conditions.

Chromosomes

DNA strands are packaged into chromosomes with proteins, which allow cells to control gene expression (and phenotypes), replication of the DNA, and separation of the genetic material into cells as they divide. Most (but not all) Bacteria and Archaea have circular chromosomes, with the DNA strands forming a continuous loop. These loops are often twisted up on themselves so the chromosomes make compact structures in the cells (https://www.nature.com/scitable/topicpage/genome-packaging-in-prokaryotes-the-circular-chromosome-9113/). The region in a cell with the condensed chromosome is called the nucleoid. Some DNA can also be housed in structures called plasmids that are more easily exchanged between organisms.

Eukaryotes organize their DNA differently. First, most of the DNA is encased in the cell nucleus, which is separated from the rest of the cell with a membrane. Within the nucleus, the DNA strands are packed into multiple linear chromosomes. DNA strands are wrapped around special proteins called histones (also present in some Archaea) and then folded into even tighter areas by additional proteins. The folding of the chromosomes and the details of the chemical structure of long chains coming off the histones

strongly influence whether or not genes on the chromosomes can be expressed. Eukaryotes also have DNA in other parts of their cells, specifically certain organelles, including mitochondria and plastids (which include chloroplasts). The DNA in organelles (orDNA) is inherited from ancient bacteria that were the ancestors of these organelles. orDNA is packaged into their own chromosomes, whose structure varies among different organisms and even during development of a single organism. In general, orDNA structure is highly variable and poorly understood relative to nuclear DNA structure and replication (see https://www.frontiersin.org/articles/10.3389/fpls.2015.00883/full)

For all DNA, the structure of the chromosomes strongly influences how and when the DNA is active and can be copied.

Key Concepts and Summary

- Nucleic acids are molecules composed of three components. The details of these components affect the function and behavior of RNA and DNA molecules
- The sequence of nitrogenous bases in DNA and RNA provides the information recorded in the molecules.
- Double-stranded DNA has a helical structure in which bases are pared with their complements on the opposite strand.
- Genes consist of DNA sequences that code for the production of specific proteins.
- The genotype of a cell consists of all of its genes and remains constant. The phenotype of a cell consists of the functions a cell is capable of due to the expression of genes. Phenotype varies through time as gene expression changes in response to environmental and biochemical signals.
- Organisms organize their DNA into chromosomes. The structure of the chromosomes changes through time and affects which genes can be expressed.

More Information

RNA World: https://www.khanacademy.org/science/ap-biology/natural-selection/origins-of-life-on-earth/a/rna-world

Structure of bacterial chromosomes: https://www.nature.com/scitable/topicpage/genome-packaging-in-prokaryotes-the-circular-chromosome-9113/

Organelle DNA organization: https://www.frontiersin.org/articles/10.3389/fpls.2015.00883/full

Content on this page, including figures, has been derived from the Nucleic Acids chapter of General Biology (OpenStax) and Chapter 11.1 of Microbiology (OpenStax). Both are licensed under CC BY-NC-SA 3.0.

DNA, RNA, Genes and Chromosomes is shared under a not declared license and was authored, remixed, and/or curated by LibreTexts.

DNA Replication

learning outcomes

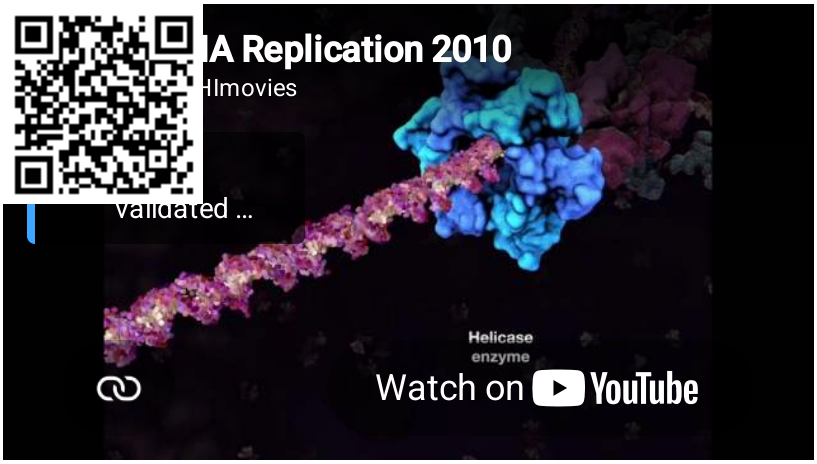
- I can explain why DNA in chromosomes has to be unwrapped and un-zipped into two strands for replication.
- I can explain why the two DNA strands have to be treated differently when the complementary bases are being added to return them to the 2-stranded state.
- I can use the similarities and differences in DNA replication in Bacteria, Archaea, and Eukarya to compare their evolutionary histories.

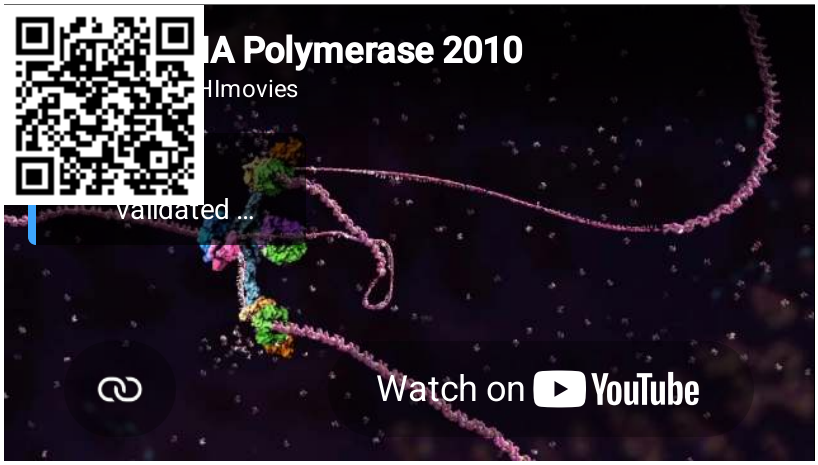
Overall Processes

DNA replication requires three processes: the **initiation** of replication, the **elongation** of the new DNA during actual copying, and the **termination** of the DNA replication process. Each of these consists of reactions between enzymes and the DNA macromolecule. And each has to be performed precisely to produce two identical strands of DNA.

The importance of DNA replication has led to it being extensively studied in cells, replicated as chemical reactions in experiments, and modeled at a molecular level. The basic processes for DNA replication are similar in Bacteria, Archaea, and Eukarya, although there are significant differences in the details of the processes. The text below describes the processes of initiation, elongation and termination generally, and then discusses some key differences among the three domains of life as well as for DNA in organelles (like plastids and mitochondria), plasmids, and viruses.

Let's start, however, with two beautiful animations of the elongation process (in a eukaryotic cell) based on a very detailed molecular simulation. The first video shows the overall process, and the second video shows how the new strand of DNA is built. Each process illustrated in the videos is caused by spontaneously chemical reactions when the right molecules are present in the right places in the cells. Evolution over billions of years has produced these impressive molecular machines.





Initiation

Chromosomal DNA is typically wrapped around histones (in Archaea and Eukarya) or histone-like proteins (in bacteria). When DNA is wrapped and twisted on itself, the DNA molecule is protected from interacting with most other molecules and can not be copied. However, specific enzymes change the shape and supercoiling of the chromosome, and these enzymes can expose the origin of replication, which is a specific nucleotide sequence that binds to the specific proteins that initiate the replication process. Every chromosome has at least one origin of replication so that it can be copied, and some Archaea and Eukarya have more than one.

The initiation of replication starts at the origin of replication and consists of converting the DNA into a strand that is accessible for replication. An enzyme called helicase binds to the DNA at the origin of replication and separates it into two strands by breaking the hydrogen bonds between the nitrogenous base pairs. As the DNA strands "un-zip", they are coated with special proteins to prevent the now single-stranded DNA from rewinding into a double helix, which is its more stable form. These stabilized single DNA strands extend outward from the helicase enzyme to produce a Y-shaped structure called a replication fork. A special RNA sequence, called a primer, binds to the DNA strands near the replication fork to help create the right chemical environment for building the complementary DNA strand for each of the original strands being copied. At this point, DNA replication can begin.

Elongation

The complementary DNA strand is added to the original DNA strand by an enzyme called DNA polymerase, which is held near the replication fork by an enzyme that facilitates smooth passage of the single DNA strand to the polymerase. As the DNA strand slides through, the DNA polymerase adds the appropriate nucleotide to complements. The addition of these nucleotides requires energy, which comes from breaking bonds in the phosphate groups attached to each nucleotide (a triphosphate nucleotide). When the bond between the phosphates is broken, diphosphate is released along with energy that allows the formation of a covalent bond between the incoming nucleotide and the growing DNA strand. The DNA polymerase catalyzes this process.

DNA polymerase can only extend the complementary strand of DNA in one specific direction defined by the geometry of the pentose sugar and phosphate groups bound to the nitrogenous bases in DNA. However, the DNA double helix is antiparallel; that is, one strand is oriented in one direction and the other is oriented in the opposite direction (see Structure and Function of DNA). Thus, during replication, one strand of the original DNA is oriented in the right direction to be copied whereas the other one is not; the two strands have to be treated differently at the replication fork. DNA polymerase adds nucleotides to the properly oriented strand, the "leading strand", without complications. However, another DNA polymerase has to add bases to the other strand, the "lagging strand", in the opposite direction. This requires the replication fork to create loops of the DNA and attach DNA polymerases to it repeatedly. In this process, a DNA polymerase attaches to the single stranded DNA and builds the complementary strand while moving away from the replication fork. Once it hits part of the DNA strand that already has the complement, it jumps back toward the replication fork to begin adding bases to a new place in the DNA. These steps produce a double-stranded DNA molecule with RNA primers located at each jump point. These RNA primers are replaced with DNA as one of the final steps in the elongation process.

Termination

Once the complete chromosome has been replicated, DNA replication is terminated. Although much is known about initiation of replication, less is known about the termination process, and it is different for Bacteria and Eukarya. For organisms with circular chromosomes (most Bacteria and Archaea), the elongation process stops when two replication forks encounter each other. If there is only one origin of replication on the circular chromosome, the two forks will encounter each other once full chromosome has been copied. However, the new chromosomes are interlocked, so they have to be broken apart and the ends have to be joined to reform the circle. For organisms with linear chromosomes, termination happens when either two replication forks meet or the end of the chromosome is reached. At an end, there is no place to add a primer on the lagging DNA strand for the DNA replicase to attache to. Thus, the ends of linear chromosomes can remain unpaired and, over time, linear chromosomes may get progressively shorter, losing information.

Variations in DNA Replication

DNA replication follows a similar process in Bacteria, Archaea, and Eukarya: they all have a genetic marker for the origin of replication, similar mechanisms for elongation, and the need for termination. However, the actual enzymes that perform the replication show some variations related to their evolutionary history. The genes that code for the enzymes that structure the replication fork are very similar in all three domains (Bell, 2017), which suggests that the basic process for duplicating DNA evolved in the last common ancestor of all life. In contrast, most of the other genes involved in DNA replication are similar in Archaea and Eukarya, but different in Bacteria (Bell, 2017). The differences between Bacteria and Archaea/Eukarya are consistent with other evolutionary relationships between the groups that suggest Archaea and Eukarya are more closely related to each other than they are to Bacteria.

Plasmids and some viruses also require DNA replication to reproduce. They lack the genes to make their own replication enzymes, so they rely on their host cells for DNA replication.

Bacteria

DNA replication has been well studied in bacteria primarily because of the small size of the genome and the mutants that are available. *E. coli* has 4.6 million base pairs (Mbp) in a single circular chromosome and all of it is replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the circle in both directions. This means that approximately 1000 nucleotides are added per second. The process is quite rapid and occurs with few errors.

Archaea

Most archaea also have a single circular chromosome, but their processes of DNA replication are less well studied. The enzymes for DNA replication in Archaea is similar to those in Eukarya, but they are in general simpler (Bell, 2017). Most archaeal chromosomes have more than one origin of replication, with four being the maximum documented to date. There are lots of unanswered research questions that can be pursued to better understand how archaea function as cells.

Eukarya Nuclear DNA

Eukaryotic genomes are much more complex and larger than bacterial and archaeal genomes and are typically composed of multiple linear chromosomes. The human genome, for example, requires the insertion of 6 billion base pairs are inserted during replication. There are multiple origins of replication on each eukaryotic chromosome; the human genome has 30,000 to 50,000 origins of replication. The rate of replication is approximately 100 nucleotides per second—10 times slower than bacterial replication.

Eukaryotic chromosomes are linear, which means that their ends sometime contain unpaired bases. Thus, over time, they may get progressively shorter as cells continue to divide. To help prevent important information from being lost, the ends of the linear chromosomes consist of noncoding repetitive sequences called telomeres. The telomeres protect coding sequences from being lost as cells continue to divide. In humans, telomeres consist of 100 to 1000 repetitions of a six base-pair sequence, TTAGGG. There is a specific enzyme that attaches to this sequence at the end of the template DNA for the lagging strand of DNA and extends it with an RNA template. Once the lagging strand template is long enough for the DNA polymerase to shift to a new primer, the polymerase can finish adding the complementary nucleotides to the end of the chromosome.

In humans, telomerase is typically active in germ cells and adult stem cells; it is not active in adult somatic cells and may be associated with the aging of these cells. Eukaryotic microbes including fungi and protozoans also produce telomerase to maintain chromosomal integrity. For her discovery of telomerase and its action, Elizabeth Blackburn (1948–) received the Nobel Prize for Medicine or Physiology in 2009.

Eukaryotic Organelles

Eukaryotes also host DNA in their organelles. This orDNA was inherited from bacteria that merged ancient ancestors to modern eukaryotes through a process called endosymbiosis. Over hundreds of millions of years, some of the bacterial genes were transferred to the host cells, some were lost, and all evolved in response to being permanently encased within another cell. One of the key processes transferred from the ancestors to the organelles to the host cells was DNA replication. The replication of orDNA is controlled by genes in the nucleus, even though orDNA replication is not necessarily coordinated with replication of nuclear DNA. The replication process is also variable among organisms, in part due to the different evolutionary paths of different eukaryotic lineages after the endosymbiosis events. Overall, orDNA replication is less well understood by scientists than nuclear DNA replication (see https://www.frontiersin.org/articles/10.3389/fpls.2015.00883/full), even though it is critical for the function of most eukaryotes.

Plasmids and Viruses

Plasmids and DNA viruses depend on host cell DNA replication processes to replicate their DNA. Plasmids are small circular molecules of double-stranded DNA that are separate from the main chromosome(s) of their host cells. They usually contain one or two non-essential genes, like antibiotic resistance, and none of the genes necessary for DNA replication. Thus, they depend on enzymes coded in genes in the host cell chromosomes to replicate their DNA. Plasmids have their own origin of replication to initiate DNA replication, but they will only be replicated if the host cell's enzymes recognize their origin of replication. Because origins of replication have different coding sequences in Bacteria, Archaea, and Eukarya, plasmids are usually specific to one domain of life or even a smaller subset of organisms. In addition, sometimes the replication process proceeds differently than for chromosomal DNA, initiating with a nick in one of the DNA strands and elongating the two strands separately.

Viruses also depend on their host cell's enzymes for replication. Some viruses contain DNA whereas others have RNA. DNA viruses do not include all the genes for DNA replication enzymes. Thus, they rely on their host cell's cellular machinery to produce more viral particles and use multiple methods for tricking host cells into replicating their DNA. RNA viruses can replicate their genetic code more easily since RNA is a reactive molecule and does not require the processes of initiation, elongation, and termination essential for DNA replication. For more information on viruses, see The Viral Life Cycle.

More Information and References

Bell, S.D., 2017. Chapter 5 - Initiation of DNA Replication in the Archaea, in H. Masai, M. Foiani (eds.), *DNA Replication*, Advances in Experimental Medicine and Biology 1042, https://doi.org/10.1007/978-981-10-6955-0_5

Content on this page, including figures, has been derived from Chapter 11.2 of Mechanisms of Microbial Genomics and is licensed under CC BY-NC-SA 3.0.

Contributor

- Template:ContribOpenSTAXMicrobiology

DNA Replication is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

How Asexual Prokaryotes Achieve Genetic Diversity

skills to develop

- Compare the processes of transformation, transduction, and conjugation
- Explain how asexual gene transfer results in prokaryotic genetic diversity
- Explain the structure and consequences for bacterial genetic diversity of transposons

Typically, when we consider genetic transfer, we think of vertical gene transfer, the transmission of genetic information from generation to generation. Vertical gene transfer is by far the main mode of transmission of genetic information in all cells. In sexually reproducing organisms, crossing-over events and independent assortment of individual chromosomes during meiosis contribute to genetic diversity in the population. Genetic diversity is also introduced during sexual reproduction, when the genetic information from two parents, each with different complements of genetic information, are combined, producing new combinations of parental genotypes in the diploid offspring. The occurrence of mutations also contributes to genetic diversity in a population. Genetic diversity of offspring is useful in changing or inconsistent environments and may be one reason for the evolutionary success of sexual reproduction.

When prokaryotes and eukaryotes reproduce asexually, they transfer a nearly identical copy of their genetic material to their offspring through vertical gene transfer. Although asexual reproduction produces more offspring more quickly, any benefits of diversity among those offspring are lost. How then do organisms whose dominant reproductive mode is asexual create genetic diversity? In prokaryotes, horizontal gene transfer (HGT), the introduction of genetic material from one organism to another organism within the same generation, is an important way to introduce genetic diversity. HGT allows even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes but that only a small fraction of the prokaryotic genome may be transferred by this type of transfer at any one time. As the phenomenon is investigated more thoroughly, it may be revealed to be even more common. Many scientists believe that HGT and mutation are significant sources of genetic variation, the raw material for the process of natural selection, in prokaryotes. Although HGT is more common among evolutionarily related organisms, it may occur between any two species that live together in a natural community.

HGT in prokaryotes is known to occur by the three primary mechanisms that are illustrated in Figure 1:

1. Transformation: naked DNA is taken up from the environment
2. Transduction: genes are transferred between cells in a virus (see The Viral Life Cycle)
3. Conjugation: use of a hollow tube called a conjugation pilus to transfer genes between cells

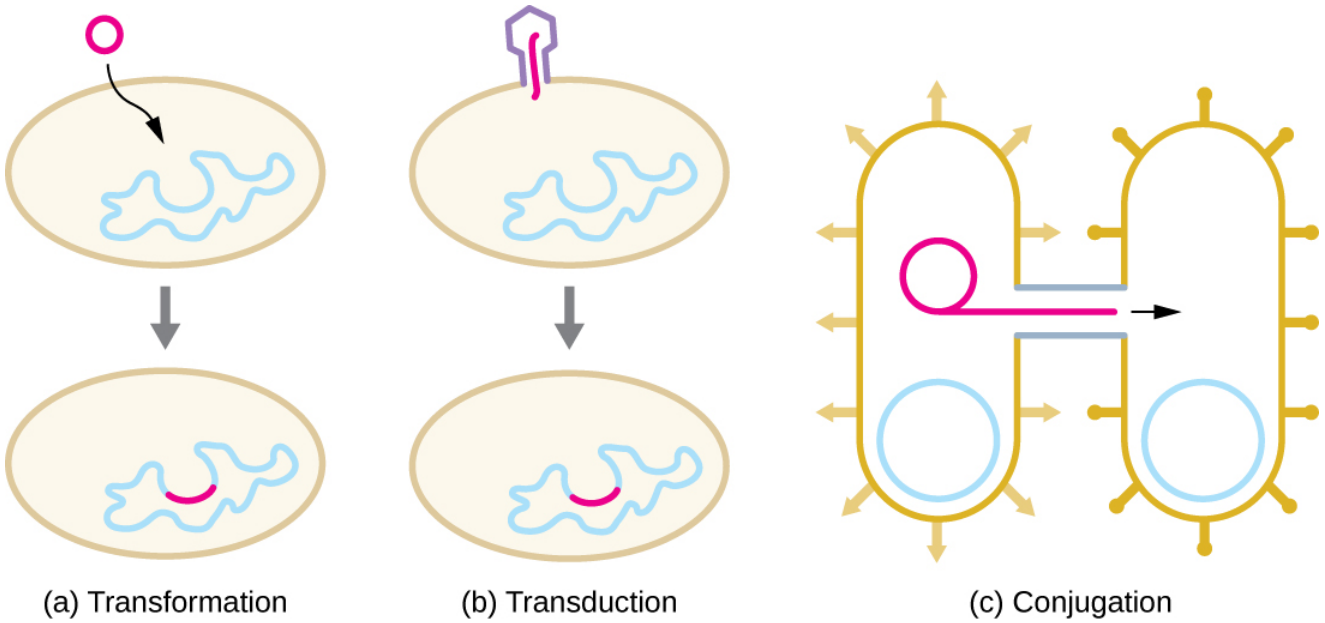


Figure 1: *There are three prokaryote-specific mechanisms leading to horizontal gene transfer in prokaryotes. a) In transformation, the cell takes up DNA directly from the environment. The DNA may remain separate as a plasmid or be incorporated into the host genome. b) In transduction, a bacteriophage injects DNA that is a hybrid of viral DNA and DNA from a previously infected bacterial cell. c) In conjugation, DNA is transferred between cells through a cytoplasmic bridge after a conjugation pilus draws the two cells close enough to form the bridge.*

Exercise 1

1. What are three ways sexual reproduction introduces genetic variation into offspring?
2. What is a benefit of asexual reproduction?
3. What are the three mechanisms of horizontal gene transfer in prokaryotes?

Transformation

Frederick Griffith was the first to demonstrate the process of transformation. In 1928, he showed that live, nonpathogenic *Streptococcus pneumoniae* bacteria could be transformed into pathogenic bacteria through exposure to a heat-killed pathogenic strain. He concluded that some sort of agent, which he called the "transforming principle," had been passed from the dead pathogenic bacteria to the live, nonpathogenic bacteria. In 1944, Oswald Avery (1877–1955), Colin MacLeod (1909–1972), and Maclyn McCarty (1911–2005) demonstrated that the transforming principle was DNA (see Using Microorganisms to Discover the Secrets of Life).

In transformation, the prokaryote takes up naked DNA found in its environment and that is derived from other cells that have lysed on death and released their contents, including their genome, into the environment. Many bacteria are naturally competent, meaning that they actively bind to environmental DNA, transport it across their cell envelopes into their cytoplasm, and make it single stranded. Typically, double-stranded foreign DNA within cells is destroyed by nucleases as a defense against viral infection. However, these nucleases are usually ineffective against single-stranded DNA, so this single-stranded DNA within the cell has the opportunity to recombine into the bacterial genome. A molecule of DNA that contains fragments of DNA from different organisms is called recombinant DNA. (Recombinant DNA will be discussed in more detail in Microbes and the Tools of Genetic Engineering.) If the bacterium incorporates the new DNA into its own genome through recombination, the bacterial cell may gain new phenotypic properties. For example, if a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and then incorporates it into its chromosome, it, too, may become pathogenic. Plasmid DNA may also be taken up by competent bacteria and confer new properties to the cell. Overall, transformation in nature is a relatively inefficient process because environmental DNA levels are low because of the activity of nucleases that are also released during cellular lysis. Additionally, genetic recombination is inefficient at incorporating new DNA sequences into the genome.

In nature, bacterial transformation is an important mechanism for the acquisition of genetic elements encoding virulence factors and antibiotic resistance. Genes encoding resistance to antimicrobial compounds have been shown to be widespread in nature, even

in environments not influenced by humans. These genes, which allow microbes living in mixed communities to compete for limited resources, can be transferred within a population by transformation, as well as by the other processes of HGT. In the laboratory, we can exploit the natural process of bacterial transformation for genetic engineering to make a wide variety of medicinal products, as discussed in Microbes and the Tools of Genetic Engineering.

Exercise 2

Why does a bacterial cell make environmental DNA brought into the cell into a single-stranded form?

Transduction

Viruses that infect bacteria (bacteriophages) may also move short pieces of chromosomal DNA from one bacterium to another in a process called transduction (see [link]). Recall that in generalized transduction, any piece of chromosomal DNA may be transferred to a new host cell by accidental packaging of chromosomal DNA into a phage head during phage assembly. By contrast, specialized transduction results from the imprecise excision of a lysogenic prophage from the bacterial chromosome such that it carries with it a piece of the bacterial chromosome from either side of the phage's integration site to a new host cell. As a result, the host may acquire new properties. This process is called lysogenic conversion. Of medical significance, a lysogenic phage may carry with it a virulence gene to its new host. Once inserted into the new host's chromosome, the new host may gain pathogenicity. Several pathogenic bacteria, including *Corynebacterium diphtheriae* (the causative agent of diphtheria) and *Clostridium botulinum* (the causative agent of botulism), are virulent because of the introduction of toxin-encoding genes by lysogenic bacteriophages, affirming the clinical relevance of transduction in the exchange of genes involved in infectious disease. Archaea have their own viruses that translocate genetic material from one individual to another.

Exercise 3

1. What is the agent of transduction of prokaryotic cells?
2. In specialized transduction, where does the transducing piece of DNA come from?

THE CLINICAL CONSEQUENCES OF TRANSDUCTION

Paul, a 23-year-old relief worker from Atlanta, traveled to Haiti in 2011 to provide aid following the 2010 earthquake. After working there for several weeks, he suddenly began experiencing abdominal distress, including severe cramping, nausea, vomiting, and watery diarrhea. He also began to experience intense muscle cramping. At a local clinic, the physician suspected that Paul's symptoms were caused by cholera because there had been a cholera outbreak after the earthquake. Because cholera is transmitted by the fecal-oral route, breaches in sanitation infrastructure, such as often occur following natural disasters, may precipitate outbreaks. The physician confirmed the presumptive diagnosis using a cholera dipstick test. He then prescribed Paul a single dose of doxycycline, as well as oral rehydration salts, instructing him to drink significant amounts of clean water.

Cholera is caused by the gram-negative curved rod *Vibrio cholerae* (Figure 2). Its symptoms largely result from the production of the cholera toxin (CT), which ultimately activates a chloride transporter to pump chloride ions out of the epithelial cells into the gut lumen. Water then follows the chloride ions, causing the prolific watery diarrhea characteristic of cholera. The gene encoding the cholera toxin is incorporated into the bacterial chromosome of *V. cholerae* through infection of the bacterium with the lysogenic filamentous CTX phage, which carries the CT gene and introduces it into the chromosome on integration of the prophage. Thus, pathogenic strains of *V. cholerae* result from horizontal gene transfer by specialized transduction.

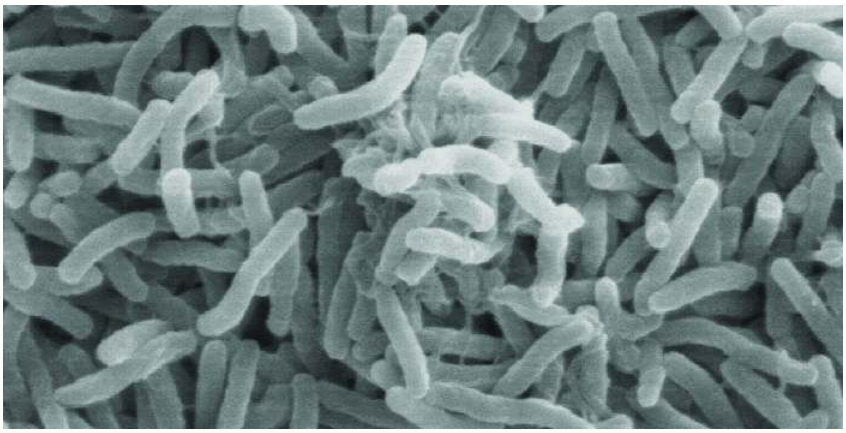


Figure 2: *A scanning electron micrograph of* Vibrio cholerae *shows its characteristic curved rod shape.*

Exercise 4

1. Why are outbreaks of cholera more common as a result of a natural disaster?
2. Why is muscle cramping a common symptom of cholera? Why is treatment with oral rehydration salts so important for the treatment of cholera?
3. In areas stricken by cholera, what are some strategies that people could use to prevent disease transmission?

Conjugation

In conjugation, DNA is directly transferred from one prokaryote to another by means of a conjugation pilus, which brings the organisms into contact with one another. In *E. coli*, the genes encoding the ability to conjugate are located on a bacterial plasmid called the F plasmid, also known as the fertility factor, and the conjugation pilus is called the F pilus. The F-plasmid genes encode both the proteins composing the F pilus and those involved in rolling circle replication of the plasmid. Cells containing the F plasmid, capable of forming an F pilus, are called F^+ cells or donor cells, and those lacking an F plasmid are called F^- cells or recipient cells.

Conjugation of the F Plasmid

During typical conjugation in *E. coli*, the F pilus of an F^+ cell comes into contact with an F^- cell and retracts, bringing the two cell envelopes into contact (Figure 3). Then a cytoplasmic bridge forms between the two cells at the site of the conjugation pilus. As rolling circle replication of the F plasmid occurs in the F^+ cell, a single-stranded copy of the F plasmid is transferred through the cytoplasmic bridge to the F^- cell, which then synthesizes the complementary strand, making it double stranded. The F^- cell now becomes an F^+ cell capable of making its own conjugation pilus. Eventually, in a mixed bacterial population containing both F^+ and F^- cells, all cells will become F^+ cells. Genes on the *E. coli* F plasmid also encode proteins preventing conjugation between F^+ cells.

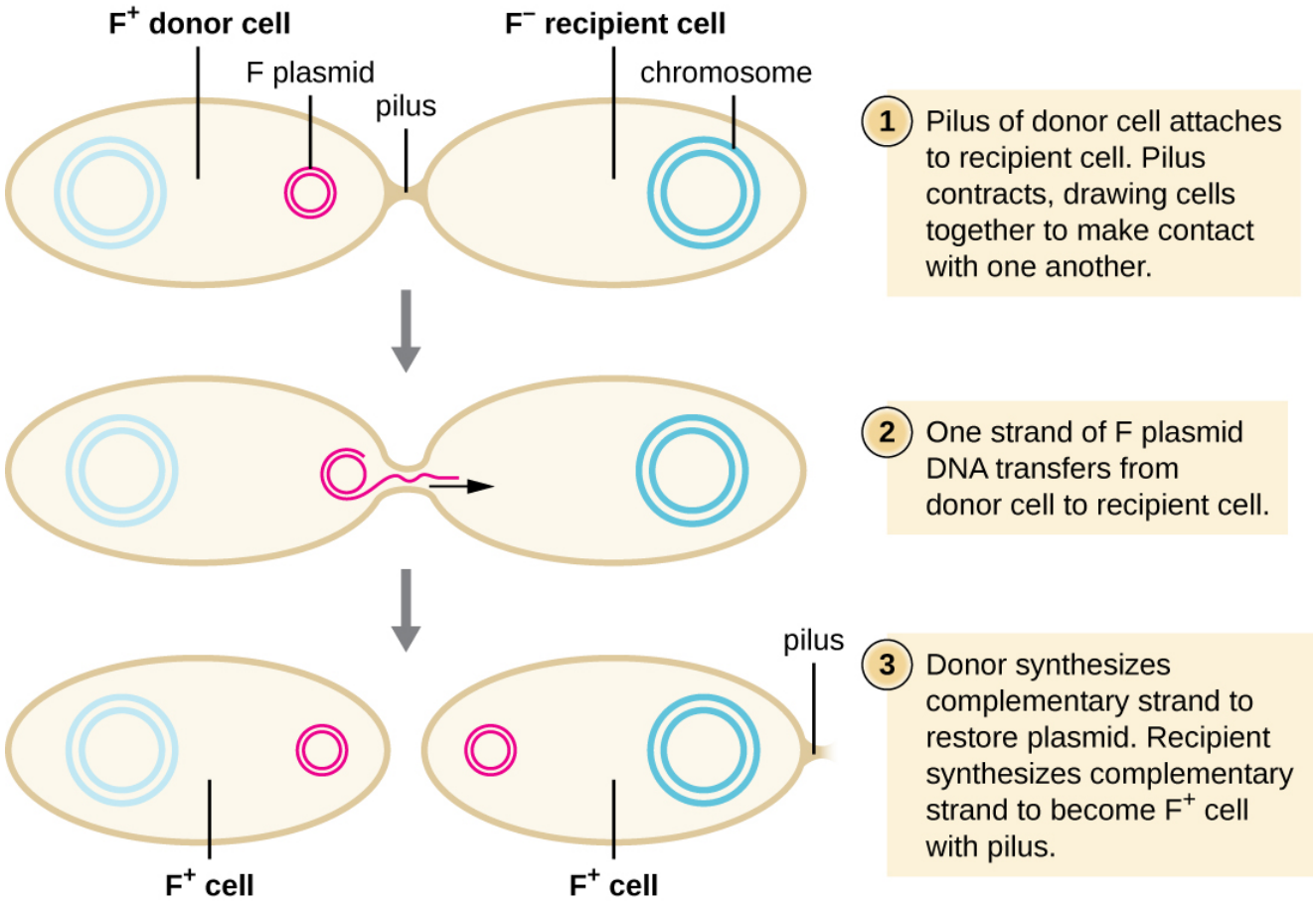


Figure 3: *Typical conjugation of the F plasmid from an F^+ cell to an F^- cell is brought about by the conjugation pilus bringing the two cells into contact. A single strand of the F plasmid is transferred to the F^- cell, which is then made double stranded.*

Conjugation of F' and Hfr Cells

Although typical conjugation in *E. coli* results in the transfer of the F-plasmid DNA only, conjugation may also transfer chromosomal DNA. This is because the F plasmid occasionally integrates into the bacterial chromosome through recombination between the plasmid and the chromosome, forming an Hfr cell (Figure 4). "Hfr" refers to the high frequency of recombination seen when recipient F^- cells receive genetic information from Hfr cells through conjugation. Similar to the imprecise excision of a prophage during specialized transduction, the integrated F plasmid may also be imprecisely excised from the chromosome, producing an F' plasmid that carries with it some chromosomal DNA adjacent to the integration site. On conjugation, this DNA is introduced to the recipient cell and may be either maintained as part of the F' plasmid or be recombined into the recipient cell's bacterial chromosome.

Hfr cells may also treat the bacterial chromosome like an enormous F plasmid and attempt to transfer a copy of it to a recipient F^- cell. Because the bacterial chromosome is so large, transfer of the entire chromosome takes a long time (Figure 5). However, contact between bacterial cells during conjugation is transient, so it is unusual for the entire chromosome to be transferred. Host chromosomal DNA near the integration site of the F plasmid, displaced by the unidirectional process of rolling circle replication, is more likely to be transferred and recombined into a recipient cell's chromosome than host genes farther away. Thus, the relative location of bacterial genes on the Hfr cell's genome can be mapped based on when they are transferred through conjugation. As a result, prior to the age of widespread bacterial genome sequencing, distances on prokaryotic genome maps were often measured in minutes.

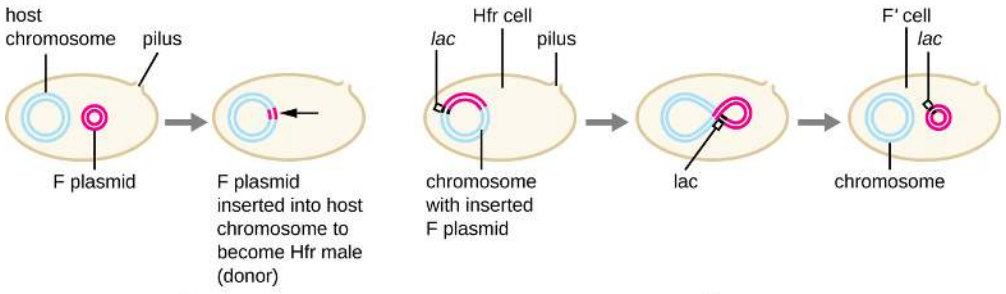


Figure 4: *(a) The F plasmid can occasionally integrate into the bacterial chromosome, producing an Hfr cell. (b) Imprecise excision of the F plasmid from the chromosome of an Hfr cell may lead to the production of an F' plasmid that carries chromosomal DNA adjacent to the integration site. This F' plasmid can be transferred to an F⁻ cell by conjugation.*

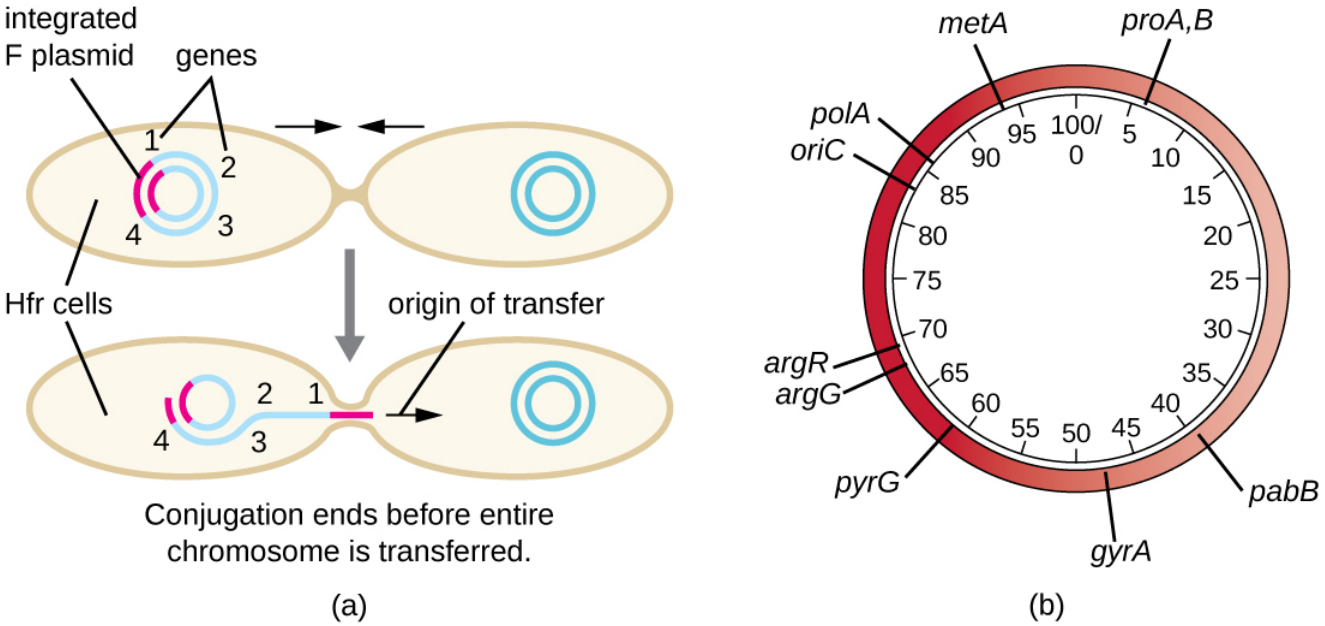


Figure 5: *(a) An Hfr cell may attempt to transfer the entire bacterial chromosome to an F⁻ cell, treating the chromosome like an extremely large F plasmid. However, contact between cells during conjugation is temporary. Chromosomal genes closest to the integration site (gene 1) that are first displaced during rolling circle replication will be transferred more quickly than genes far away from the integration site (gene 4). Hence, they are more likely to be recombined into the recipient F⁻ cell's chromosome. (b) The time it takes for a gene to be transferred, as detected by recombination into the F⁻ cell's chromosome, can be used to generate a map of the bacterial genome, such as this genomic map of E. coli. Note that it takes approximately 100 minutes for the entire genome (4.6 Mbp) of an Hfr strain of E. coli to be transferred by conjugation.*

Consequences and Applications of Conjugation

Plasmids are an important type of extrachromosomal DNA element in bacteria and, in those cells that harbor them, are considered to be part of the bacterial genome. From a clinical perspective, plasmids often code for genes involved in virulence. For example, genes encoding proteins that make a bacterial cell resistant to a particular antibiotic are encoded on R plasmids. R plasmids, in addition to their genes for antimicrobial resistance, contain genes that control conjugation and transfer of the plasmid. R plasmids are able to transfer between cells of the same species and between cells of different species. Single R plasmids commonly contain multiple genes conferring resistance to multiple antibiotics.

Genes required for the production of various toxins and molecules important for colonization during infection may also be found encoded on plasmids. For example, verotoxin-producing strains of *E. coli* (VTEC) appear to have acquired the genes encoding the Shiga toxin from its gram-negative relative *Shigella dysenteriae* through the acquisition of a large plasmid encoding this toxin. VTEC causes severe diarrheal disease that may result in hemolytic uremic syndrome(HUS), which may be lead to kidney failure and death.

In nonclinical settings, bacterial genes that encode metabolic enzymes needed to degrade specialized atypical compounds like polycyclic aromatic hydrocarbons (PAHs) are also frequently encoded on plasmids. Additionally, certain plasmids have the ability

to move from bacterial cells to other cell types, like those of plants and animals, through mechanisms distinct from conjugation. Such mechanisms and their use in genetic engineering are covered in Modern Applications of Microbial Genetics.

Click through this animation to learn more about the process of conjugation.

Exercise 5

1. What type of replication occurs during conjugation?
2. What occurs to produce an Hfr *E. coli* cell?
3. What types of traits are encoded on plasmids?

Transposition

Genetic elements called transposons (transposable elements), or "jumping genes," are molecules of DNA that include special inverted repeat sequences at their ends and a gene encoding the enzyme transposase (Figure 6). Transposons allow the entire sequence to independently excise from one location in a DNA molecule and integrate into the DNA elsewhere through a process called transposition. Transposons were originally discovered in maize (corn) by American geneticist Barbara McClintock (1902–1992) in the 1940s. Transposons have since been found in all types of organisms, both prokaryotes and eukaryotes. Thus, unlike the three previous mechanisms discussed, transposition is not prokaryote-specific. Most transposons are nonreplicative, meaning they move in a "cut-and-paste" fashion. Some may be replicative, however, retaining their location in the DNA while making a copy to be inserted elsewhere ("copy and paste"). Because transposons can move within a DNA molecule, from one DNA molecule to another, or even from one cell to another, they have the ability to introduce genetic diversity. Movement within the same DNA molecule can alter phenotype by inactivating or activating a gene.

Transposons may carry with them additional genes, moving these genes from one location to another with them. For example, bacterial transposons can relocate antibiotic resistance genes, moving them from chromosomes to plasmids. This mechanism has been shown to be responsible for the colocalization of multiple antibiotic resistance genes on a single R plasmid in *Shigella* strains causing bacterial dysentery. Such an R plasmid can then be easily transferred among a bacterial population through the process of conjugation.

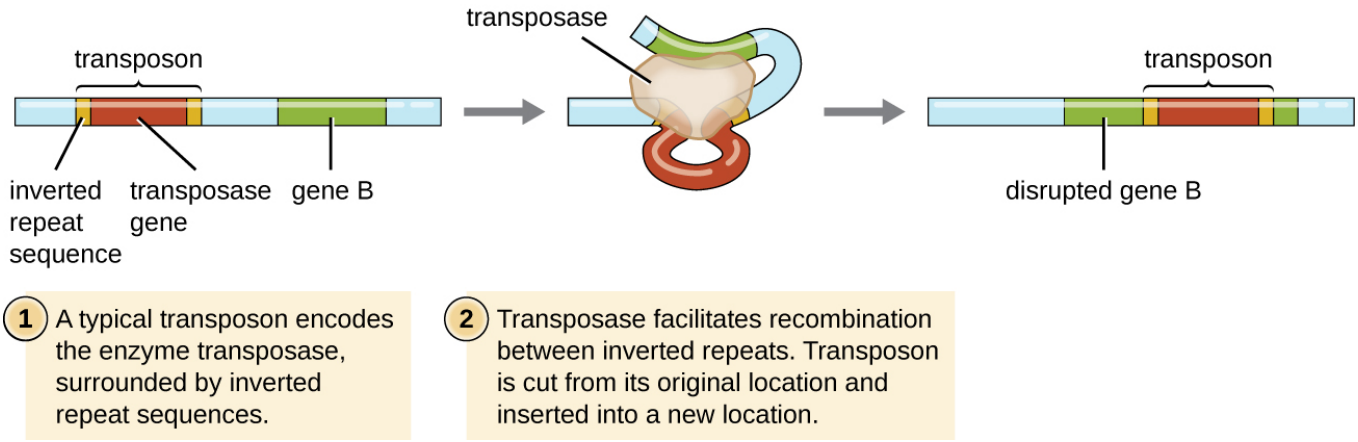


Figure 6: Transposons are segments of DNA that have the ability to move from one location to another because they code for the enzyme transposase. In this example, a nonreplicative transposon has disrupted gene B. The consequence of that the transcription of gene B may now have been interrupted.

Exercise 6

What are two ways a transposon can affect the phenotype of a cell it moves to?

Table 1 summarizes the processes discussed in this section.

***Table** 1: Summary of Mechanisms of Genetic Diversity in Prokaryotes*

Term	Definition
Conjugation	Transfer of DNA through direct contact using a conjugation pilus
Transduction	Mechanism of horizontal gene transfer in bacteria in which genes are transferred through viral infection
Transformation	Mechanism of horizontal gene transfer in which naked environmental DNA is taken up by a bacterial cell
Transposition	Process whereby DNA independently excises from one location in a DNA molecule and integrates elsewhere

Clinical Focus: PART 3

Despite continued antibiotic treatment, Mark's infection continued to progress rapidly. The infected region continued to expand, and he had to be put on a ventilator to help him breathe. Mark's physician ordered surgical removal of the infected tissue. Following an initial surgery, Mark's wound was monitored daily to ensure that the infection did not return, but it continued to spread.

After two additional rounds of surgery, the infection finally seemed to be contained. A few days later, Mark was removed from the ventilator and was able to breathe on his own. However, he had lost a great deal of skin and soft tissue on his lower leg.

Exercise 7

1. Why does the removal of infected tissue stem the infection?
2. What are some likely complications of this method of treatment?

Key Concepts and Summary

- **Horizontal gene transfer** is an important way for asexually reproducing organisms like prokaryotes to acquire new traits.
- There are three mechanisms of horizontal gene transfer typically used by bacteria: **transformation**, **transduction**, and **conjugation**.
- Transformation allows for competent cells to take up naked DNA, released from other cells on their death, into their cytoplasm, where it may recombine with the host genome.
- In **generalized transduction**, any piece of chromosomal DNA may be transferred by accidental packaging of the degraded host chromosome into a phage head. In **specialized transduction**, only chromosomal DNA adjacent to the integration site of a lysogenic phage may be transferred as a result of imprecise excision of the prophage.
- Conjugation is mediated by the **F plasmid,** which encodes a **conjugation pilus** that brings an F plasmid-containing **F^+ cell** into contact with an **F^- cell**.
- The rare integration of the F plasmid into the bacterial chromosome, generating an **Hfr cell**, allows for transfer of chromosomal DNA from the donor to the recipient. Additionally, imprecise excision of the F plasmid from the chromosome may generate an F' plasmid that may be transferred to a recipient by conjugation.
- Conjugation transfer of **R plasmids** is an important mechanism for the spread of antibiotic resistance in bacterial communities.
- **Transposons** are molecules of DNA with inverted repeats at their ends that also encode the enzyme transposase, allowing for their movement from one location in DNA to another. Although found in both prokaryotes and eukaryotes, transposons are clinically relevant in bacterial pathogens for the movement of virulence factors, including antibiotic resistance genes.

Multiple Choice

Which is the mechanism by which improper excision of a prophage from a bacterial chromosome results in packaging of bacterial genes near the integration site into a phage head?

A. conjugation
B. generalized transduction

C. specialized transduction
D. transformation

C

Which of the following refers to the uptake of naked DNA from the surrounding environment?

A. conjugation
B. generalized transduction
C. specialized transduction
D. transformation

D

The F plasmid is involved in which of the following processes?

A. conjugation
B. transduction
C. transposition
D. transformation

A

Which of the following refers to the mechanism of horizontal gene transfer naturally responsible for the spread of antibiotic resistance genes within a bacterial population?

A. conjugation
B. generalized transduction
C. specialized transduction
D. transformation

A

Fill in the Blank

A small DNA molecule that has the ability to independently excise from one location in a larger DNA molecule and integrate into the DNA elsewhere is called a _____.

---

transposon or transposable element

_____ is a group of mechanisms that allow for the introduction of genetic material from one organism to another organism within the same generation.

Horizontal gene transfer

True/False

Asexually reproducing organisms lack mechanisms for generating genetic diversity within a population.

False

Short Answer

Briefly describe two ways in which chromosomal DNA from a donor cell may be transferred to a recipient cell during the process of conjugation.

Describe what happens when a nonsense mutation is introduced into the gene encoding transposase within a transposon.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled How Asexual Prokaryotes Achieve Genetic Diversity is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

Mutations

skills to develop

- Compare point mutations and frameshift mutations
- Describe the differences between missense, nonsense, and silent mutations
- Describe the differences between light and dark repair
- Explain how different mutagens act
- Explain why the Ames test can be used to detect carcinogens
- Analyze sequences of DNA and identify examples of types of mutations
- e following laws within the Ideal Gas Law

A mutation is a heritable change in the DNA sequence of an organism. The resulting organism, called a mutant, may have a recognizable change in phenotype compared to the wild type, which is the phenotype most commonly observed in nature. A change in the DNA sequence is conferred to mRNA through transcription, and may lead to an altered amino acid sequence in a protein on translation. Because proteins carry out the vast majority of cellular functions, a change in amino acid sequence in a protein may lead to an altered phenotype for the cell and organism.

Effects of Mutations on DNA Sequence

There are several types of mutations that are classified according to how the DNA molecule is altered. One type, called a point mutation, affects a single base and most commonly occurs when one base is substituted or replaced by another. Mutations also result from the addition of one or more bases, known as an insertion, or the removal of one or more bases, known as a deletion.

Exercise 1

What type of a mutation occurs when a gene has two fewer nucleotides in its sequence?

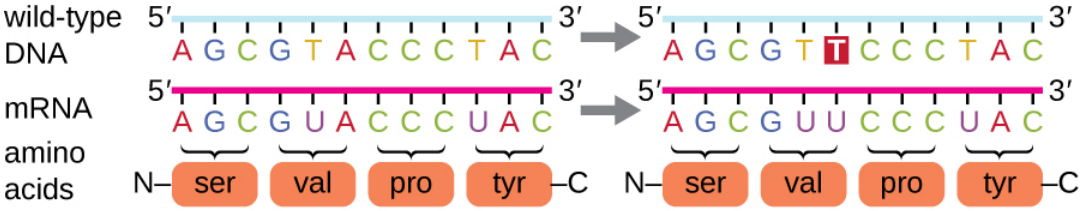
Effects of Mutations on Protein Structure and Function

Point mutations may have a wide range of effects on protein function (Figure 1). As a consequence of the degeneracy of the genetic code, a point mutation will commonly result in the same amino acid being incorporated into the resulting polypeptide despite the sequence change. This change would have no effect on the protein's structure, and is thus called a silent mutation. A missense mutation results in a different amino acid being incorporated into the resulting polypeptide. The effect of a missense mutation depends on how chemically different the new amino acid is from the wild-type amino acid. The location of the changed amino acid within the protein also is important. For example, if the changed amino acid is part of the enzyme's active site, then the effect of the missense mutation may be significant. Many missense mutations result in proteins that are still functional, at least to some degree. Sometimes the effects of missense mutations may be only apparent under certain environmental conditions; such missense mutations are called conditional mutations. Rarely, a missense mutation may be beneficial. Under the right environmental conditions, this type of mutation may give the organism that harbors it a selective advantage. Yet another type of point mutation, called a nonsense mutation, converts a codon encoding an amino acid (a sense codon) into a stop codon (a nonsense codon). Nonsense mutations result in the synthesis of proteins that are shorter than the wild type and typically not functional.

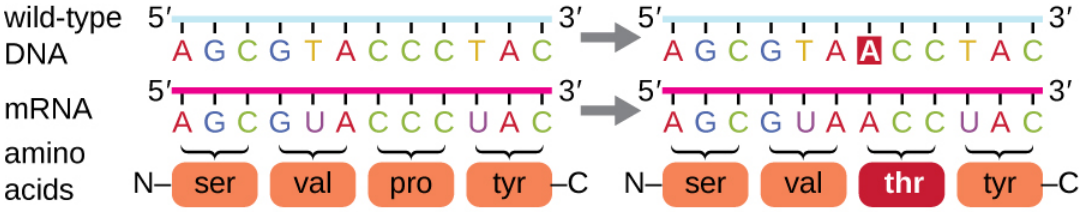
Deletions and insertions also cause various effects. Because codons are triplets of nucleotides, insertions or deletions in groups of three nucleotides may lead to the insertion or deletion of one or more amino acids and may not cause significant effects on the resulting protein's functionality. However, frameshift mutations, caused by insertions or deletions of a number of nucleotides that are not a multiple of three are extremely problematic because a shift in the reading frame results (Figure 1). Because ribosomes read the mRNA in triplet codons, frameshift mutations can change every amino acid after the point of the mutation. The new reading frame may also include a stop codon before the end of the coding sequence. Consequently, proteins made from genes containing frameshift mutations are nearly always nonfunctional.

point mutation: substitution of a single base

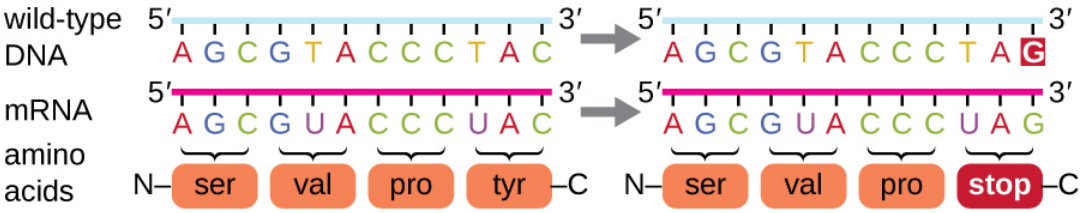
silent: has no effect on the protein sequence



missense: results in an amino acid substitution



nonsense: substitutes a stop codon for an amino acid



frameshift mutation: insertion or deletion of one or more bases

Insertion or **deletion** results in a shift in the reading frame.

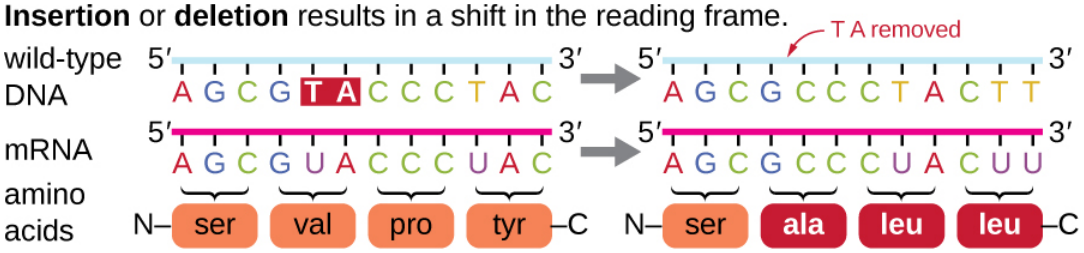


Figure 1: Mutations can lead to changes in the protein sequence encoded by the DNA.

Exercise 2

1. What are the reasons a nucleotide change in a gene for a protein might not have any effect on the phenotype of that gene?
2. Is it possible for an insertion of three nucleotides together after the fifth nucleotide in a protein-coding gene to produce a protein that is shorter than normal? How or how not?

A BENEFICIAL MUTATION

Since the first case of infection with human immunodeficiency virus (HIV) was reported in 1981, nearly 40 million people have died from HIV infection,[1] the virus that causes acquired immune deficiency syndrome (AIDS). The virus targets helper T cells that play a key role in bridging the innate and adaptive immune response, infecting and killing cells normally involved in the body's response to infection. There is no cure for HIV infection, but many drugs have been developed to slow or block the progression of the virus. Although individuals around the world may be infected, the highest prevalence among people 15–49

years old is in sub-Saharan Africa, where nearly one person in 20 is infected, accounting for greater than 70% of the infections worldwide[2] (Figure 2). Unfortunately, this is also a part of the world where prevention strategies and drugs to treat the infection are the most lacking.

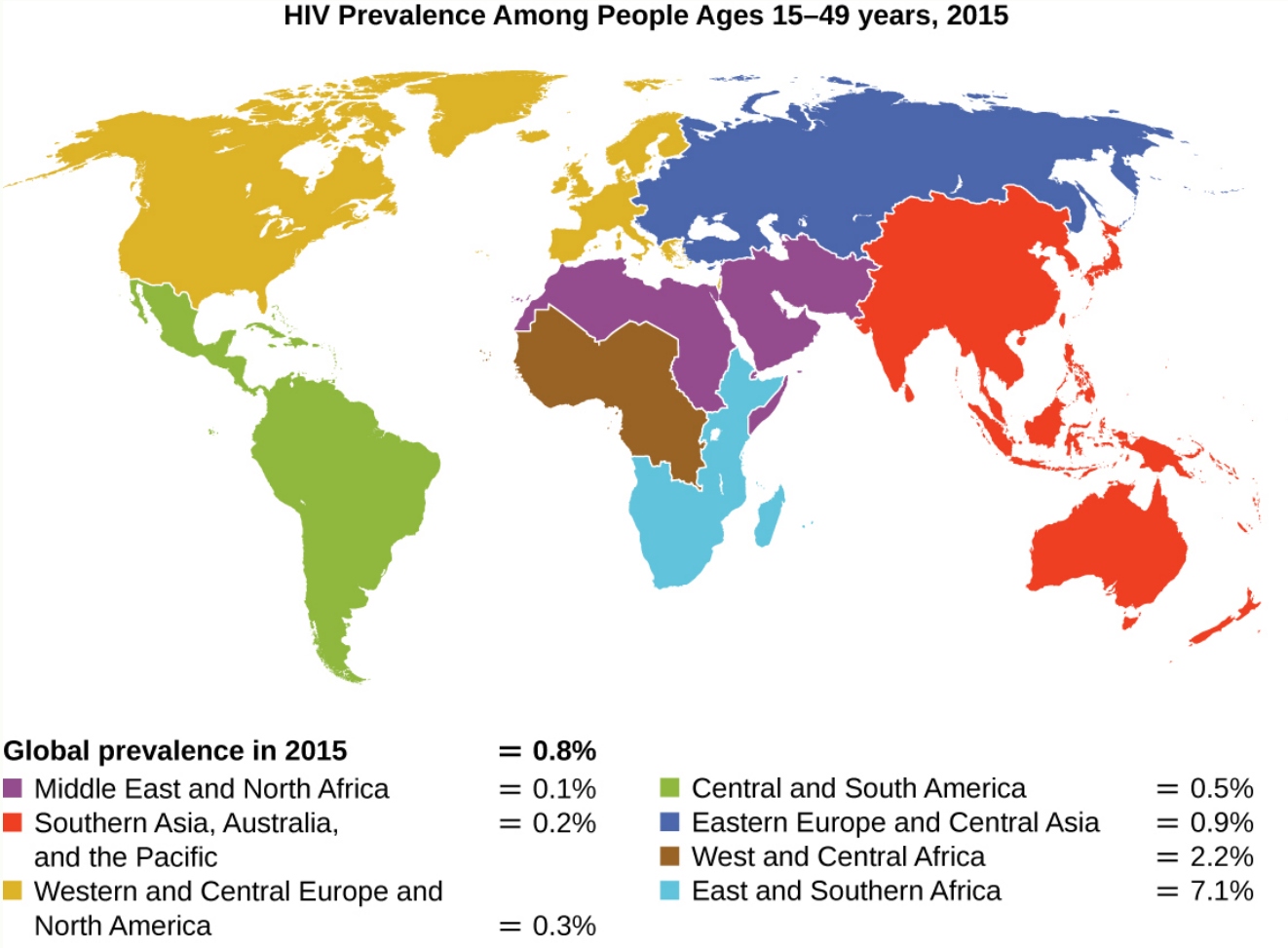


Figure 2: HIV is highly prevalent in sub-Saharan Africa, but its prevalence is quite low in some other parts of the world.

In recent years, scientific interest has been piqued by the discovery of a few individuals from northern Europe who are resistant to HIV infection. In 1998, American geneticist Stephen J. O'Brien at the National Institutes of Health (NIH) and colleagues published the results of their genetic analysis of more than 4,000 individuals. These indicated that many individuals of Eurasian descent (up to 14% in some ethnic groups) have a deletion mutation, called CCR5-delta 32, in the gene encoding CCR5. CCR5 is a coreceptor found on the surface of T cells that is necessary for many strains of the virus to enter the host cell. The mutation leads to the production of a receptor to which HIV cannot effectively bind and thus blocks viral entry. People homozygous for this mutation have greatly reduced susceptibility to HIV infection, and those who are heterozygous have some protection from infection as well.

It is not clear why people of northern European descent, specifically, carry this mutation, but its prevalence seems to be highest in northern Europe and steadily decreases in populations as one moves south. Research indicates that the mutation has been present since before HIV appeared and may have been selected for in European populations as a result of exposure to the plague or smallpox. This mutation may protect individuals from plague (caused by the bacterium *Yersinia pestis*) and smallpox (caused by the variola virus) because this receptor may also be involved in these diseases. The age of this mutation is a matter of debate, but estimates suggest it appeared between 1875 years to 225 years ago, and may have been spread from Northern Europe through Viking invasions.

This exciting finding has led to new avenues in HIV research, including looking for drugs to block CCR5 binding to HIV in individuals who lack the mutation. Although DNA testing to determine which individuals carry the CCR5-delta 32 mutation is

possible, there are documented cases of individuals homozygous for the mutation contracting HIV. For this reason, DNA testing for the mutation is not widely recommended by public health officials so as not to encourage risky behavior in those who carry the mutation. Nevertheless, inhibiting the binding of HIV to CCR5 continues to be a valid strategy for the development of drug therapies for those infected with HIV.

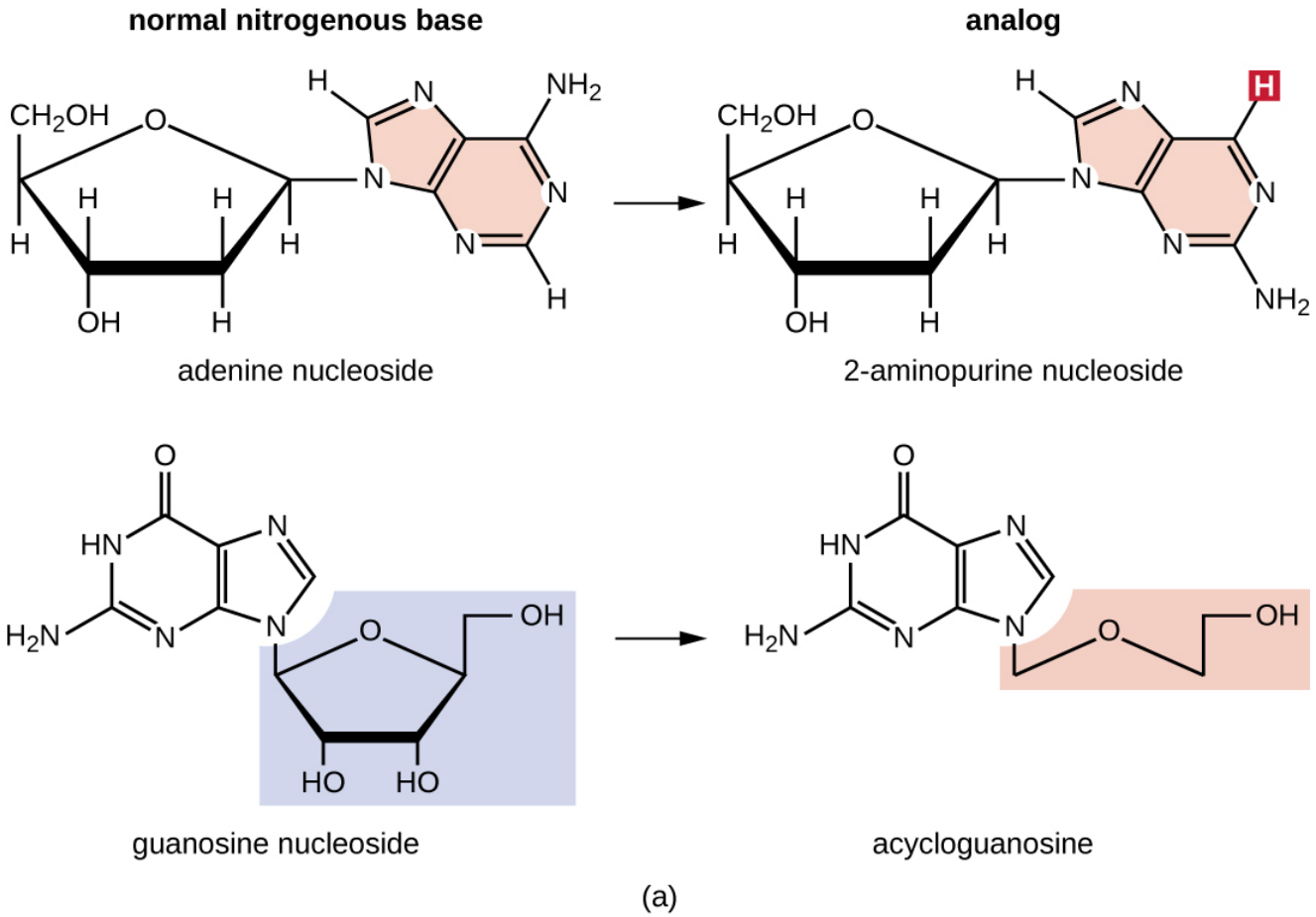
Causes of Mutations

Mistakes in the process of DNA replication can cause spontaneous mutations to occur. The error rate of DNA polymerase is one incorrect base per billion base pairs replicated. Exposure to mutagens can cause induced mutations, which are various types of chemical agents or radiation (Table 1). Exposure to a mutagen can increase the rate of mutation more than 1000-fold. Mutagens are often also carcinogens, agents that cause cancer. However, whereas nearly all carcinogens are mutagenic, not all mutagens are necessarily carcinogens.

Chemical Mutagens

Various types of chemical mutagens interact directly with DNA either by acting as nucleoside analogs or by modifying nucleotide bases. Chemicals called nucleoside analogs are structurally similar to normal nucleotide bases and can be incorporated into DNA during replication (Figure 3). These base analogs induce mutations because they often have different base-pairing rules than the bases they replace. Other chemical mutagens can modify normal DNA bases, resulting in different base-pairing rules. For example, nitrous acid deaminates cytosine, converting it to uracil. Uracil then pairs with adenine in a subsequent round of replication, resulting in the conversion of a GC base pair to an AT base pair. Nitrous acid also deaminates adenine to hypoxanthine, which base pairs with cytosine instead of thymine, resulting in the conversion of a TA base pair to a CG base pair.

Chemical mutagens known as intercalating agents work differently. These molecules slide between the stacked nitrogenous bases of the DNA double helix, distorting the molecule and creating atypical spacing between nucleotide base pairs (Figure 4). As a result, during DNA replication, DNA polymerase may either skip replicating several nucleotides (creating a deletion) or insert extra nucleotides (creating an insertion). Either outcome may lead to a frameshift mutation. Combustion products like polycyclic aromatic hydrocarbons are particularly dangerous intercalating agents that can lead to mutation-caused cancers. The intercalating agents ethidium bromide and acridine orange are commonly used in the laboratory to stain DNA for visualization and are potential mutagens.



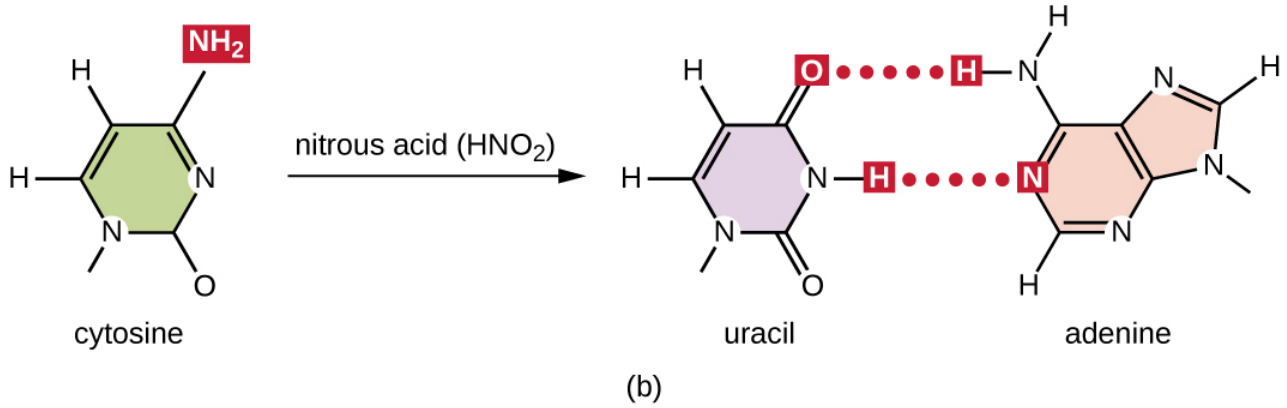


Figure 3: (a) 2-aminopurine nucleoside (2AP) structurally is a nucleoside analog to adenine nucleoside, whereas 5-bromouracil (5BU) is a nucleoside analog to thymine nucleoside. 2AP base pairs with C, converting an AT base pair to a GC base pair after several rounds of replication. 5BU pairs with G, converting an AT base pair to a GC base pair after several rounds of replication. (b) Nitrous acid is a different type of chemical mutagen that modifies already existing nucleoside bases like C to produce U, which base pairs with A. This chemical modification, as shown here, results in converting a CG base pair to a TA base pair.

https://geo.libretexts.org/@go/page/6188

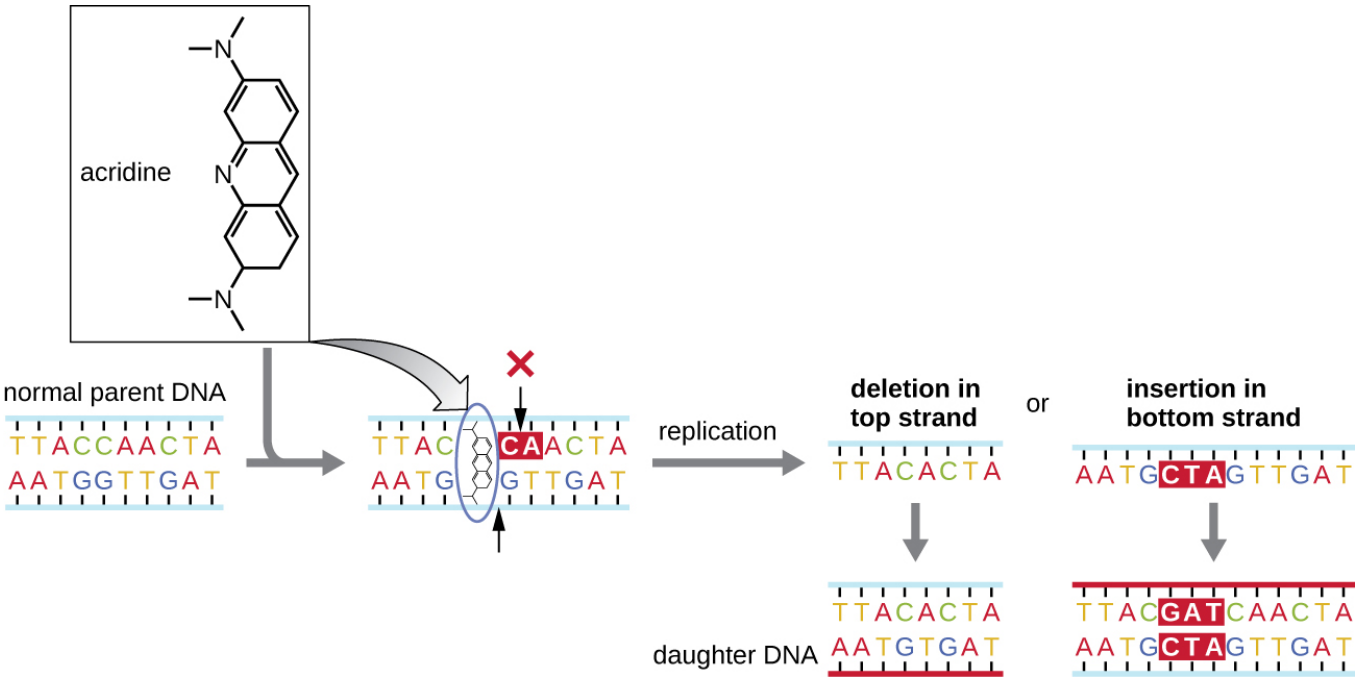


Figure 4: Intercalating agents, such as acridine, introduce atypical spacing between base pairs, resulting in DNA polymerase introducing either a deletion or an insertion, leading to a potential frameshift mutation.

Radiation

Exposure to either ionizing or nonionizing radiation can each induce mutations in DNA, although by different mechanisms. Strong ionizing radiation like X-rays and gamma rays can cause single- and double-stranded breaks in the DNA backbone through the formation of hydroxyl radicals on radiation exposure (Figure 5). Ionizing radiation can also modify bases; for example, the deamination of cytosine to uracil, analogous to the action of nitrous acid.[3] Ionizing radiation exposure is used to kill microbes to sterilize medical devices and foods, because of its dramatic nonspecific effect in damaging DNA, proteins, and other cellular components (see Using Physical Methods to Control Microorganisms).

Nonionizing radiation, like ultraviolet light, is not energetic enough to initiate these types of chemical changes. However, nonionizing radiation can induce dimer formation between two adjacent pyrimidine bases, commonly two thymines, within a nucleotide strand. During thymine dimer formation, the two adjacent thymines become covalently linked and, if left unrepaired, both DNA replication and transcription are stalled at this point. DNA polymerase may proceed and replicate the dimer incorrectly, potentially leading to frameshift or point mutations.

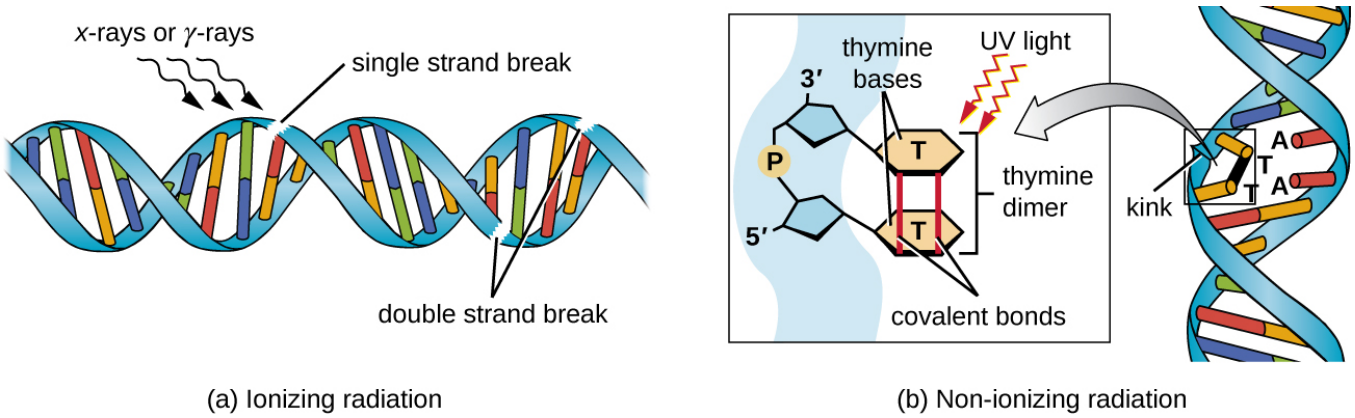


Figure 5: (a) Ionizing radiation may lead to the formation of single-stranded and double-stranded breaks in the sugar-phosphate backbone of DNA, as well as to the modification of bases (not shown). (b) Nonionizing radiation like ultraviolet light can lead to the formation of thymine dimers, which can stall replication and transcription and introduce frameshift or point mutations.

https://geo.libretexts.org/@go/page/6188

Table 1: A Summary of Mutagenic Agents

Mutagenic Agents	Mode of Action	Effect on DNA	Resulting Type of Mutation
Nucleoside analogs			
2-aminopurine	Is inserted in place of A but base pairs with C	Converts AT to GC base pair	Point
5-bromouracil	Is inserted in place of T but base pairs with G	Converts AT to GC base pair	Point
Nucleotide-modifying agent			
Nitrous oxide	Deaminates C to U	Converts GC to AT base pair	Point
Intercalating agents			
Acridine orange, ethidium bromide, polycyclic aromatic hydrocarbons	Distorts double helix, creates unusual spacing between nucleotides	Introduces small deletions and insertions	Frameshift
Ionizing radiation			
X-rays, γ-rays	Forms hydroxyl radicals	Causes single- and double-strand DNA breaks	Repair mechanisms may introduce mutations
X-rays, γ-rays	Modifies bases (e.g., deaminating C to U)	Converts GC to AT base pair	Point
Nonionizing radiation			
Ultraviolet	Forms pyrimidine (usually thymine) dimers	Causes DNA replication errors	Frameshift or point

Exercise 3

1. How does a base analog introduce a mutation?
2. How does an intercalating agent introduce a mutation?
3. What type of mutagen causes thymine dimers?

DNA Repair

The process of DNA replication is highly accurate, but mistakes can occur spontaneously or be induced by mutagens. Uncorrected mistakes can lead to serious consequences for the phenotype. Cells have developed several repair mechanisms to minimize the number of mutations that persist.

Proofreading

Most of the mistakes introduced during DNA replication are promptly corrected by most DNA polymerases through a function called proofreading. In proofreading, the DNA polymerase reads the newly added base, ensuring that it is complementary to the corresponding base in the template strand before adding the next one. If an incorrect base has been added, the enzyme makes a cut to release the wrong nucleotide and a new base is added.

Mismatch Repair

Some errors introduced during replication are corrected shortly after the replication machinery has moved. This mechanism is called mismatch repair. The enzymes involved in this mechanism recognize the incorrectly added nucleotide, excise it, and replace it with the correct base. One example is the methyl-directed mismatch repair in *E. coli*. The DNA is hemimethylated. This means that the parental strand is methylated while the newly synthesized daughter strand is not. It takes several minutes before the new strand is methylated. Proteins MutS, MutL, and MutH bind to the hemimethylated site where the incorrect nucleotide is found.

MutH cuts the nonmethylated strand (the new strand). An exonuclease removes a portion of the strand (including the incorrect nucleotide). The gap formed is then filled in by DNA pol III and ligase.

Repair of Thymine Dimers

Because the production of thymine dimers is common (many organisms cannot avoid ultraviolet light), mechanisms have evolved to repair these lesions. In nucleotide excision repair (also called dark repair), enzymes remove the pyrimidine dimer and replace it with the correct nucleotides (Figure 6). In *E. coli*, the DNA is scanned by an enzyme complex. If a distortion in the double helix is found that was introduced by the pyrimidine dimer, the enzyme complex cuts the sugar-phosphate backbone several bases upstream and downstream of the dimer, and the segment of DNA between these two cuts is then enzymatically removed. DNA pol I replaces the missing nucleotides with the correct ones and DNA ligase seals the gap in the sugar-phosphate backbone.

The direct repair (also called light repair) of thymine dimers occurs through the process of photoreactivation in the presence of visible light. An enzyme called photolyase recognizes the distortion in the DNA helix caused by the thymine dimer and binds to the dimer. Then, in the presence of visible light, the photolyase enzyme changes conformation and breaks apart the thymine dimer, allowing the thymines to again correctly base pair with the adenines on the complementary strand. Photoreactivation appears to be present in all organisms, with the exception of placental mammals, including humans. Photoreactivation is particularly important for organisms chronically exposed to ultraviolet radiation, like plants, photosynthetic bacteria, algae, and corals, to prevent the accumulation of mutations caused by thymine dimer formation.

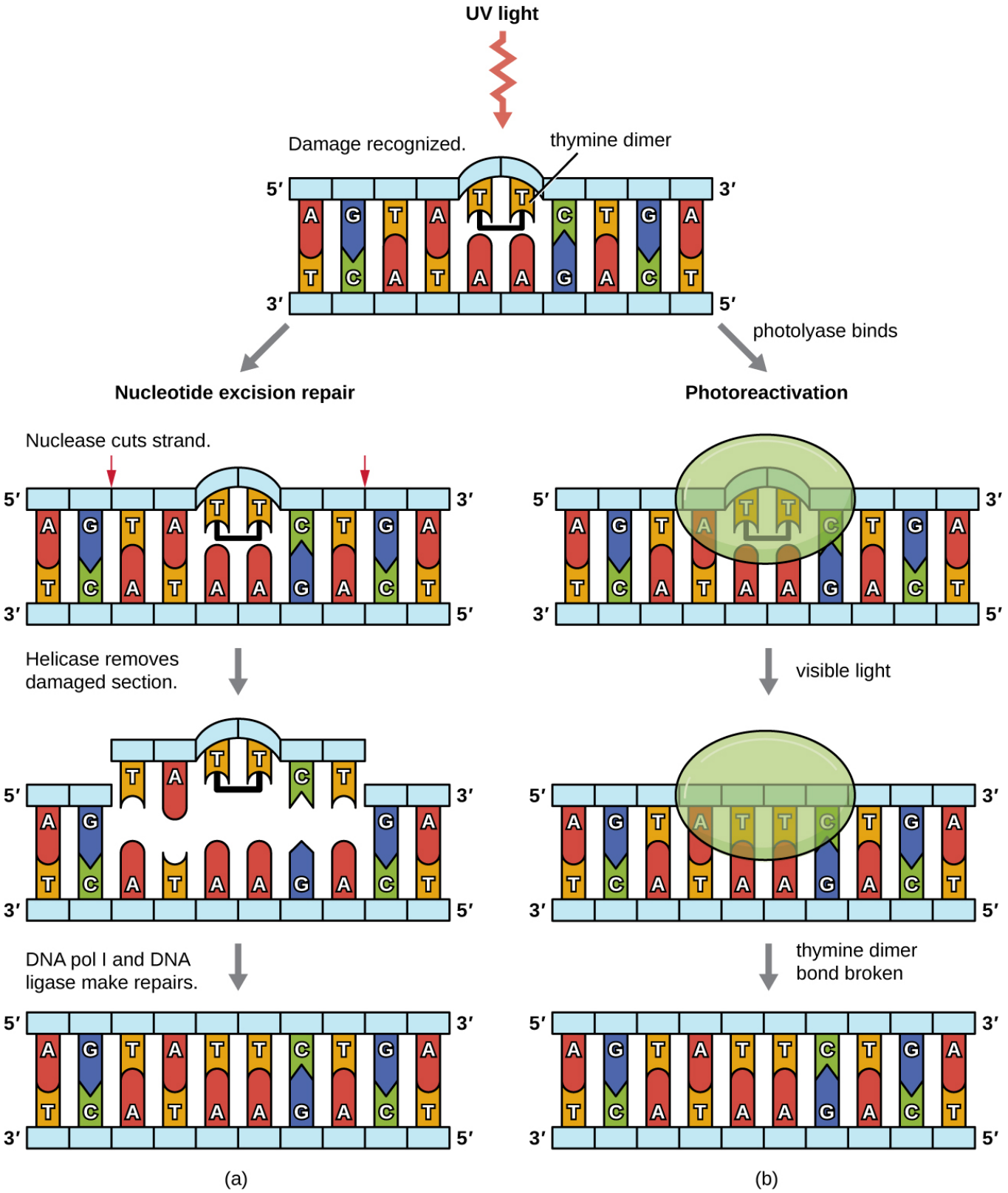


Figure 6: Bacteria have two mechanisms for repairing thymine dimers. (a) In nucleotide excision repair, an enzyme complex recognizes the distortion in the DNA complex around the thymine dimer and cuts and removes the damaged DNA strand. The correct nucleotides are replaced by DNA pol I and the nucleotide strand is sealed by DNA ligase. (b) In photoreactivation, the enzyme photolyase binds to the thymine dimer and, in the presence of visible light, breaks apart the dimer, restoring the base pairing of the thymines with complementary adenines on the opposite DNA strand.

https://geo.libretexts.org/@go/page/6188

Exercise 4

1. During mismatch repair, how does the enzyme recognize which is the new and which is the old strand?
2. How does an intercalating agent introduce a mutation?
3. What type of mutation does photolyase repair?

Identifying Bacterial Mutants

One common technique used to identify bacterial mutants is called replica plating. This technique is used to detect nutritional mutants, called auxotrophs, which have a mutation in a gene encoding an enzyme in the biosynthesis pathway of a specific nutrient, such as an amino acid. As a result, whereas wild-type cells retain the ability to grow normally on a medium lacking the specific nutrient, auxotrophs are unable to grow on such a medium. During replica plating (Figure 7), a population of bacterial cells is mutagenized and then plated as individual cells on a complex nutritionally complete plate and allowed to grow into colonies. Cells from these colonies are removed from this master plate, often using sterile velvet. This velvet, containing cells, is then pressed in the same orientation onto plates of various media. At least one plate should also be nutritionally complete to ensure that cells are being properly transferred between the plates. The other plates lack specific nutrients, allowing the researcher to discover various auxotrophic mutants unable to produce specific nutrients. Cells from the corresponding colony on the nutritionally complete plate can be used to recover the mutant for further study.

Exercise 5

Why are cells plated on a nutritionally complete plate in addition to nutrient-deficient plates when looking for a mutant?

The Ames Test

The Ames test, developed by Bruce Ames (1928–) in the 1970s, is a method that uses bacteria for rapid, inexpensive screening of the carcinogenic potential of new chemical compounds. The test measures the mutation rate associated with exposure to the compound, which, if elevated, may indicate that exposure to this compound is associated with greater cancer risk. The Ames test uses as the test organism a strain of *Salmonella typhimurium* that is a histidine auxotroph, unable to synthesize its own histidine because of a mutation in an essential gene required for its synthesis. After exposure to a potential mutagen, these bacteria are plated onto a medium lacking histidine, and the number of mutants regaining the ability to synthesize histidine is recorded and compared with the number of such mutants that arise in the absence of the potential mutagen (Figure 8). Chemicals that are more mutagenic will bring about more mutants with restored histidine synthesis in the Ames test. Because many chemicals are not directly mutagenic but are metabolized to mutagenic forms by liver enzymes, rat liver extract is commonly included at the start of this experiment to mimic liver metabolism. After the Ames test is conducted, compounds identified as mutagenic are further tested for their potential carcinogenic properties by using other models, including animal models like mice and rats.

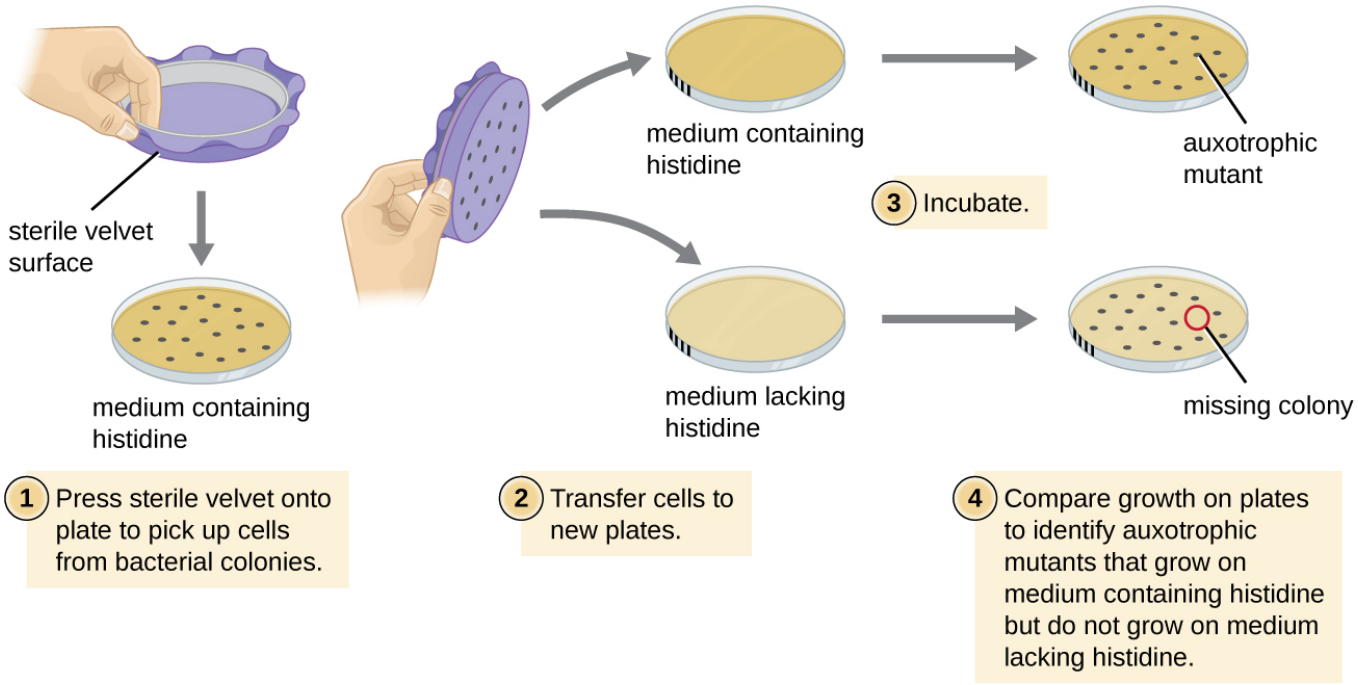


Figure 7: Identification of auxotrophic mutants, like histidine auxotrophs, is done using replica plating. After mutagenesis, colonies that grow on nutritionally complete medium but not on medium lacking histidine are identified as histidine auxotrophs.

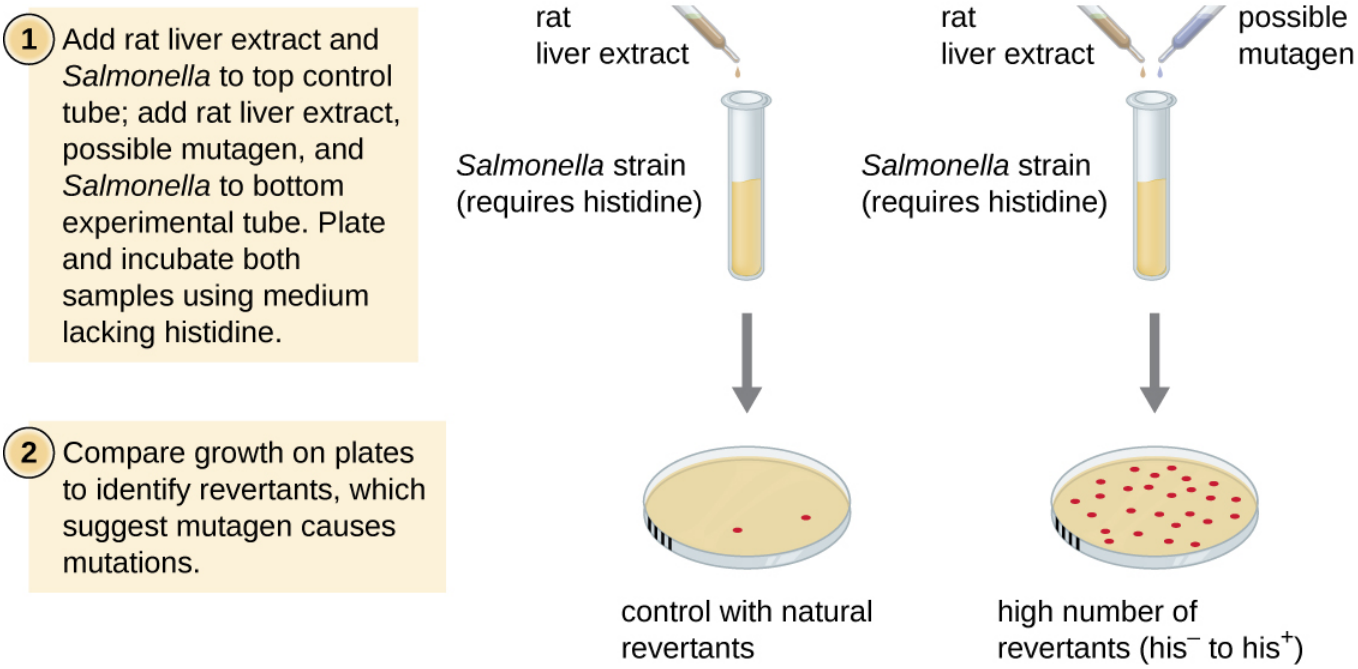


Figure 8: The Ames test is used to identify mutagenic, potentially carcinogenic chemicals. A Salmonella histidine auxotroph is used as the test strain, exposed to a potential mutagen/carcinogen. The number of reversion mutants capable of growing in the absence of supplied histidine is counted and compared with the number of natural reversion mutants that arise in the absence of the potential mutagen.

Exercise 6

1. What mutation is used as an indicator of mutation rate in the Ames test?
2. Why can the Ames test work as a test for carcinogenicity?

Key Concepts and Summary

- A **mutation** is a heritable change in DNA. A mutation may lead to a change in the amino-acid sequence of a protein, possibly affecting its function.
- A **point mutation** affects a single base pair. A point mutation may cause a **silent mutation** if the mRNA codon codes for the same amino acid, a **missense mutation** if the mRNA codon codes for a different amino acid, or a **nonsense mutation** if the mRNA codon becomes a stop codon.
- Missense mutations may retain function, depending on the chemistry of the new amino acid and its location in the protein. Nonsense mutations produce truncated and frequently nonfunctional proteins.
- A **frameshift mutation** results from an insertion or deletion of a number of nucleotides that is not a multiple of three. The change in reading frame alters every amino acid after the point of the mutation and results in a nonfunctional protein.
- **Spontaneous mutations** occur through DNA replication errors, whereas **induced mutations** occur through exposure to a **mutagen**.
- Mutagenic agents are frequently carcinogenic but not always. However, nearly all carcinogens are mutagenic.
- Chemical mutagens include base analogs and chemicals that modify existing bases. In both cases, mutations are introduced after several rounds of DNA replication.
- **Ionizing radiation,** such as X-rays and γ-rays, leads to breakage of the phosphodiester backbone of DNA and can also chemically modify bases to alter their base-pairing rules.
- **Nonionizing radiation** like ultraviolet light may introduce pyrimidine (thymine) dimers, which, during DNA replication and transcription, may introduce frameshift or point mutations.
- Cells have mechanisms to repair naturally occurring mutations. DNA polymerase has proofreading activity. Mismatch repair is a process to repair incorrectly incorporated bases after DNA replication has been completed.
- Pyrimidine dimers can also be repaired. In **nucleotide excision repair (dark repair)**, enzymes recognize the distortion introduced by the pyrimidine dimer and replace the damaged strand with the correct bases, using the undamaged DNA strand as a template. Bacteria and other organisms may also use **direct repair**, in which the photolyase enzyme, in the presence of visible light, breaks apart the pyrimidines.
- Through comparison of growth on the complete plate and lack of growth on media lacking specific nutrients, specific loss-of-function mutants called **auxotrophs** can be identified.
- The **Ames test** is an inexpensive method that uses auxotrophic bacteria to measure mutagenicity of a chemical compound. Mutagenicity is an indicator of carcinogenic potential.

Multiple Choice

Which of the following is a change in the sequence that leads to formation of a stop codon?

A. missense mutation
B. nonsense mutation
C. silent mutation
D. deletion mutation

B

The formation of pyrimidine dimers results from which of the following?

A. spontaneous errors by DNA polymerase
B. exposure to gamma radiation
C. exposure to ultraviolet radiation
D. exposure to intercalating agents

C

Which of the following is an example of a frameshift mutation?

A. a deletion of a codon
B. missense mutation
C. silent mutation
D. deletion of one nucleotide

D

Which of the following is the type of DNA repair in which thymine dimers are directly broken down by the enzyme photolyase?

A. direct repair
B. nucleotide excision repair
C. mismatch repair
D. proofreading

A

Which of the following regarding the Ames test is true?

A. It is used to identify newly formed auxotrophic mutants.
B. It is used to identify mutants with restored biosynthetic activity.
C. It is used to identify spontaneous mutants.
D. It is used to identify mutants lacking photoreactivation activity.

B

Fill in the Blank

A chemical mutagen that is structurally similar to a nucleotide but has different base-pairing rules is called a _____.

nucleoside analog

The enzyme used in light repair to split thymine dimers is called _____.

photolyase

The phenotype of an organism that is most commonly observed in nature is called the _____.

wild type

True/False

Carcinogens are typically mutagenic.

True

Short Answer

Why is it more likely that insertions or deletions will be more detrimental to a cell than point mutations?

Critical Thinking

Below are several DNA sequences that are mutated compared with the wild-type sequence: 3’-T A C T G A C T G A C G A T C-5’. Envision that each is a section of a DNA molecule that has separated in preparation for transcription, so you are only seeing the template strand. Construct the complementary DNA sequences (indicating 5’ and 3’ ends) for each mutated DNA sequence, then transcribe (indicating 5’ and 3’ ends) the template strands, and translate the mRNA molecules using the genetic code, recording the resulting amino acid sequence (indicating the N and C termini). What type of mutation is each?

Mutated DNA Template Strand #1: 3’-T A C T G T C T G A C G A T C-5’ Complementary DNA sequence: mRNA sequence transcribed from template: Amino acid sequence of peptide: Type of mutation:
Mutated DNA Template Strand #2: 3’-T A C G G A C T G A C G A T C-5’ Complementary DNA sequence: mRNA sequence transcribed from template: Amino acid sequence of peptide: Type of mutation:
Mutated DNA Template Strand #3: 3’-T A C T G A C T G A C T A T C-5’ Complementary DNA sequence: mRNA sequence transcribed from template: Amino acid sequence of peptide: Type of mutation:
Mutated DNA Template Strand #4: 3’-T A C G A C T G A C T A T C-5’ Complementary DNA sequence: mRNA sequence transcribed from template: Amino acid sequence of peptide: Type of mutation:

Why do you think the Ames test is preferable to the use of animal models to screen chemical compounds for mutagenicity?

Footnotes

1. 1 World Health Organization. “ Global Health Observatory (GHO) Data, HIV/AIDS.” http://www.who.int/gho/hiv/en/. Accessed August 5, 2016.
2. 2 World Health Organization. “ Global Health Observatory (GHO) Data, HIV/AIDS.” http://www.who.int/gho/hiv/en/. Accessed August 5, 2016.
3. 3 K.R. Tindall et al. “Changes in DNA Base Sequence Induced by Gamma-Ray Mutagenesis of Lambda Phage and Prophage.” *Genetics* 118 no. 4 (1988):551–560.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled Mutations is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

Operon Theory

skills to develop

- Compare inducible operons and repressible operons
- Describe why regulation of operons is important

Each nucleated cell in a multicellular organism contains copies of the same DNA. Similarly, all cells in two pure bacterial cultures inoculated from the same starting colony contain the same DNA, with the exception of changes that arise from spontaneous mutations. If each cell in a multicellular organism has the same DNA, then how is it that cells in different parts of the organism's body exhibit different characteristics? Similarly, how is it that the same bacterial cells within two pure cultures exposed to different environmental conditions can exhibit different phenotypes? In both cases, each genetically identical cell does not turn on, or express, the same set of genes. Only a subset of proteins in a cell at a given time is expressed.

Genomic DNA contains both structural genes, which encode products that serve as cellular structures or enzymes, and regulatory genes, which encode products that regulate gene expression. The expression of a gene is a highly regulated process. Whereas regulating gene expression in multicellular organisms allows for cellular differentiation, in single-celled organisms like prokaryotes, it primarily ensures that a cell's resources are not wasted making proteins that the cell does not need at that time.

Elucidating the mechanisms controlling gene expression is important to the understanding of human health. Malfunctions in this process in humans lead to the development of cancer and other diseases. Understanding the interaction between the gene expression of a pathogen and that of its human host is important for the understanding of a particular infectious disease. Gene regulation involves a complex web of interactions within a given cell among signals from the cell's environment, signaling molecules within the cell, and the cell's DNA. These interactions lead to the expression of some genes and the suppression of others, depending on circumstances.

Prokaryotes and eukaryotes share some similarities in their mechanisms to regulate gene expression; however, gene expression in eukaryotes is more complicated because of the temporal and spatial separation between the processes of transcription and translation. Thus, although most regulation of gene expression occurs through transcriptional control in prokaryotes, regulation of gene expression in eukaryotes occurs at the transcriptional level and post-transcriptionally (after the primary transcript has been made).

Prokaryotic Gene Regulation

In bacteria and archaea, structural proteins with related functions are usually encoded together within the genome in a block called an operon and are transcribed together under the control of a single promoter, resulting in the formation of a polycistronic transcript (Figure 1). In this way, regulation of the transcription of all of the structural genes encoding the enzymes that catalyze the many steps in a single biochemical pathway can be controlled simultaneously, because they will either all be needed at the same time, or none will be needed. For example, in *E. coli*, all of the structural genes that encode enzymes needed to use lactose as an energy source lie next to each other in the lactose (or *lac*) operon under the control of a single promoter, the *lac* promoter. French scientists François Jacob (1920–2013) and Jacques Monod at the Pasteur Institute were the first to show the organization of bacterial genes into operons, through their studies on the *lac* operon of *E. coli*. For this work, they won the Nobel Prize in Physiology or Medicine in 1965. Although eukaryotic genes are not organized into operons, prokaryotic operons are excellent models for learning about gene regulation generally. There are some gene clusters in eukaryotes that function similar to operons. Many of the principles can be applied to eukaryotic systems and contribute to our understanding of changes in gene expression in eukaryotes that can result pathological changes such as cancer.

Each operon includes DNA sequences that influence its own transcription; these are located in a region called the regulatory region. The regulatory region includes the promoter and the region surrounding the promoter, to which transcription factors, proteins encoded by regulatory genes, can bind. Transcription factors influence the binding of RNA polymerase to the promoter and allow its progression to transcribe structural genes. A repressor is a transcription factor that suppresses transcription of a gene in response to an external stimulus by binding to a DNA sequence within the regulatory region called the operator, which is located between the RNA polymerase binding site of the promoter and the transcriptional start site of the first structural gene. Repressor binding physically blocks RNA polymerase from transcribing structural genes. Conversely, an activator is a transcription factor that increases the transcription of a gene in response to an external stimulus by facilitating RNA polymerase binding to the promoter.

An inducer, a third type of regulatory molecule, is a small molecule that either activates or represses transcription by interacting with a repressor or an activator.

In prokaryotes, there are examples of operons whose gene products are required rather consistently and whose expression, therefore, is unregulated. Such operons are constitutively expressed, meaning they are transcribed and translated continuously to provide the cell with constant intermediate levels of the protein products. Such genes encode enzymes involved in housekeeping functions required for cellular maintenance, including DNA replication, repair, and expression, as well as enzymes involved in core metabolism. In contrast, there are other prokaryotic operons that are expressed only when needed and are regulated by repressors, activators, and inducers.

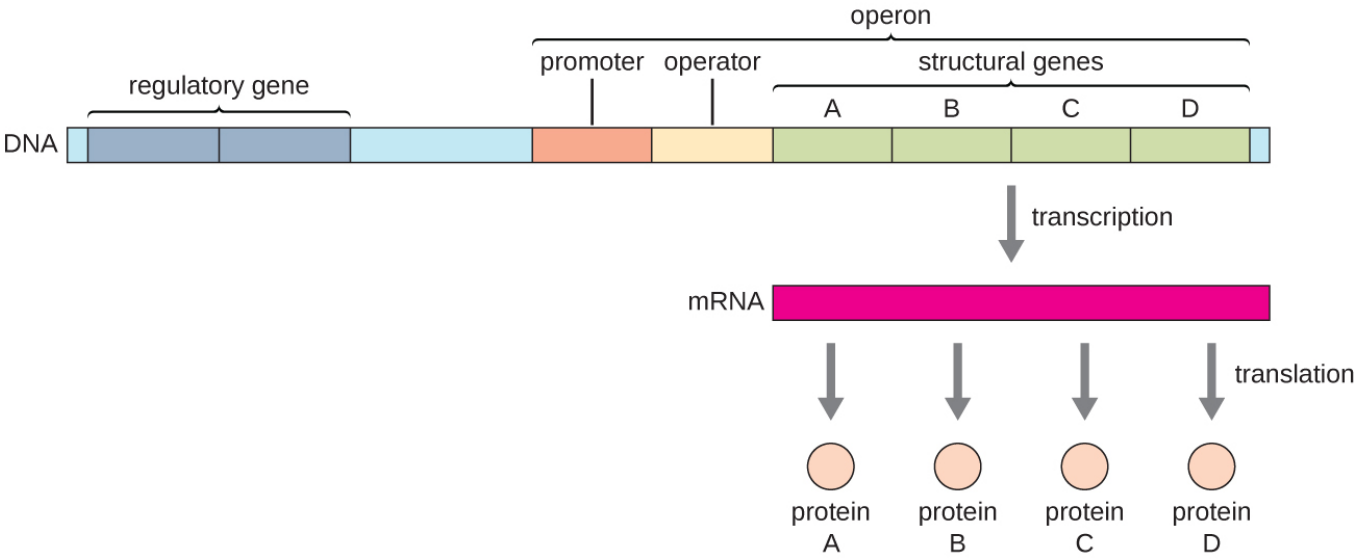


Figure 1: In prokaryotes, structural genes of related function are often organized together on the genome and transcribed together under the control of a single promoter. The operon's regulatory region includes both the promoter and the operator. If a repressor binds to the operator, then the structural genes will not be transcribed. Alternatively, activators may bind to the regulatory region, enhancing transcription.

Exercise 1

1. What are the parts in the DNA sequence of an operon?
2. What types of regulatory molecules are there?

Regulation by Repression

Prokaryotic operons are commonly controlled by the binding of repressors to operator regions, thereby preventing the transcription of the structural genes. Such operons are classified as either **repressible operons** or inducible operons. Repressible operons, like the tryptophan (*trp*) operon, typically contain genes encoding enzymes required for a biosynthetic pathway. As long as the product of the pathway, like tryptophan, continues to be required by the cell, a repressible operon will continue to be expressed. However, when the product of the biosynthetic pathway begins to accumulate in the cell, removing the need for the cell to continue to make more, the expression of the operon is repressed. Conversely, **inducible operons**, like the *lac* operon of *E. coli*, often contain genes encoding enzymes in a pathway involved in the metabolism of a specific substrate like lactose. These enzymes are only required when that substrate is available, thus expression of the operons is typically induced only in the presence of the substrate.

The trp Operon: A Repressible Operon

E. coli can synthesize tryptophan using enzymes that are encoded by five structural genes located next to each other in the *trp* operon (Figure 2). When environmental tryptophan is low, the operon is turned on. This means that transcription is initiated, the genes are expressed, and tryptophan is synthesized. However, if tryptophan is present in the environment, the *trp* operon is turned off. Transcription does not occur and tryptophan is not synthesized.

When tryptophan is not present in the cell, the repressor by itself does not bind to the operator; therefore, the operon is active and tryptophan is synthesized. However, when tryptophan accumulates in the cell, two tryptophan molecules bind to the *trp* repressor

molecule, which changes its shape, allowing it to bind to the *trp* operator. This binding of the active form of the *trp* repressor to the operator blocks RNA polymerase from transcribing the structural genes, stopping expression of the operon. Thus, the actual product of the biosynthetic pathway controlled by the operon regulates the expression of the operon.

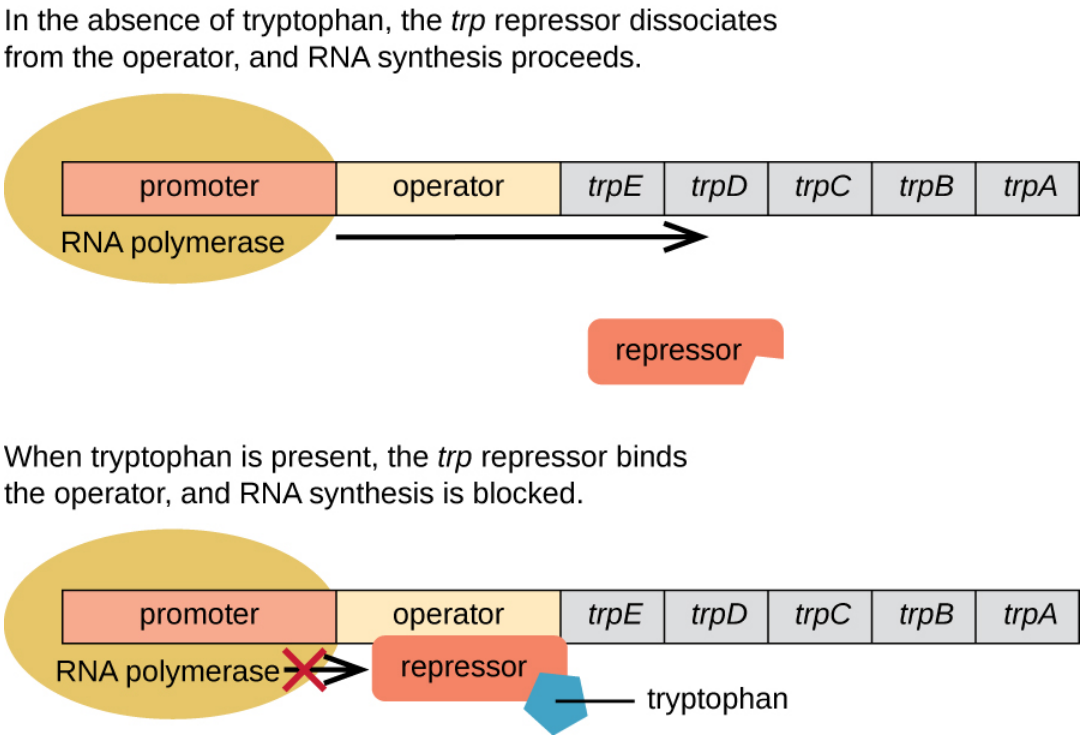


Figure 2: *The five structural genes needed to synthesize tryptophan in E. coli are located next to each other in the trp operon. When tryptophan is absent, the repressor protein does not bind to the operator, and the genes are transcribed. When tryptophan is plentiful, tryptophan binds the repressor protein at the operator sequence. This physically blocks the RNA polymerase from transcribing the tryptophan biosynthesis genes.*

Watch this video to learn more about the *trp* operon.

The *lac* Operon: An Inducible Operon

The *lac* operon is an example of an inducible operon that is also subject to activation in the absence of glucose (Figure 3). The *lac* operon encodes three structural genes necessary to acquire and process the disaccharide lactose from the environment, breaking it down into the simple sugars glucose and galactose. For the *lac* operon to be expressed, lactose must be present. This makes sense for the cell because it would be energetically wasteful to create the enzymes to process lactose if lactose was not available.

In the absence of lactose, the *lac* repressor is bound to the operator region of the *lac* operon, physically preventing RNA polymerase from transcribing the structural genes. However, when lactose is present, the lactose inside the cell is converted to allolactose. Allolactose serves as an inducer molecule, binding to the repressor and changing its shape so that it is no longer able to bind to the operator DNA. Removal of the repressor in the presence of lactose allows RNA polymerase to move through the operator region and begin transcription of the *lac* structural genes.

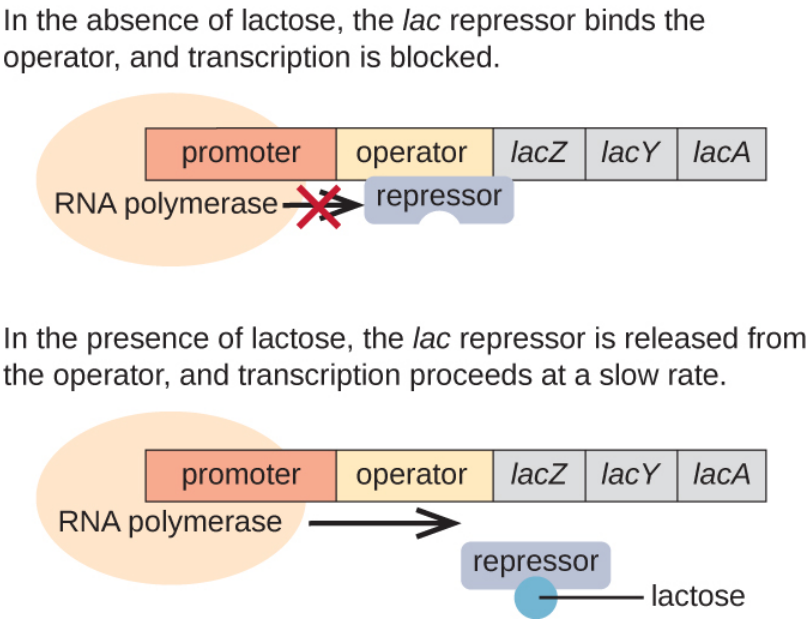


Figure 3: The three structural genes that are needed to degrade lactose in E. coli are located next to each other in the lac operon. When lactose is absent, the repressor protein binds to the operator, physically blocking the RNA polymerase from transcribing the lac structural genes. When lactose is available, a lactose molecule binds the repressor protein, preventing the repressor from binding to the operator sequence, and the genes are transcribed.

The *lac* Operon: Activation by Catabolite Activator Protein

Bacteria typically have the ability to use a variety of substrates as carbon sources. However, because glucose is usually preferable to other substrates, bacteria have mechanisms to ensure that alternative substrates are only used when glucose has been depleted. Additionally, bacteria have mechanisms to ensure that the genes encoding enzymes for using alternative substrates are expressed only when the alternative substrate is available. In the 1940s, Jacques Monod was the first to demonstrate the preference for certain substrates over others through his studies of *E. coli*'s growth when cultured in the presence of two different substrates simultaneously. Such studies generated diauxic growth curves, like the one shown in Figure 4. Although the preferred substrate glucose is used first, *E. coli* grows quickly and the enzymes for lactose metabolism are absent. However, once glucose levels are depleted, growth rates slow, inducing the expression of the enzymes needed for the metabolism of the second substrate, lactose. Notice how the growth rate in lactose is slower, as indicated by the lower steepness of the growth curve.

The ability to switch from glucose use to another substrate like lactose is a consequence of the activity of an enzyme called Enzyme IIA (EIIA). When glucose levels drop, cells produce less ATP from catabolism (see Catabolism of Carbohydrates), and EIIA becomes phosphorylated. Phosphorylated EIIA activates adenylyl cyclase, an enzyme that converts some of the remaining ATP to cyclic AMP (cAMP), a cyclic derivative of AMP and important signaling molecule involved in glucose and energy metabolism in *E. coli*. As a result, cAMP levels begin to rise in the cell (Figure 5).

The *lac* operon also plays a role in this switch from using glucose to using lactose. When glucose is scarce, the accumulating cAMP caused by increased adenylyl cyclase activity binds to catabolite activator protein (CAP), also known as cAMP receptor protein (CRP). The complex binds to the promoter region of the *lac* operon (Figure 6). In the regulatory regions of these operons, a CAP binding site is located upstream of the RNA polymerase binding site in the promoter. Binding of the CAP-cAMP complex to this site increases the binding ability of RNA polymerase to the promoter region to initiate the transcription of the structural genes. Thus, in the case of the *lac* operon, for transcription to occur, lactose must be present (removing the lac repressor protein) and glucose levels must be depleted (allowing binding of an activating protein). When glucose levels are high, there is catabolite repression of operons encoding enzymes for the metabolism of alternative substrates. Because of low cAMP levels under these conditions, there is an insufficient amount of the CAP-cAMP complex to activate transcription of these operons. See Table 1 for a summary of the regulation of the lac operon.

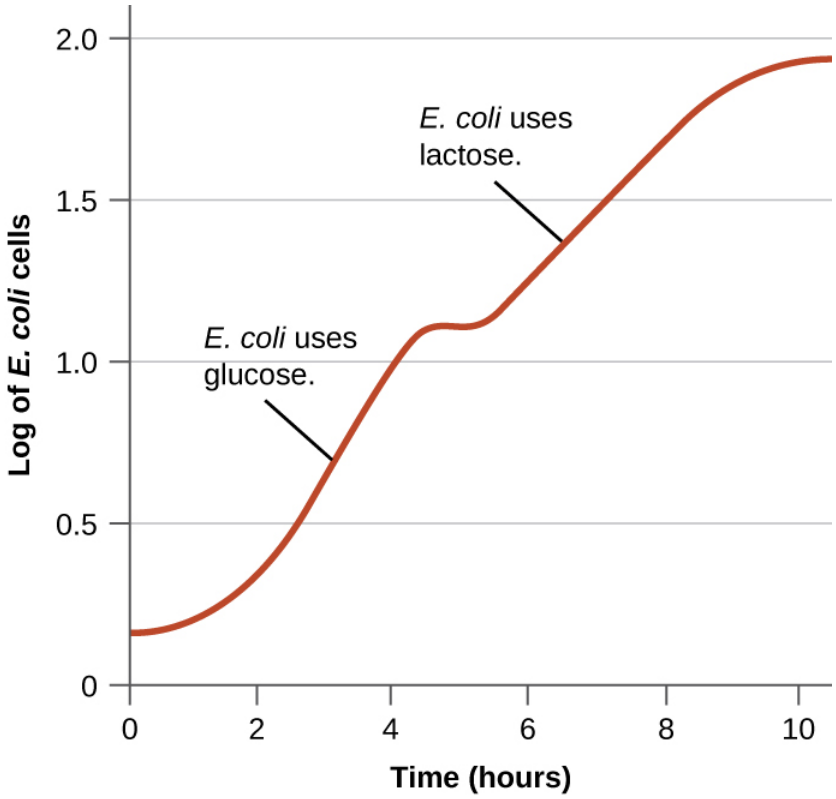


Figure 4: *When grown in the presence of two substrates, E. coli uses the preferred substrate (in this case glucose) until it is depleted. Then, enzymes needed for the metabolism of the second substrate are expressed and growth resumes, although at a slower rate.*

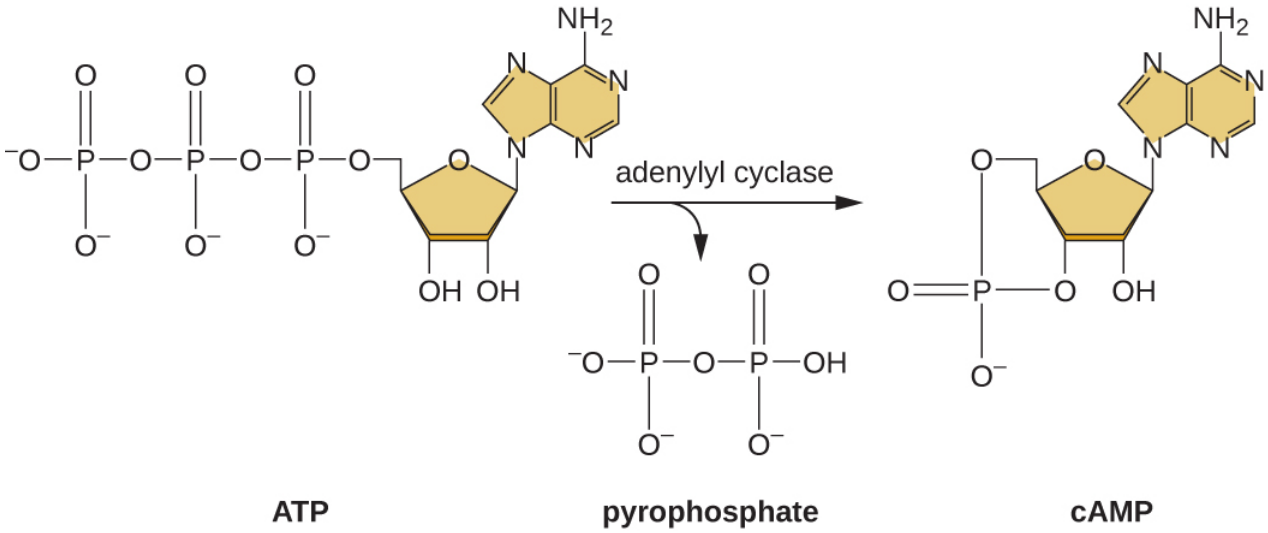


Figure 5: When ATP levels decrease due to depletion of glucose, some remaining ATP is converted to cAMP by adenylyl cyclase. Thus, increased cAMP levels signal glucose depletion.

https://geo.libretexts.org/@go/page/6190

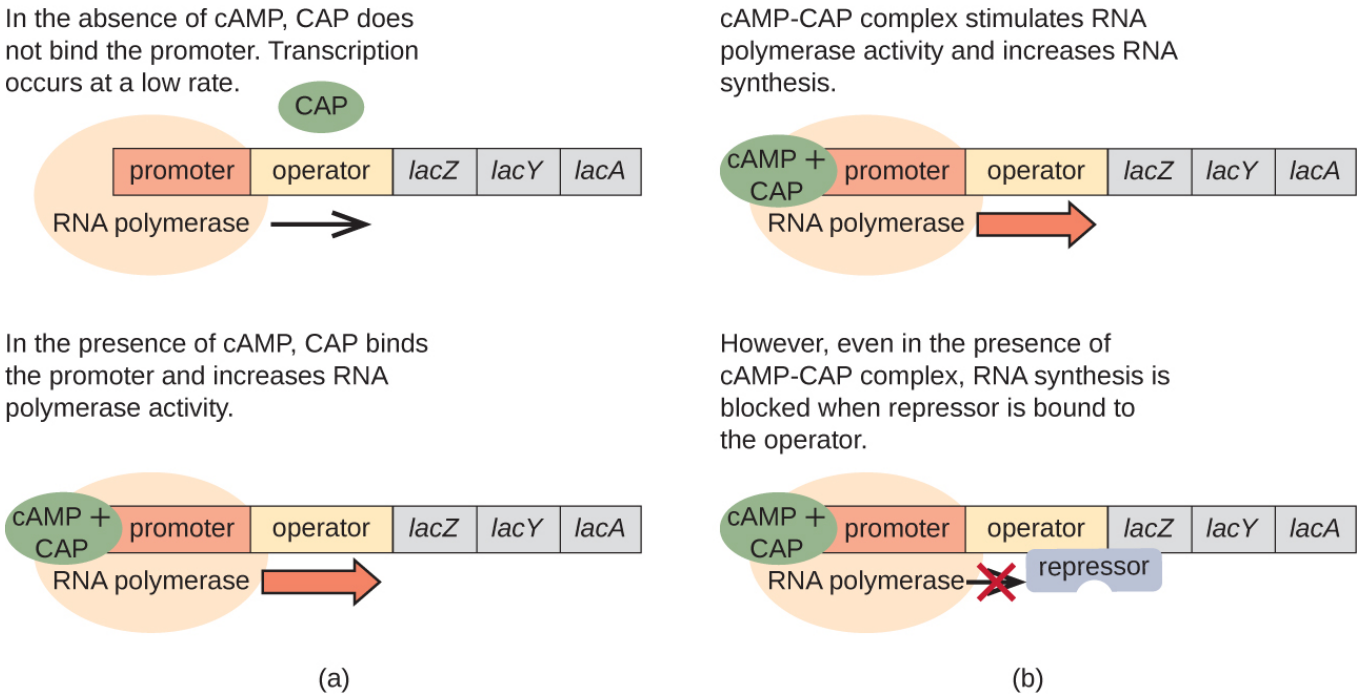


Figure 6: (a) In the presence of cAMP, CAP binds to the promoters of operons, like the lac operon, that encode genes for enzymes for the use of alternate substrates. (b) For the lac operon to be expressed, there must be activation by cAMP-CAP as well as removal of the lac repressor from the operator.

Table* 1*: *Conditions Affecting Transcription of the lac Operon*

Glucose	CAP binds	Lactose	Repressor binds	Transcription
+	–	–	+	No
+	–	+	–	Some
–	+	–	+	No
–	+	+	–	Yes

Watch an animated tutorial about the workings of lac operon here.

Exercise 2

1. What affects the binding of the *trp* operon repressor to the operator?
2. How and when is the behavior of the *lac* repressor protein altered?
3. In addition to being repressible, how else is the *lac* operon regulated?

Global Responses of Prokaryotes

In prokaryotes, there are also several higher levels of gene regulation that have the ability to control the transcription of many related operons simultaneously in response to an environmental signal. A group of operons all controlled simultaneously is called a regulon.

Alarmones

When sensing impending stress, prokaryotes alter the expression of a wide variety of operons to respond in coordination. They do this through the production of alarmones, which are small intracellular nucleotide derivatives. Alarmones change which genes are expressed and stimulate the expression of specific stress-response genes. The use of alarmones to alter gene expression in response to stress appears to be important in pathogenic bacteria. On encountering host defense mechanisms and other harsh conditions during infection, many operons encoding virulence genes are upregulated in response to alarmone signaling. Knowledge of these

https://geo.libretexts.org/@go/page/6190

responses is key to being able to fully understand the infection process of many pathogens and to the development of therapies to counter this process.

Alternate σ Factors

Since the σ subunit of bacterial RNA polymerase confers specificity as to which promoters should be transcribed, altering the σ factor used is another way for bacteria to quickly and globally change what regulons are transcribed at a given time. The σ factor recognizes sequences within a bacterial promoter, so different σ factors will each recognize slightly different promoter sequences. In this way, when the cell senses specific environmental conditions, it may respond by changing which σ factor it expresses, degrading the old one and producing a new one to transcribe the operons encoding genes whose products will be useful under the new environmental condition. For example, in sporulating bacteria of the genera *Bacillus* and *Clostridium* (which include many pathogens), a group of σ factors controls the expression of the many genes needed for sporulation in response to sporulation-stimulating signals.

Exercise 3

1. What is the name given to a collection of operons that can be regulated as a group?
2. What type of stimulus would trigger the transcription of a different σ factor?

Additional Methods of Regulation in Bacteria: Attenuation and Riboswitches

Although most gene expression is regulated at the level of transcription initiation in prokaryotes, there are also mechanisms to control both the completion of transcription as well as translation concurrently. Since their discovery, these mechanisms have been shown to control the completion of transcription and translation of many prokaryotic operons. Because these mechanisms link the regulation of transcription and translation directly, they are specific to prokaryotes, because these processes are physically separated in eukaryotes.

One such regulatory system is attenuation, whereby secondary stem-loop structures formed within the 5’ end of an mRNA being transcribed determine if transcription to complete the synthesis of this mRNA will occur and if this mRNA will be used for translation. Beyond the transcriptional repression mechanism already discussed, attenuation also controls expression of the *trp* operon in *E. coli* (Figure 7). The *trp* operon regulatory region contains a leader sequence called *trpL* between the operator and the first structural gene, which has four stretches of RNA that can base pair with each other in different combinations. When a terminator stem-loop forms, transcription terminates, releasing RNA polymerase from the mRNA. However, when an antiterminator stem-loop forms, this prevents the formation of the terminator stem-loop, so RNA polymerase can transcribe the structural genes.

A related mechanism of concurrent regulation of transcription and translation in prokaryotes is the use of a riboswitch, a small region of noncoding RNA found within the 5’ end of some prokaryotic mRNA molecules (Figure 8). A riboswitch may bind to a small intracellular molecule to stabilize certain secondary structures of the mRNA molecule. The binding of the small molecule determines which stem-loop structure forms, thus influencing the completion of mRNA synthesis and protein synthesis.

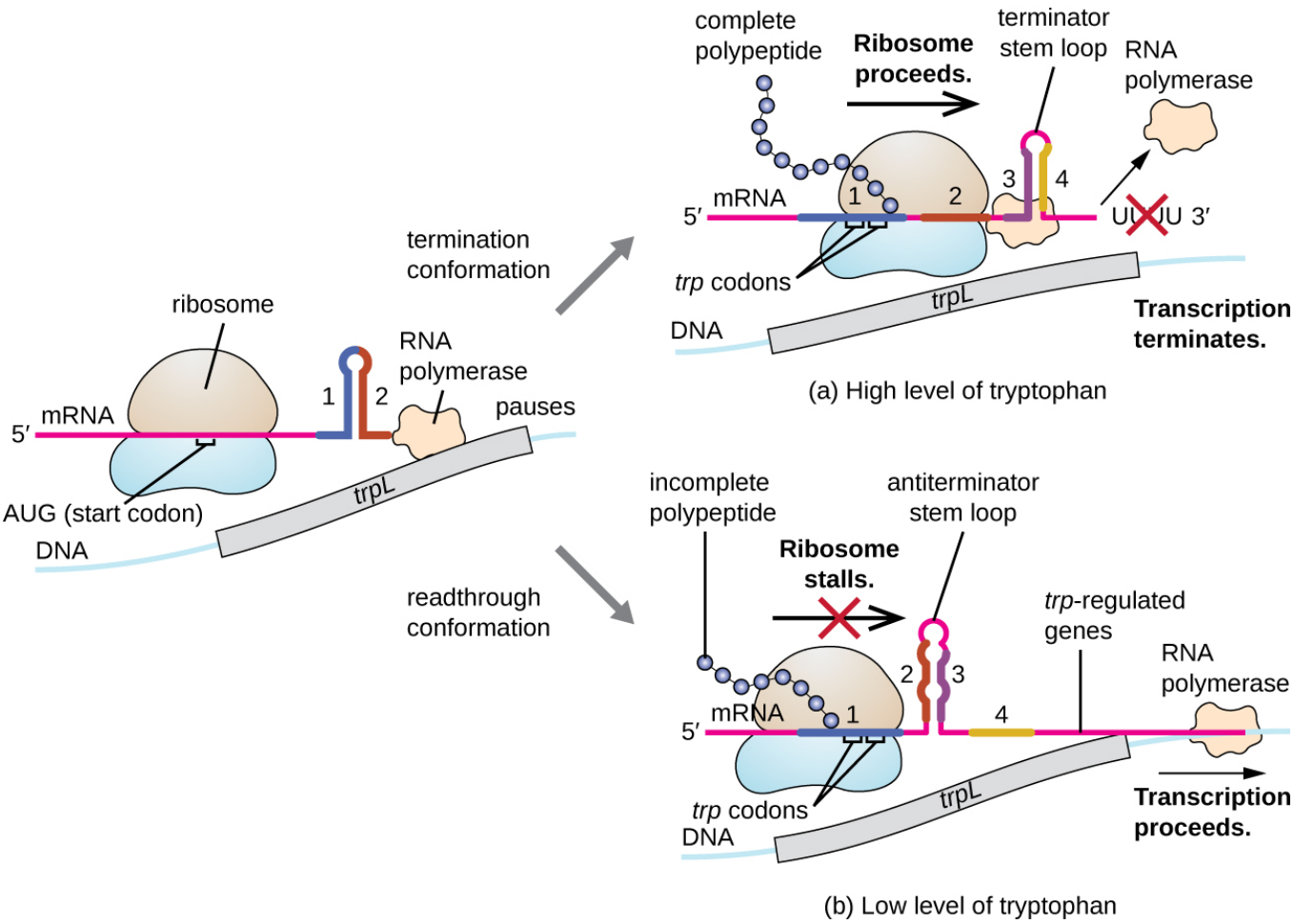


Figure 7: *When tryptophan is plentiful, translation of the short leader peptide encoded by trpL proceeds, the terminator loop between regions 3 and 4 forms, and transcription terminates. When tryptophan levels are depleted, translation of the short leader peptide stalls at region 1, allowing regions 2 and 3 to form an antiterminator loop, and RNA polymerase can transcribe the structural genes of the trp operon.*

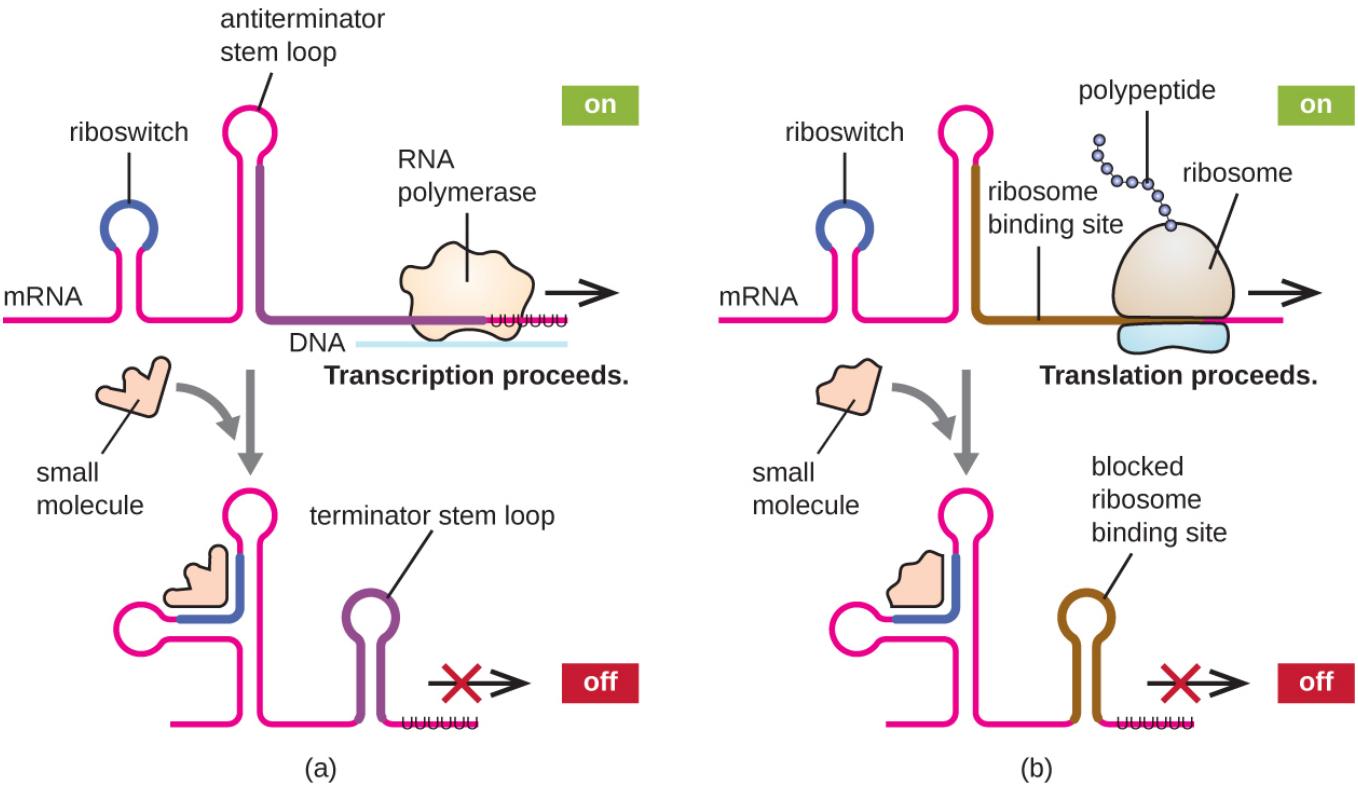


Figure 8: Riboswitches found within prokaryotic mRNA molecules can bind to small intracellular molecules, stabilizing certain RNA structures, influencing either the completion of the synthesis of the mRNA molecule itself (left) or the protein made using that mRNA (right).

Other Factors Affecting Gene Expression in Prokaryotes and Eukaryotes

Although the focus on our discussion of transcriptional control used prokaryotic operons as examples, eukaryotic transcriptional control is similar in many ways. As in prokaryotes, eukaryotic transcription can be controlled through the binding of transcription factors including repressors and activators. Interestingly, eukaryotic transcription can be influenced by the binding of proteins to regions of DNA, called enhancers, rather far away from the gene, through DNA looping facilitated between the enhancer and the promoter (Figure 9). Overall, regulating transcription is a highly effective way to control gene expression in both prokaryotes and eukaryotes. However, the control of gene expression in eukaryotes in response to environmental and cellular stresses can be accomplished in additional ways without the binding of transcription factors to regulatory regions.

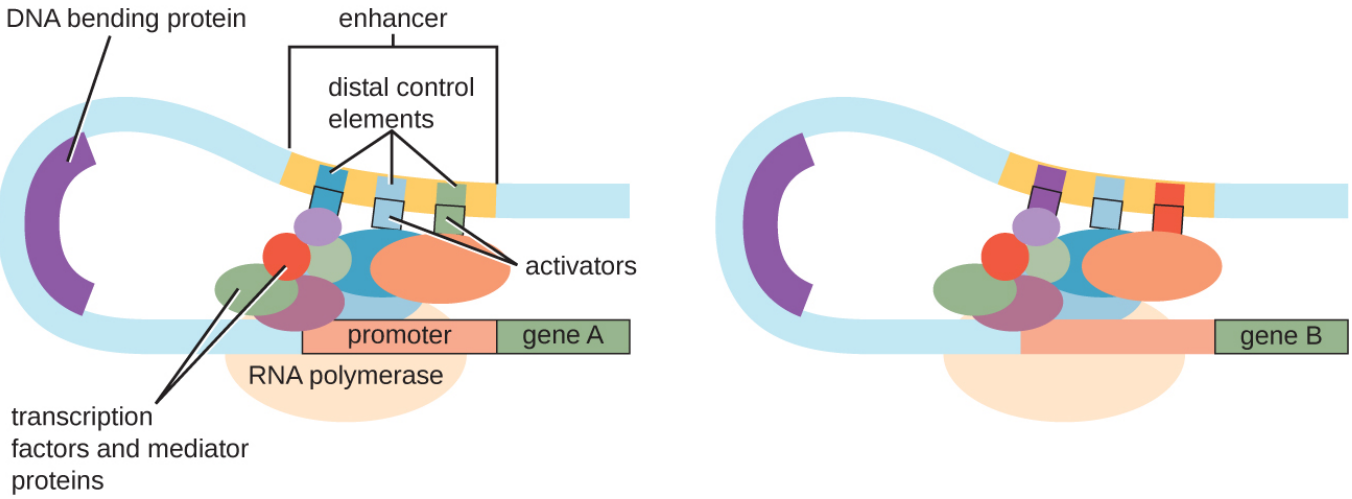


Figure 9: In eukaryotes, an enhancer is a DNA sequence that promotes transcription. Each enhancer is made up of short DNA sequences called distal control elements. Activators bound to the distal control elements interact with mediator proteins and transcription factors. Two different genes may have the same promoter but different distal control elements, enabling differential gene expression.

DNA-Level Control

In eukaryotes, the DNA molecules or associated histones can be chemically modified in such a way as to influence transcription; this is called epigenetic regulation. Methylation of certain cytosine nucleotides in DNA in response to environmental factors has been shown to influence use of such DNA for transcription, with DNA methylation commonly correlating to lowered levels of gene expression. Additionally, in response to environmental factors, histone proteins for packaging DNA can also be chemically modified in multiple ways, including acetylation and deacetylation, influencing the packaging state of DNA and thus affecting the availability of loosely wound DNA for transcription. These chemical modifications can sometimes be maintained through multiple rounds of cell division, making at least some of these epigenetic changes heritable.

This video describes how epigenetic regulation controls gene expression.

Exercise Runaway argument for \eatSpaces?

1. What stops or allows transcription to proceed when attenuation is operating?
2. What determines the state of a riboswitch?
3. Describe the function of an enhancer.
4. Describe two mechanisms of epigenetic regulation in eukaryotes.

Clinical Focus: RESOLUTION

Although Mark survived his bout with necrotizing fasciitis, he would now have to undergo a skin-grafting surgery, followed by long-term physical therapy. Based on the amount of muscle mass he lost, it is unlikely that his leg will return to full strength, but his physical therapist is optimistic that he will regain some use of his leg.

Laboratory testing revealed the causative agent of Mark's infection was a strain of group A streptococcus (Group A strep). As required by law, Mark's case was reported to the state health department and ultimately to the Centers for Disease Control and Prevention (CDC). At the CDC, the strain of group A strep isolated from Mark was analyzed more thoroughly for methicillin resistance.

Methicillin resistance is genetically encoded and is becoming more common in group A strep through horizontal gene transfer. In necrotizing fasciitis, blood flow to the infected area is typically limited because of the action of various genetically encoded bacterial toxins. This is why there is typically little to no bleeding as a result of the incision test. Unfortunately, these bacterial toxins limit the effectiveness of intravenous antibiotics in clearing infection from the skin and underlying tissue, meaning that antibiotic resistance alone does not explain the ineffectiveness of Mark's treatment. Nevertheless, intravenous antibiotic therapy was warranted to help minimize the possible outcome of sepsis, which is a common outcome of necrotizing fasciitis. Through genomic analysis by the CDC of the strain isolated from Mark, several of the important virulence genes were shown to be

encoded on prophages, indicating that transduction is important in the horizontal gene transfer of these genes from one bacterial cell to another.

Key Concepts and Summary

- **Gene expression** is a tightly regulated process.
- Gene expression in prokaryotes is largely regulated at the point of transcription. Gene expression in eukaryotes is additionally regulated post-transcriptionally.
- Prokaryotic structural genes of related function are often organized into **operons**, all controlled by transcription from a single promoter. The regulatory region of an operon includes the promoter itself and the region surrounding the promoter to which transcription factors can bind to influence transcription.
- Although some operons are **constitutively expressed**, most are subject to regulation through the use of **transcription factors** (repressors and activators). A **repressor** binds to an **operator**, a DNA sequence within the regulatory region between the RNA polymerase binding site in the promoter and first structural gene, thereby physically blocking transcription of these operons. An **activator** binds within the regulatory region of an operon, helping RNA polymerase bind to the promoter, thereby enhancing the transcription of this operon. An **inducer**influences transcription through interacting with a repressor or activator.
- The *trp* operon is a classic example of a **repressible operon**. When tryptophan accumulates, tryptophan binds to a repressor, which then binds to the operator, preventing further transcription.
- The *lac* operon is a classic example an **inducible operon**. When lactose is present in the cell, it is converted to allolactose. Allolactose acts as an inducer, binding to the repressor and preventing the repressor from binding to the operator. This allows transcription of the structural genes.
- The *lac* operon is also subject to activation. When glucose levels are depleted, some cellular ATP is converted into cAMP, which binds to the **catabolite activator protein (CAP)**. The cAMP-CAP complex activates transcription of the *lac* operon. When glucose levels are high, its presence prevents transcription of the *lac* operon and other operons by **catabolite repression**.
- Small intracellular molecules called **alarmones** are made in response to various environmental stresses, allowing bacteria to control the transcription of a group of operons, called a regulon.
- Bacteria have the ability to change which ***σ* factor** of RNA polymerase they use in response to environmental conditions to quickly and globally change which regulons are transcribed.
- Prokaryotes have regulatory mechanisms, including **attenuation** and the use of **riboswitches**, to simultaneously control the completion of transcription and translation from that transcript. These mechanisms work through the formation of stem loops in the 5’ end of an mRNA molecule currently being synthesized.
- There are additional points of regulation of gene expression in prokaryotes and eukaryotes. In eukaryotes, **epigenetic regulation** by chemical modification of DNA or histones, and regulation of RNA processing are two methods.

Multiple Choice

An operon of genes encoding enzymes in a biosynthetic pathway is likely to be which of the following?

A. inducible
B. repressible
C. constitutive
D. monocistronic

B

An operon encoding genes that are transcribed and translated continuously to provide the cell with constant intermediate levels of the protein products is said to be which of the following?

A. repressible
B. inducible

C. constitutive
D. activated

C

Which of the following conditions leads to maximal expression of the *lac* operon?

A. lactose present, glucose absent
B. lactose present, glucose present
C. lactose absent, glucose absent
D. lactose absent, glucose present

A

Which of the following is a type of regulation of gene expression unique to eukaryotes?

A. attenuation
B. use of alternate σ factor
C. chemical modification of histones
D. alarmones

C

Fill in the Blank

The DNA sequence, to which repressors may bind, that lies between the promoter and the first structural gene is called the _____.

---

operator

The prevention of expression of operons encoding substrate use pathways for substrates other than glucose when glucose is present is called _____.

---

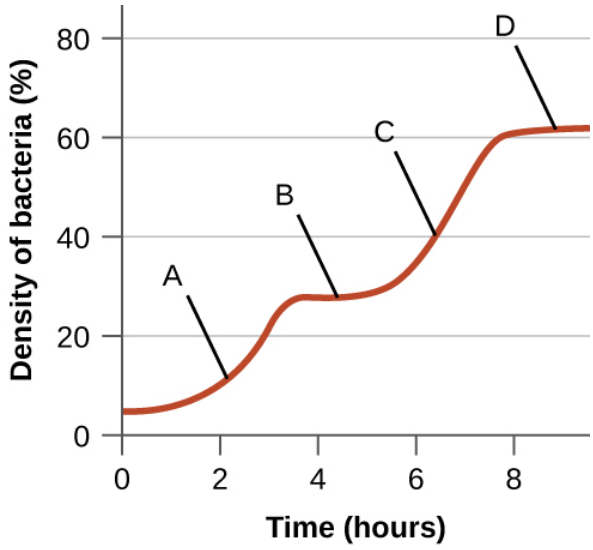
catabolite repression

Short Answer

What are two ways that bacteria can influence the transcription of multiple different operons simultaneously in response to a particular environmental condition?

Critical Thinking

The following figure is from Monod's original work on diauxic growth showing the growth of *E. coli* in the simultaneous presence of xylose and glucose as the only carbon sources. Explain what is happening at points A–D with respect to the carbon source being used for growth, and explain whether the xylose-use operon is being expressed (and why). Note that expression of the enzymes required for xylose use is regulated in a manner similar to the expression of the enzymes required for lactose use.



Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled Operon Theory is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

Protein Synthesis (Translation)

skills to develop

- Describe the genetic code and explain why it is considered almost universal
- Explain the process of translation and the functions of the molecular machinery of translation
- Compare translation in eukaryotes and prokaryotes

The synthesis of proteins consumes more of a cell's energy than any other metabolic process. In turn, proteins account for more mass than any other macromolecule of living organisms. They perform virtually every function of a cell, serving as both functional (e.g., enzymes) and structural elements. The process of translation, or protein synthesis, the second part of gene expression, involves the decoding by a ribosome of an mRNA message into a polypeptide product.

The Genetic Code

Translation of the mRNA template converts nucleotide-based genetic information into the "language" of amino acids to create a protein product. A protein sequence consists of 20 commonly occurring amino acids. Each amino acid is defined within the mRNA by a triplet of nucleotides called a codon. The relationship between an mRNA codon and its corresponding amino acid is called the genetic code.

The three-nucleotide code means that there is a total of 64 possible combinations (4^3, with four different nucleotides possible at each of the three different positions within the codon). This number is greater than the number of amino acids and a given amino acid is encoded by more than one codon (Figure 1). This redundancy in the genetic code is called degeneracy. Typically, whereas the first two positions in a codon are important for determining which amino acid will be incorporated into a growing polypeptide, the third position, called the wobble position, is less critical. In some cases, if the nucleotide in the third position is changed, the same amino acid is still incorporated.

Whereas 61 of the 64 possible triplets code for amino acids, three of the 64 codons do not code for an amino acid; they terminate protein synthesis, releasing the polypeptide from the translation machinery. These are called stop codons or nonsense codons. Another codon, AUG, also has a special function. In addition to specifying the amino acid methionine, it also typically serves as the start codon to initiate translation. The reading frame, the way nucleotides in mRNA are grouped into codons, for translation is set by the AUG start codon near the 5' end of the mRNA. Each set of three nucleotides following this start codon is a codon in the mRNA message.

The genetic code is nearly universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis, which is powerful evidence that all extant life on earth shares a common origin. However, unusual amino acids such as selenocysteine and pyrrolysine have been observed in archaea and bacteria. In the case of selenocysteine, the codon used is UGA (normally a stop codon). However, UGA can encode for selenocysteine using a stem-loop structure (known as the selenocysteine insertion sequence, or SECIS element), which is found at the 3' untranslated region of the mRNA. Pyrrolysine uses a different stop codon, UAG. The incorporation of pyrrolysine requires the *pylS* gene and a unique transfer RNA (tRNA) with a CUA anticodon.

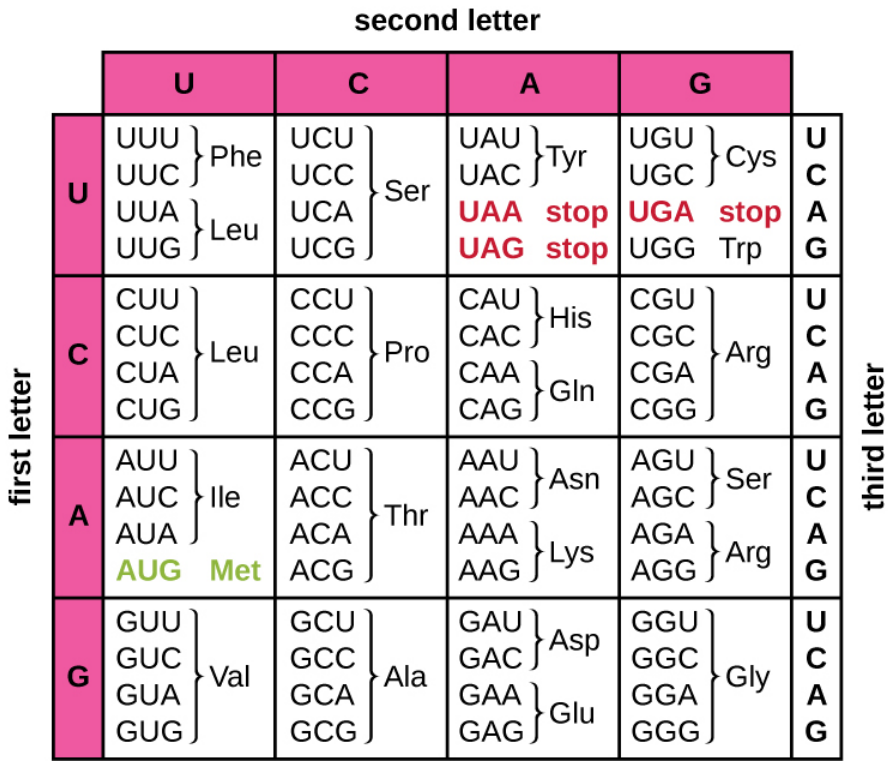


Figure 1: *This figure shows the genetic code for translating each nucleotide triplet in mRNA into an amino acid or a termination signal in a nascent protein. The first letter of a codon is shown vertically on the left, the second letter of a codon is shown horizontally across the top, and the third letter of a codon is shown vertically on the right. (credit: modification of work by National Institutes of Health)*

Exercise 1

1. How many bases are in each codon?
2. What amino acid is coded for by the codon AAU?
3. What happens when a stop codon is reached?

The Protein Synthesis Machinery

In addition to the mRNA template, many molecules and macromolecules contribute to the process of translation. The composition of each component varies across taxa; for instance, ribosomes may consist of different numbers of ribosomal RNAs (rRNAs) and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors.

Ribosomes

A ribosome is a complex macromolecule composed of catalytic rRNAs (called ribozymes) and structural rRNAs, as well as many distinct polypeptides. Mature rRNAs make up approximately 50% of each ribosome. Prokaryotes have 70S ribosomes, whereas eukaryotes have 80S ribosomes in the cytoplasm and rough endoplasmic reticulum, and 70S ribosomes in mitochondria and chloroplasts. Ribosomes dissociate into large and small subunits when they are not synthesizing proteins and reassociate during the initiation of translation. In *E. coli*, the small subunit is described as 30S (which contains the 16S rRNA subunit), and the large subunit is 50S (which contains the 5S and 23S rRNA subunits), for a total of 70S (Svedberg units are not additive). Eukaryote ribosomes have a small 40S subunit (which contains the 18S rRNA subunit) and a large 60S subunit (which contains the 5S, 5.8S and 28S rRNA subunits), for a total of 80S. The small subunit is responsible for binding the mRNA template, whereas the large subunit binds tRNAs (discussed in the next subsection).

Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction: reading the mRNA from 5’ to 3’ and synthesizing the polypeptide from the N terminus to the C terminus. The complete structure containing an mRNA with multiple associated ribosomes is called a polyribosome (or polysome). In both bacteria and archaea, before

transcriptional termination occurs, each protein-encoding transcript is already being used to begin synthesis of numerous copies of the encoded polypeptide(s) because the processes of transcription and translation can occur concurrently, forming polyribosomes (Figure 2). The reason why transcription and translation can occur simultaneously is because both of these processes occur in the same 5' to 3' direction, they both occur in the cytoplasm of the cell, and because the RNA transcript is not processed once it is transcribed. This allows a prokaryotic cell to respond to an environmental signal requiring new proteins very quickly. In contrast, in eukaryotic cells, simultaneous transcription and translation is not possible. Although polyribosomes also form in eukaryotes, they cannot do so until RNA synthesis is complete and the RNA molecule has been modified and transported out of the nucleus.

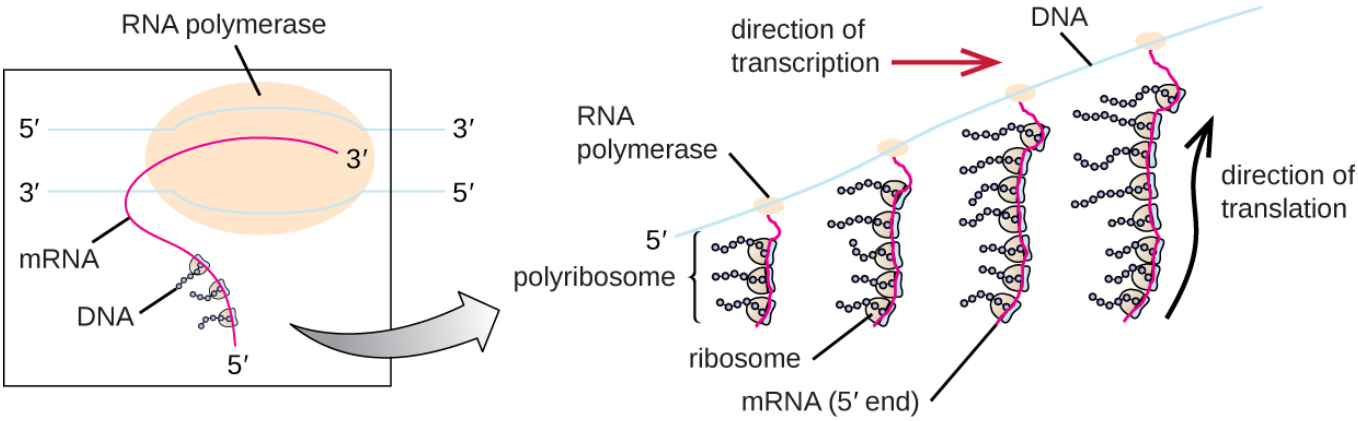


Figure 2: *In prokaryotes, multiple RNA polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. In this way, a specific protein can rapidly reach a high concentration in the bacterial cell.*

Transfer RNAs

Transfer RNAs (tRNAs) are structural RNA molecules and, depending on the species, many different types of tRNAs exist in the cytoplasm. Bacterial species typically have between 60 and 90 types. Serving as adaptors, each tRNA type binds to a specific codon on the mRNA template and adds the corresponding amino acid to the polypeptide chain. Therefore, tRNAs are the molecules that actually "translate" the language of RNA into the language of proteins. As the adaptor molecules of translation, it is surprising that tRNAs can fit so much specificity into such a small package. The tRNA molecule interacts with three factors: aminoacyl tRNA synthetases, ribosomes, and mRNA.

Mature tRNAs take on a three-dimensional structure when complementary bases exposed in the single-stranded RNA molecule hydrogen bond with each other (Figure 3). This shape positions the amino-acid binding site, called the CCA amino acid binding end, which is a cytosine-cytosine-adenine sequence at the 3' end of the tRNA, and the anticodonat the other end. The anticodon is a three-nucleotide sequence that bonds with an mRNA codon through complementary base pairing.

An amino acid is added to the end of a tRNA molecule through the process of tRNA "charging," during which each tRNA molecule is linked to its correct or cognate amino acid by a group of enzymes called aminoacyl tRNA synthetases. At least one type of aminoacyl tRNA synthetase exists for each of the 20 amino acids. During this process, the amino acid is first activated by the addition of adenosine monophosphate (AMP) and then transferred to the tRNA, making it a charged tRNA, and AMP is released.

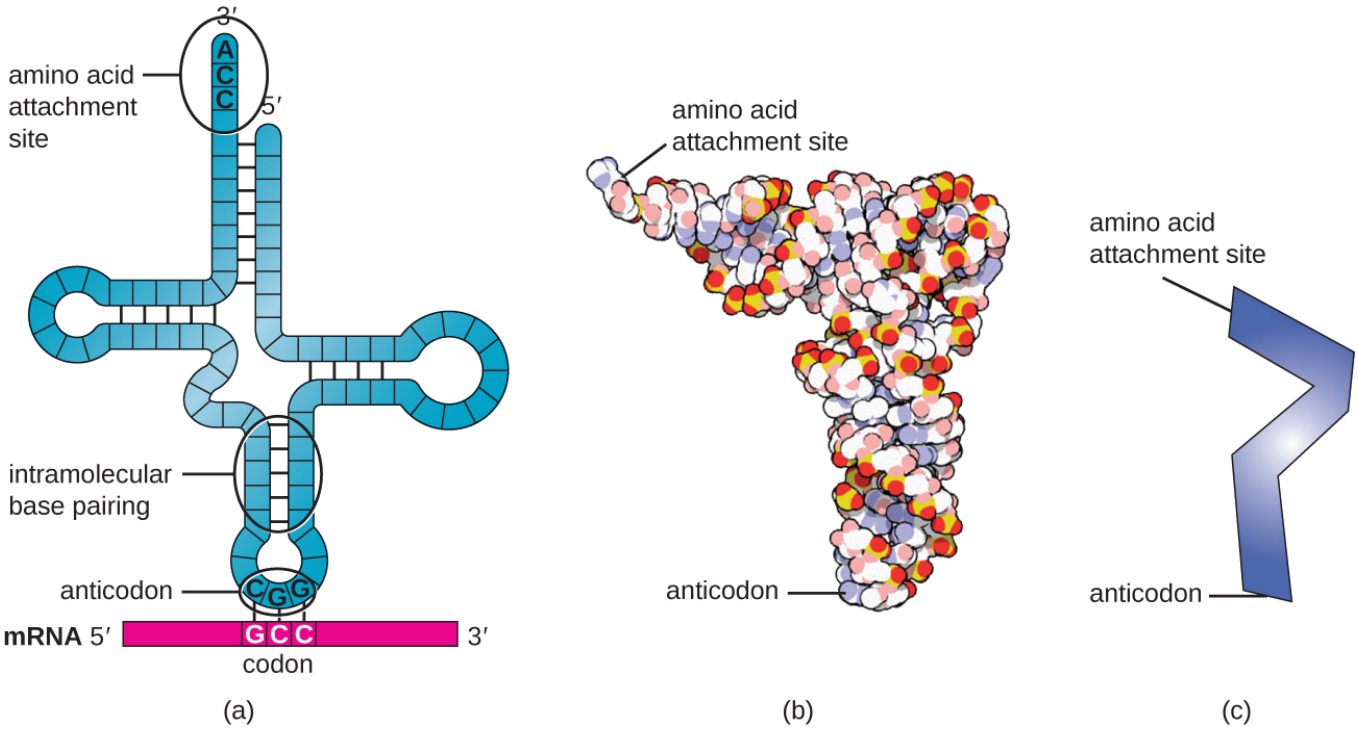


Figure 3: (a) After folding caused by intramolecular base pairing, a tRNA molecule has one end that contains the anticodon, which interacts with the mRNA codon, and the CCA amino acid binding end. (b) A space-filling model is helpful for visualizing the three-dimensional shape of tRNA. (c) Simplified models are useful when drawing complex processes such as protein synthesis.

Exercise 2

1. Describe the structure and composition of the prokaryotic ribosome.
2. In what direction is the mRNA template read?
3. Describe the structure and function of a tRNA.

The Mechanism of Protein Synthesis

Translation is similar in prokaryotes and eukaryotes. Here we will explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between bacterial and eukaryotic translation.

Initiation

The initiation of protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small 30S ribosome, the mRNA template, three initiation factors that help the ribosome assemble correctly, guanosine triphosphate (GTP) that acts as an energy source, and a special initiator tRNA carrying *N*-formyl-methionine(fMet-tRNA^{fMet}) (Figure 4). The initiator tRNA interacts with the start codon AUG of the mRNA and carries a formylated methionine (fMet). Because of its involvement in initiation, fMet is inserted at the beginning (N terminus) of every polypeptide chain synthesized by *E. coli*. In *E. coli* mRNA, a leader sequence upstream of the first AUG codon, called the Shine-Dalgarno sequence (also known as the ribosomal binding site AGGAGG), interacts through complementary base pairing with the rRNA molecules that compose the ribosome. This interaction anchors the 30S ribosomal subunit at the correct location on the mRNA template. At this point, the 50S ribosomal subunit then binds to the initiation complex, forming an intact ribosome.

In eukaryotes, initiation complex formation is similar, with the following differences:

- The initiator tRNA is a different specialized tRNA carrying methionine, called Met-tRNAi
- Instead of binding to the mRNA at the Shine-Dalgarno sequence, the eukaryotic initiation complex recognizes the 5' cap of the eukaryotic mRNA, then tracks along the mRNA in the 5' to 3' direction until the AUG start codon is recognized. At this point, the 60S subunit binds to the complex of Met-tRNAi, mRNA, and the 40S subunit.

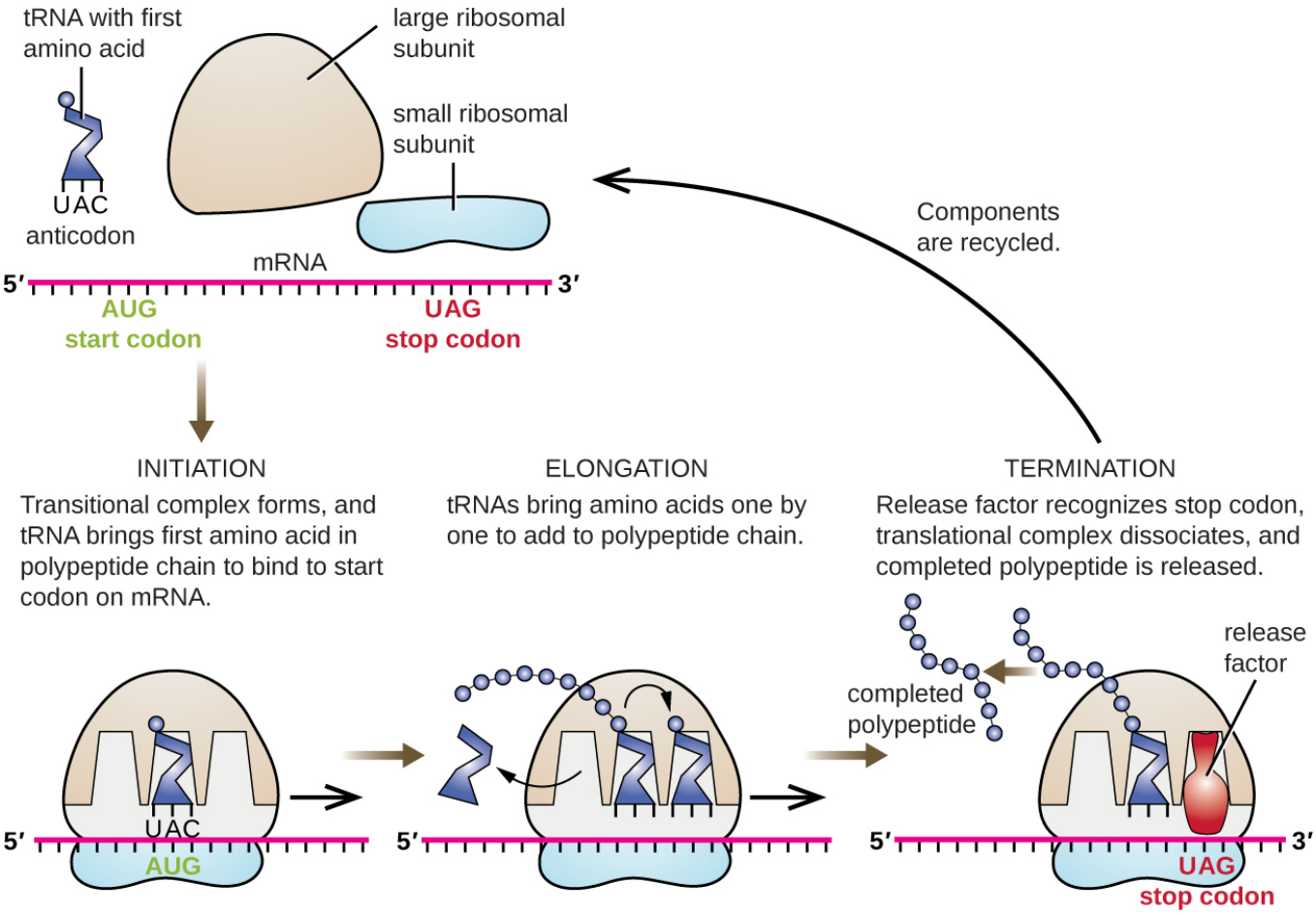


Figure 4: *Translation in bacteria begins with the formation of the initiation complex, which includes the small ribosomal subunit, the mRNA, the initiator tRNA carrying N-formyl-methionine, and initiation factors. Then the 50S subunit binds, forming an intact ribosome.*

Elongation

In prokaryotes and eukaryotes, the basics of elongation of translation are the same. In *E. coli*, the binding of the 50S ribosomal subunit to produce the intact ribosome forms three functionally important ribosomal sites: The A (aminoacyl) site binds incoming charged aminoacyl tRNAs. The P (peptidyl) site binds charged tRNAs carrying amino acids that have formed peptide bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E (exit) site releases dissociated tRNAs so that they can be recharged with free amino acids. There is one notable exception to this assembly line of tRNAs: During initiation complex formation, bacterial fMet−tRNA^{fMet} or eukaryotic Met-tRNAi enters the P site directly without first entering the A site, providing a free A site ready to accept the tRNA corresponding to the first codon after the AUG.

Elongation proceeds with single-codon movements of the ribosome each called a translocation event. During each translocation event, the charged tRNAs enter at the A site, then shift to the P site, and then finally to the E site for removal. Ribosomal movements, or steps, are induced by conformational changes that advance the ribosome by three bases in the 3’ direction. Peptide bonds form between the amino group of the amino acid attached to the A-site tRNA and the carboxyl group of the amino acid attached to the P-site tRNA. The formation of each peptide bond is catalyzed by peptidyl transferase, an RNA-based ribozyme that is integrated into the 50S ribosomal subunit. The amino acid bound to the P-site tRNA is also linked to the growing polypeptide chain. As the ribosome steps across the mRNA, the former P-site tRNA enters the E site, detaches from the amino acid, and is expelled. Several of the steps during elongation, including binding of a charged aminoacyl tRNA to the A site and translocation, require energy derived from GTP hydrolysis, which is catalyzed by specific elongation factors. Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200 amino-acid protein can be translated in just 10 seconds.

https://geo.libretexts.org/@go/page/6187

Termination

The termination of translation occurs when a nonsense codon (UAA, UAG, or UGA) is encountered for which there is no complementary tRNA. On aligning with the A site, these nonsense codons are recognized by release factors in prokaryotes and eukaryotes that result in the P-site amino acid detaching from its tRNA, releasing the newly made polypeptide. The small and large ribosomal subunits dissociate from the mRNA and from each other; they are recruited almost immediately into another translation init iation complex.

In summary, there are several key features that distinguish prokaryotic gene expression from that seen in eukaryotes. These are illustrated in Figure 5 and listed in Figure 6.

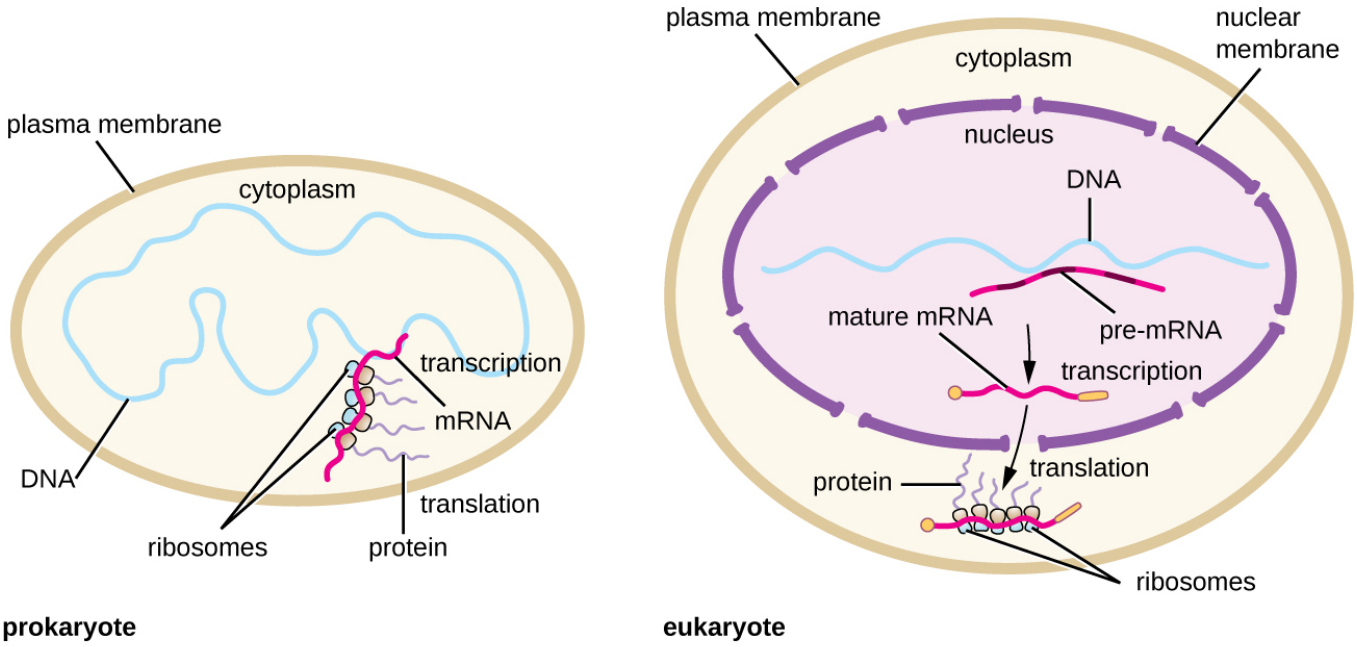


Figure 5: (a) In prokaryotes, the processes of transcription and translation occur simultaneously in the cytoplasm, allowing for a rapid cellular response to an environmental cue. (b) In eukaryotes, transcription is localized to the nucleus and translation is localized to the cytoplasm, separating these processes and necessitating RNA processing for stability.

Comparison of Translation in Bacteria Versus Eukaryotes

Property	Bacteria	Eukaryotes
Ribosomes	70S • 30S (small subunit) with 16S rRNA subunit • 50S (large subunit) with 5S and 23S rRNA subunits	80S • 40S (small subunit) with 18S rRNA subunit • 60S (large subunit) with 5S, 5.8S, and 28S rRNA subunits
Amino acid carried by initiator tRNA	fMet	Met
Shine-Dalgarno sequence in mRNA	Present	Absent
Simultaneous transcription and translation	Yes	No

Figure 6: Comparison of translation in bacteria versus eukaryotes

Protein Targeting, Folding, and Modification

During and after translation, polypeptides may need to be modified before they are biologically active. Post-translational modifications include:

1. removal of translated signal sequences—short tails of amino acids that aid in directing a protein to a specific cellular compartment
2. proper “folding” of the polypeptide and association of multiple polypeptide subunits, often facilitated by chaperone proteins, into a distinct three-dimensional structure
3. proteolytic processing of an inactive polypeptide to release an active protein component, and
4. various chemical modifications (e.g., phosphorylation, methylation, or glycosylation) of individual amino acids.

- What are the components of the initiation complex for translation in prokaryotes?
- What are two differences between initiation of prokaryotic and eukaryotic translation?
- What occurs at each of the three active sites of the ribosome?
- What causes termination of translation?

Key Concepts and Summary

- In **translation**, polypeptides are synthesized using mRNA sequences and cellular machinery, including tRNAs that match mRNA **codons** to specific amino acids and ribosomes composed of RNA and proteins that catalyze the reaction.
- The **genetic code** is **degenerate** in that several mRNA codons code for the same amino acids. The genetic code is almost universal among living organisms.
- Prokaryotic (70S) and cytoplasmic eukaryotic (80S) ribosomes are each composed of a large subunit and a small subunit of differing sizes between the two groups. Each subunit is composed of rRNA and protein. Organelle ribosomes in eukaryotic cells resemble prokaryotic ribosomes.
- Some 60 to 90 species of tRNA exist in bacteria. Each tRNA has a three-nucleotide **anticodon** as well as a binding site for a **cognate amino acid**. All tRNAs with a specific anticodon will carry the same amino acid.
- **Initiation** of translation occurs when the small ribosomal subunit binds with **initiation factors** and an initiator tRNA at the **start codon** of an mRNA, followed by the binding to the initiation complex of the large ribosomal subunit.
- In prokaryotic cells, the start codon codes for N-formyl-methionine carried by a special initiator tRNA. In eukaryotic cells, the start codon codes for methionine carried by a special initiator tRNA. In addition, whereas ribosomal binding of the mRNA in prokaryotes is facilitated by the Shine-Dalgarno sequence within the mRNA, eukaryotic ribosomes bind to the 5’ cap of the mRNA.
- During the **elongation** stage of translation, a **charged tRNA** binds to mRNA in the **A site** of the ribosome; a peptide bond is catalyzed between the two adjacent amino acids, breaking the bond between the first amino acid and its tRNA; the ribosome moves one codon along the mRNA; and the first tRNA is moved from the **P site** of the ribosome to the **E site** and leaves the ribosomal complex.
- **Termination** of translation occurs when the ribosome encounters a **stop codon**, which does not code for a tRNA. Release factors cause the polypeptide to be released, and the ribosomal complex dissociates.
- In prokaryotes, transcription and translation may be coupled, with translation of an mRNA molecule beginning as soon as transcription allows enough mRNA exposure for the binding of a ribosome, prior to transcription termination. Transcription and translation are not coupled in eukaryotes because transcription occurs in the nucleus, whereas translation occurs in the cytoplasm or in association with the rough endoplasmic reticulum.
- Polypeptides often require one or more **post-translational modifications** to become biologically active.

Multiple Choice

Which of the following is the name of the three-base sequence in the mRNA that binds to a tRNA molecule?

A. P site
B. codon
C. anticodon
D. CCA binding site

B

Which component is the last to join the initiation complex during the initiation of translation?

A. the mRNA molecule
B. the small ribosomal subunit
C. the large ribosomal subunit
D. the initiator tRNA

C

During elongation in translation, to which ribosomal site does an incoming charged tRNA molecule bind?

A. A site
B. P site
C. E site
D. B site

A

Which of the following is the amino acid that appears at the N-terminus of all newly translated prokaryotic and eukaryotic polypeptides?

A. tryptophan
B. methionine
C. selenocysteine
D. glycine

B

When the ribosome reaches a nonsense codon, which of the following occurs?

A. a methionine is incorporated
B. the polypeptide is released
C. a peptide bond forms
D. the A site binds to a charged tRNA

B

Fill in the Blank

The third position within a codon, in which changes often result in the incorporation of the same amino acid into the growing polypeptide, is called the _____.

wobble position

The enzyme that adds an amino acid to a tRNA molecule is called _____.

aminoacyl-tRNA synthetase

True/False

Each codon within the genetic code encodes a different amino acid.

False

Short Answer

Why does translation terminate when the ribosome reaches a stop codon? What happens?

How does the process of translation differ between prokaryotes and eukaryotes?

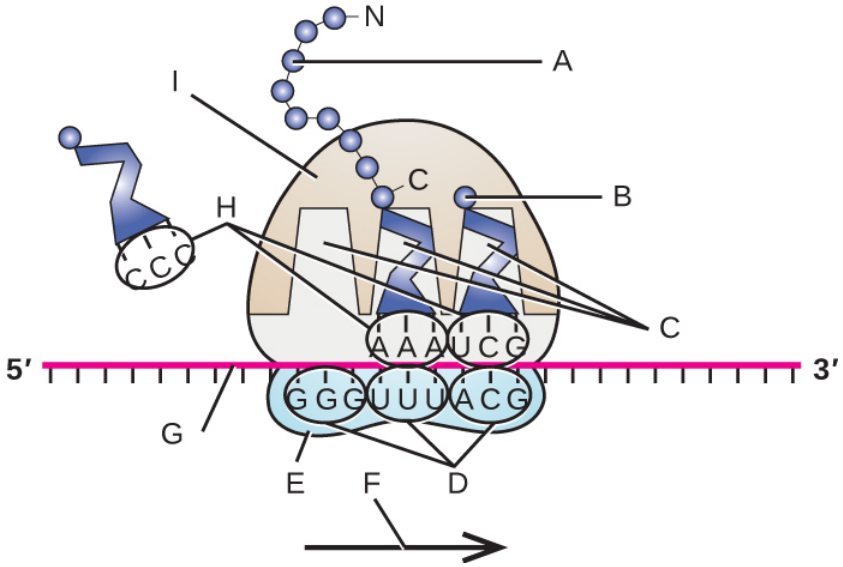
What is meant by the genetic code being nearly universal?

Below is an antisense DNA sequence. Translate the mRNA molecule synthesized using the genetic code, recording the resulting amino acid sequence, indicating the N and C termini.

Antisense DNA strand: 3'-T A C T G A C T G A C G A T C-5'

Critical Thinking

Label the following in the figure: ribosomal E, P, and A sites; mRNA; codons; anticodons; growing polypeptide; incoming amino acid; direction of translocation; small ribosomal unit; large ribosomal unit.



Prior to the elucidation of the genetic code, prominent scientists, including Francis Crick, had predicted that each mRNA codon, coding for one of the 20 amino acids, needed to be at least three nucleotides long. Why is it not possible for codons to be any shorter?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled Protein Synthesis (Translation) is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

RNA Transcription

skills to develop

- Explain how RNA is synthesized using DNA as a template
- Distinguish between transcription in prokaryotes and eukaryotes

During the process of transcription, the information encoded within the DNA sequence of one or more genes is transcribed into a strand of RNA, also called an RNA transcript. The resulting single-stranded RNA molecule, composed of ribonucleotides containing the bases adenine (A), cytosine (C), guanine (G), and uracil (U), acts as a mobile molecular copy of the original DNA sequence. Transcription in prokaryotes and in eukaryotes requires the DNA double helix to partially unwind in the region of RNA synthesis. The unwound region is called a transcription bubble. Transcription of a particular gene always proceeds from one of the two DNA strands that acts as a template, the so-called antisense strand. The RNA product is complementary to the template strand of DNA and is almost identical to the nontemplate DNA strand, or the sense strand. The only difference is that in RNA, all of the T nucleotides are replaced with U nucleotides; during RNA synthesis, U is incorporated when there is an A in the complementary antisense strand.

Transcription in Bacteria

Bacteria use the same RNA polymerase to transcribe all of their genes. Like DNA polymerase, RNA polymerase adds nucleotides one by one to the 3'-OH group of the growing nucleotide chain. One critical difference in activity between DNA polymerase and RNA polymerase is the requirement for a 3'-OH onto which to add nucleotides: DNA polymerase requires such a 3'-OH group, thus necessitating a primer, whereas RNA polymerase does not. During transcription, a ribonucleotide complementary to the DNA template strand is added to the growing RNA strand and a covalent phosphodiester bond is formed by dehydration synthesis between the new nucleotide and the last one added. In *E. coli*, RNA polymerase comprises six polypeptide subunits, five of which compose the polymerase core enzyme responsible for adding RNA nucleotides to a growing strand. The sixth subunit is known as sigma (σ). The σ factor enables RNA polymerase to bind to a specific promoter, thus allowing for the transcription of various genes. There are various σ factors that allow for transcription of various genes.

Initiation

The initiation of transcription begins at a promoter, a DNA sequence onto which the transcription machinery binds and initiates transcription. The nucleotide pair in the DNA double helix that corresponds to the site from which the first 5' RNA nucleotide is transcribed is the initiation site. Nucleotides preceding the initiation site are designated "upstream," whereas nucleotides following the initiation site are called "downstream" nucleotides. In most cases, promoters are located just upstream of the genes they regulate. Although promoter sequences vary among bacterial genomes, a few elements are conserved. At the –10 and –35 positions within the DNA prior to the initiation site (designated +1), there are two promoter consensus sequences, or regions that are similar across all promoters and across various bacterial species. The –10 consensus sequence, called the TATA box, is TATAAT. The –35 sequence is recognized and bound by σ.

Elongation

The elongation in transcription phase begins when the σ subunit dissociates from the polymerase, allowing the core enzyme to synthesize RNA complementary to the DNA template in a 5' to 3' direction at a rate of approximately 40 nucleotides per second. As elongation proceeds, the DNA is continuously unwound ahead of the core enzyme and rewound behind it (Figure 1).

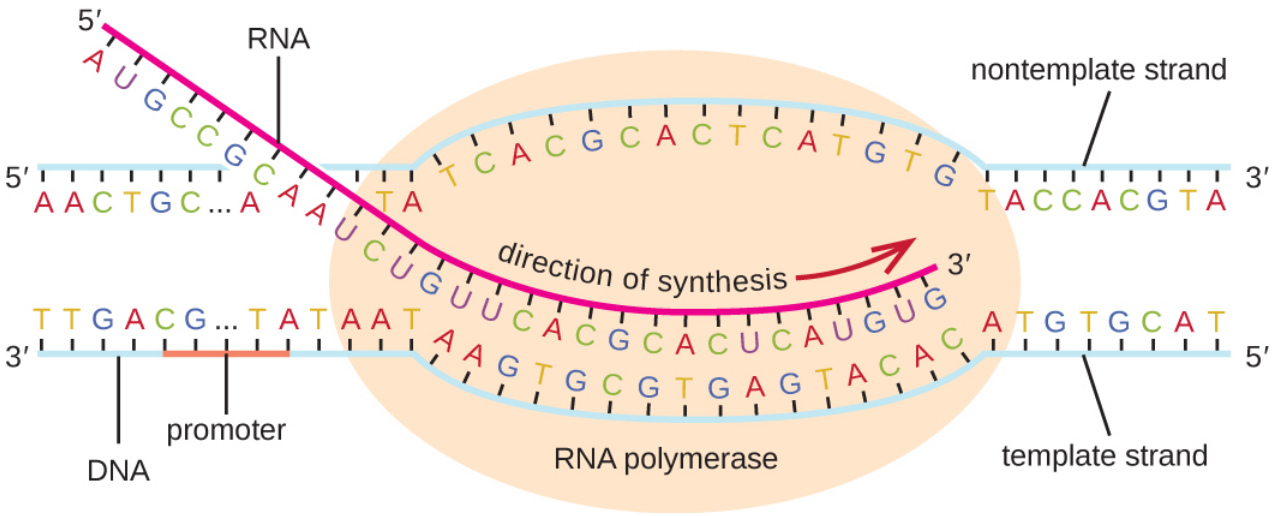


Figure 1: *During elongation, the bacterial RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds and rewinds the DNA as it is read.*

Termination

Once a gene is transcribed, the bacterial polymerase must dissociate from the DNA template and liberate the newly made RNA. This is referred to as termination of transcription. The DNA template includes repeated nucleotide sequences that act as termination signals, causing RNA polymerase to stall and release from the DNA template, freeing the RNA transcript.

Exercise 1

1. Where does σ factor of RNA polymerase bind DNA to start transcription?
2. What occurs to initiate the polymerization activity of RNA polymerase?
3. Where does the signal to end transcription come from?

Transcription in Eukaryotes

Prokaryotes and eukaryotes perform fundamentally the same process of transcription, with a few significant differences (see Table 1). Eukaryotes use three different polymerases, RNA polymerases I, II, and III, all structurally distinct from the bacterial RNA polymerase. Each transcribes a different subset of genes. Interestingly, archaea contain a single RNA polymerase that is more closely related to eukaryotic RNA polymerase II than to its bacterial counterpart. Eukaryotic mRNAs are also usually monocistronic, meaning that they each encode only a single polypeptide, whereas prokaryotic mRNAs of bacteria and archaea are commonly polycistronic, meaning that they encode multiple polypeptides.

The most important difference between prokaryotes and eukaryotes is the latter's membrane-bound nucleus, which influences the ease of use of RNA molecules for protein synthesis. With the genes bound in a nucleus, the eukaryotic cell must transport protein-encoding RNA molecules to the cytoplasm to be translated. Protein-encoding primary transcripts, the RNA molecules directly synthesized by RNA polymerase, must undergo several processing steps to protect these RNA molecules from degradation during the time they are transferred from the nucleus to the cytoplasm and translated into a protein. For example, eukaryotic mRNAs may last for several hours, whereas the typical prokaryotic mRNA lasts no more than 5 seconds.

The primary transcript (also called pre-mRNA) is first coated with RNA-stabilizing proteins to protect it from degradation while it is processed and exported out of the nucleus. The first type of processing begins while the primary transcript is still being synthesized; a special 7-methylguanosine nucleotide, called the 5' cap, is added to the 5' end of the growing transcript. In addition to preventing degradation, factors involved in subsequent protein synthesis recognize the cap, which helps initiate translation by ribosomes. Once elongation is complete, another processing enzyme then adds a string of approximately 200 adenine nucleotides to the 3' end, called the poly-A tail. This modification further protects the pre-mRNA from degradation and signals to cellular factors that the transcript needs to be exported to the cytoplasm.

Eukaryotic genes that encode polypeptides are composed of coding sequences called exons (*ex*-on signifies that they are *ex*pressed) and intervening sequences called introns (*int*-ron denotes their *int*ervening role). Transcribed RNA sequences corresponding to introns do not encode regions of the functional polypeptide and are removed from the pre-mRNA during processing. It is essential that all of the intron-encoded RNA sequences are completely and precisely removed from a pre-mRNA before protein synthesis so that the exon-encoded RNA sequences are properly joined together to code for a functional polypeptide. If the process errs by even a single nucleotide, the sequences of the rejoined exons would be shifted, and the resulting polypeptide would be nonfunctional. The process of removing intron-encoded RNA sequences and reconnecting those encoded by exons is called RNA splicing and is facilitated by the action of a spliceosome containing small nuclear ribonucleo proteins (snRNPs). Intron-encoded RNA sequences are removed from the pre-mRNA while it is still in the nucleus. Although they are not translated, introns appear to have various functions, including gene regulation and mRNA transport. On completion of these modifications, the mature transcript, the mRNA that encodes a polypeptide, is transported out of the nucleus, destined for the cytoplasm for translation. Introns can be spliced out differently, resulting in various exons being included or excluded from the final mRNA product. This process is known as alternative splicing. The advantage of alternative splicing is that different types of mRNA transcripts can be generated, all derived from the same DNA sequence. In recent years, it has been shown that some archaea also have the ability to splice their pre-mRNA.

***Table** 1: Comparison of Transcription in Bacteria Versus Eukaryotes*

Property	Bacteria	Eukaryotes
Number of polypeptides encoded per mRNA	Monocistronic or polycistronic	Exclusively monocistronic
Strand elongation	core + σ = holoenzyme	RNA polymerases I, II, or III
Addition of 5’ cap	No	Yes
Addition of 3’ poly-A tail	No	Yes
Splicing of pre-mRNA	No	Yes

Visualize how mRNA splicing happens by watching the process in action in this video. See how introns are removed during RNA splicing here.

Exercise 2

1. In eukaryotic cells, how is the RNA transcript from a gene for a protein modified after it is transcribed?
2. Do exons or introns contain information for protein sequences?

Clinical Focus: PART 2

In the emergency department, a nurse told Mark that he had made a good decision to come to the hospital because his symptoms indicated an infection that had gotten out of control. Mark’s symptoms had progressed, with the area of skin affected and the amount of swelling increasing. Within the affected area, a rash had begun, blistering and small gas pockets underneath the outermost layer of skin had formed, and some of the skin was becoming gray. Based on the putrid smell of the pus draining from one of the blisters, the rapid progression of the infection, and the visual appearance of the affected skin, the physician immediately began treatment for necrotizing fasciitis. Mark’s physician ordered a culture of the fluid draining from the blister and also ordered blood work, including a white blood cell count.

Mark was admitted to the intensive care unit and began intravenous administration of a broad-spectrum antibiotic to try to minimize further spread of the infection. Despite antibiotic therapy, Mark’s condition deteriorated quickly. Mark became confused and dizzy. Within a few hours of his hospital admission, his blood pressure dropped significantly and his breathing became shallower and more rapid. Additionally, blistering increased, with the blisters intensifying in color to purplish black, and the wound itself seemed to be progressing rapidly up Mark’s leg.

Exercise 3

1. What are possible causative agents of Mark’s necrotizing fasciitis?
2. What are some possible explanations for why the antibiotic treatment does not seem to be working?

Key Concepts and Summary

- During **transcription**, the information encoded in DNA is used to make RNA.
- **RNA polymerase** synthesizes RNA, using the antisense strand of the DNA as template by adding complementary RNA nucleotides to the 3’ end of the growing strand.
- RNA polymerase binds to DNA at a sequence called a **promoter** during the **initiation of transcription**.
- Genes encoding proteins of related functions are frequently transcribed under the control of a single promoter in prokaryotes, resulting in the formation of a **polycistronic mRNA** molecule that encodes multiple polypeptides.
- Unlike DNA polymerase, RNA polymerase does not require a 3’-OH group to add nucleotides, so a **primer** is not needed during initiation.
- **Termination of transcription** in bacteria occurs when the RNA polymerase encounters specific DNA sequences that lead to stalling of the polymerase. This results in release of RNA polymerase from the DNA template strand, freeing the **RNA transcript**.
- Eukaryotes have three different RNA polymerases. Eukaryotes also have monocistronic mRNA, each encoding only a single polypeptide.
- Eukaryotic primary transcripts are processed in several ways, including the addition of a **5’ cap** and a 3′-**poly-A tail**, as well as **splicing**, to generate a mature mRNA molecule that can be transported out of the nucleus and that is protected from degradation.

Multiple Choice

During which stage of bacterial transcription is the σ subunit of the RNA polymerase involved?

A. initiation
B. elongation
C. termination
D. splicing

A

Which of the following components is involved in the initiation of transcription?

A. primer
B. origin
C. promoter
D. start codon

C

Which of the following is not a function of the 5’ cap and 3’ poly-A tail of a mature eukaryotic mRNA molecule?

A. to facilitate splicing
B. to prevent mRNA degradation
C. to aid export of the mature transcript to the cytoplasm
D. to aid ribosome binding to the transcript

A

Mature mRNA from a eukaryote would contain each of these features except which of the following?

A. exon-encoded RNA
B. intron-encoded RNA
C. 5’ cap
D. 3’ poly-A tail

B

Fill in the Blank

A _____ mRNA is one that codes for multiple polypeptides.

polycistronic

The protein complex responsible for removing intron-encoded RNA sequences from primary transcripts in eukaryotes is called the _____.

Spliceosome

Short Answer

What is the purpose of RNA processing in eukaryotes? Why don’t prokaryotes require similar processing?

Below is a DNA sequence. Envision that this is a section of a DNA molecule that has separated in preparation for transcription, so you are only seeing the antisense strand. Construct the mRNA sequence transcribed from this template.

Antisense DNA strand: 3’-T A C T G A C T G A C G A T C-5’

Critical Thinking

Predict the effect of an alteration in the sequence of nucleotides in the –35 region of a bacterial promoter.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled RNA Transcription is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

What Are Genes?

skills to develop

- Explain the two functions of the genome
- Explain the meaning of the central dogma of molecular biology
- Differentiate between genotype and phenotype and explain how environmental factors influence phenotype

Clinical Focus: Part 1

Mark is 60-year-old software engineer who suffers from type II diabetes, which he monitors and keeps under control largely through diet and exercise. One spring morning, while doing some gardening, he scraped his lower leg while walking through blackberry brambles. He continued working all day in the yard and did not bother to clean the wound and treat it with antibiotic ointment until later that evening. For the next 2 days, his leg became increasingly red, swollen, and warm to the touch. It was sore not only on the surface, but deep in the muscle. After 24 hours, Mark developed a fever and stiffness in the affected leg. Feeling increasingly weak, he called a neighbor, who drove him to the emergency department.

Exercise 1

1. Did Mark wait too long to seek medical attention? At what point do his signs and symptoms warrant seeking medical attention?
2. What types of infections or other conditions might be responsible for Mark's symptoms?

DNA serves two essential functions that deal with cellular information. First, DNA is the genetic material responsible for inheritance and is passed from parent to offspring for all life on earth. To preserve the integrity of this genetic information, DNA must be replicated with great accuracy, with minimal errors that introduce changes to the DNA sequence. A genome contains the full complement of DNA within a cell and is organized into smaller, discrete units called genes that are arranged on chromosomes and plasmids. The second function of DNA is to direct and regulate the construction of the proteins necessary to a cell for growth and reproduction in a particular cellular environment.

A gene is composed of DNA that is "read" or transcribed to produce an RNA molecule during the process of transcription. One major type of RNA molecule, called messenger RNA (mRNA), provides the information for the ribosome to catalyze protein synthesis in a process called translation. The processes of transcription and translation are collectively referred to as gene expression. Gene expression is the synthesis of a specific protein with a sequence of amino acids that is encoded in the gene. The flow of genetic information from DNA to RNA to protein is described by the central dogma (Figure 1). This central dogma of molecular biology further elucidates the mechanism behind Beadle and Tatum's "one gene-one enzyme" hypothesis (see Using Microorganisms to Discover the Secrets of Life). Each of the processes of replication, transcription, and translation includes the stages of 1) initiation, 2) elongation (polymerization), and 3) termination. These stages will be described in more detail in this chapter.



Figure 1: The central dogma states that DNA encodes messenger RNA, which, in turn, encodes protein.

A cell's genotype is the full collection of genes it contains, whereas its phenotype is the set of observable characteristics that result from those genes. The phenotype is the product of the array of proteins being produced by the cell at a given time, which is influenced by the cell's genotype as well as interactions with the cell's environment. Genes code for proteins that have functions in the cell. Production of a specific protein encoded by an individual gene often results in a distinct phenotype for the cell compared with the phenotype without that protein. For this reason, it is also common to refer to the genotype of an individual gene and its phenotype. Although a cell's genotype remains constant, not all genes are used to direct the production of their proteins simultaneously. Cells carefully regulate expression of their genes, only using genes to make specific proteins when those proteins are needed (Figure 2).

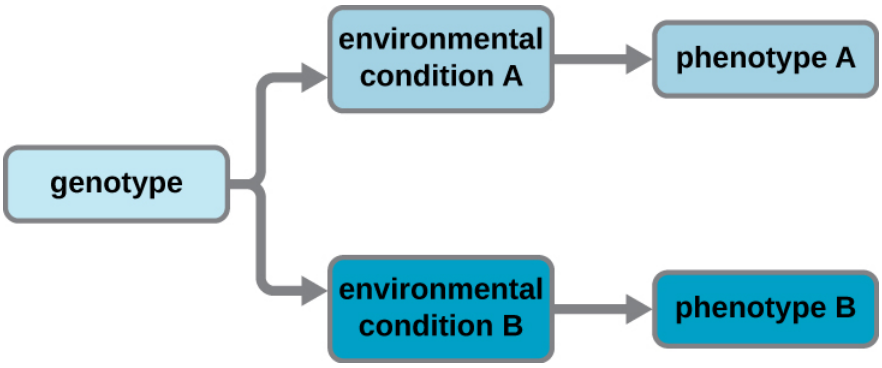


Figure 2: Phenotype is determined by the specific genes within a genotype that are expressed under specific conditions. Although multiple cells may have the same genotype, they may exhibit a wide range of phenotypes resulting from differences in patterns of gene expression in response to different environmental conditions.

Exercise 2

1. What are the two functions of DNA?
2. Distinguish between the genotype and phenotype of a cell.
3. How can cells have the same genotype but differ in their phenotype?

USE AND ABUSE OF GENOME DATA

Why can some humans harbor opportunistic pathogens like *Haemophilus influenzae*, *Staphylococcus aureus*, or *Streptococcus pyogenes*, in their upper respiratory tracts but remain asymptomatic carriers, while other individuals become seriously ill when infected? There is evidence suggesting that differences in susceptibility to infection between patients may be a result, at least in part, of genetic differences between human hosts. For example, genetic differences in human leukocyte antigens (HLAs) and red blood cell antigens among hosts have been implicated in different immune responses and resulting disease progression from infection with *H. influenzae*.

Because the genetic interplay between pathogen and host may contribute to disease outcomes, understanding differences in genetic makeup between individuals may be an important clinical tool. Ecological genomics is a relatively new field that seeks to understand how the genotypes of different organisms interact with each other in nature. The field answers questions about how gene expression of one organism affects gene expression of another. Medical applications of ecological genomics will focus on how pathogens interact with specific individuals, as opposed to humans in general. Such analyses would allow medical professionals to use knowledge of an individual's genotype to apply more individualized plans for treatment and prevention of disease.

With the advent of next-generation sequencing, it is relatively easy to obtain the entire genomic sequences of pathogens; a bacterial genome can be sequenced in as little as a day.[1] The speed and cost of sequencing the human genome has also been greatly reduced and, already, individuals can submit samples to receive extensive reports on their personal genetic traits, including ancestry and carrier status for various genetic diseases. As sequencing technologies progress further, such services will continue to become less expensive, more extensive, and quicker.

However, as this day quickly approaches, there are many ethical concerns with which society must grapple. For example, should genome sequencing be a standard practice for everybody? Should it be required by law or by employers if it will lower health-care costs? If one refuses genome sequencing,

does he or she forfeit his or her right to health insurance coverage? For what purposes should the data be used? Who should oversee proper use of these data? If genome sequencing reveals predisposition to a particular disease, do insurance companies have the right to increase rates? Will employers treat an employee differently? Knowing that environmental influences also affect disease development, how should the data on the presence of a particular disease-causing allele in an individual be used ethically? The Genetic Information Nondiscrimination Act of 2008 (GINA) currently prohibits discriminatory practices based on genetic information by both health insurance companies and employers. However, GINA does not cover life, disability, or long-term care insurance policies. Clearly, all members of society must continue to engage in conversations about these issues so that such genomic data can be used to improve health care while simultaneously protecting an individual's rights.

Key Concepts and Summary

- DNA serves two important cellular functions: It is the genetic material passed from parent to offspring and it serves as the information to direct and regulate the construction of the proteins necessary for the cell to perform all of its functions.
- The **central dogma** states that DNA organized into genes specifies the sequences of messenger RNA (mRNA), which, in turn, specifies the amino acid sequence of proteins.
- The genotype of a cell is the full collection of genes a cell contains. Not all genes are used to make proteins simultaneously. The phenotype is a cell's observable characteristics resulting from the proteins it is producing at a given time under specific environmental conditions.

Multiple Choice

DNA does all but which of the following?

A. serves as the genetic material passed from parent to offspring
B. remains constant despite changes in environmental conditions
C. provides the instructions for the synthesis of messenger RNA
D. is read by ribosomes during the process of translation

D

According to the central dogma, which of the following represents the flow of genetic information in cells?

A. protein to DNA to RNA
B. DNA to RNA to protein
C. RNA to DNA to protein
D. DNA to protein to RNA

B

True/False

Cells are always producing proteins from every gene they possess.

False

Fill in the Blank

The process of making an RNA copy of a gene is called _____.

transcription

A cell's _____ remains constant whereas its phenotype changes in response to environmental influences.

genotype or genome

Short Answer

Can two observably different cells have the same genotype? Explain.

Critical Thinking

A pure culture of an unknown bacterium was streaked onto plates of a variety of media. You notice that the colony morphology is strikingly different on plates of minimal media with glucose compared to that seen on trypticase soy agar plates. How can you explain these differences in colony morphology?

Footnotes

1. 1 D.J. Edwards, K.E. Holt. "Beginner's Guide to Comparative Bacterial Genome Analysis Using Next-Generation Sequence Data." *Microbial Informatics and Experimentation* 3 no. 1 (2013):2.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled What Are Genes? is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

CHAPTER OVERVIEW

4: Tracing the History of Evolution

The evolutionary history of life on Earth is preserved in the genetics of living organisms, body fossils preserved in the rock record, and chemical proxies also preserved in the rock record. This history is often represented by evolutionary trees using techniques developed in the field of phylogenetics.

4.1: Phylogenetic Trees

4.2: Limitations of Phylogenetic Trees

4.3: The Levels of Classification

4: Tracing the History of Evolution is shared under a not declared license and was authored, remixed, and/or curated by LibreTexts.

4.1: Phylogenetic Trees

LEARNING OBJECTIVES

- Understand how life can be organized
- Describe how phylogenetic trees show how we organize life

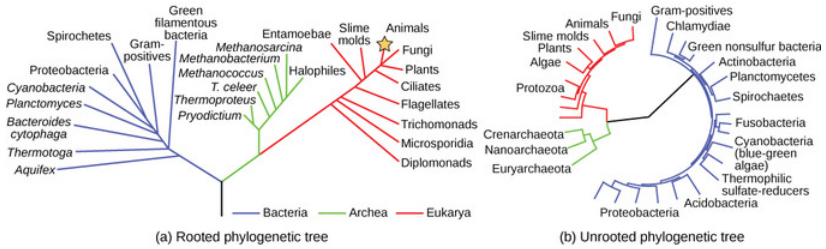
Categorizing Life

We interpret all life on Earth as related based on its shared characteristics. For example, all life uses DNA to store genetic information, that DNA is translated into RNA, and RNA is transcribed into proteins that do the biochemistry of cells. Various lineages of life share similar characteristics within a lineage, but they differ from other lineages. For example, the composition of bacterial cell walls are similar to each other but differ from those of animals in important ways. Similarly, the symmetry in the bodies of different types of animals vary in systematic ways; echinoderms have 5-fold symmetry whereas bilaterians have 2-fold symmetry. Most of these similarities and differences in characteristics reflect historical evolutionary processes, and we use those that do to classify subsets of life and to reconstruct the evolutionary history of life. One of the ways we perform, evaluate, and interpret the classifications is by making phylogenetic trees.

Phylogenetic trees are diagrams that show relationships among organisms. Scientists consider phylogenetic trees as hypotheses of the evolutionary past built from the observable characteristics of the organisms in the tree. In other words, a “tree of life”, as it is sometimes called, can be constructed to illustrate the relationships among different organisms. These organisms can be modern or fossil with the trees based on data from genomes, function, or morphology. The trees illustrate hypotheses about when different organisms diverged from their ancient common ancestors and how they evolved.

The hypothesized relationships are graphically represented by lines that connect the organisms at the tips of the lines to their ancestors deeper in the tree. The lines branch where one lineage of life evolved (or split) into two lineages. These branch points and their order in the tree record the hypothesized relationships among the organisms. The length of each line represents the relative evolutionary difference of the organism at the tip to the most recent common ancestor with other lineages at the branch point; long lines represent significant amounts of evolutionary difference, whereas short lines represent closer evolutionary relationships among the organisms. Sometimes the lines are calibrated to time, with the location of each branch point corresponding to the hypothesized time the younger lineages diverged.

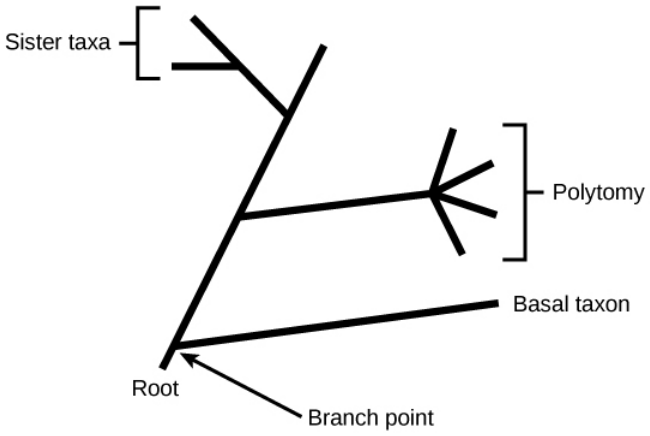
If a phylogenetic tree has a line at the base (usually drawn at the bottom or left; see phylogenetic tree (a) in the figure below), the tree is "rooted". Rooted trees can be read like a map of evolutionary history, starting from a single lineage at the base of the tree, which represents a common ancestor to all of the life shown in the tree, and up through the branches to the tips, which represent living organisms or the most recent fossil representative of the lineage. The rooted phylogenetic tree (a) shown below includes the three domains of life (Bacteria, Archaea, and Eukarya), with the "last common ancestor" of all life diverging into two Bacteria and Archaea lineages first. At some later point in time, the last common ancestor to Archaea and Eukarya diverged into two lineages, leading to modern Archaea and Eukarya. The Eukarya lineage eventually diverged into many more lineages, including plants and animals (including humans). The short lines between plants and animals show that they are more closely related to each other than any of the bacteria are to animals, for example. Similarly, the location of the branch point between plants and animals near the outside of the tree shows that they shared a common ancestor in much more recent times than the last common ancestor between animals and any of the Archaea, for example. Unrooted trees (see phylogenetic tree (b) in the figure below) do not show a last common ancestor to all the life in the tree. The branch geometry shows evolutionary relationships among the organisms, but the central point does not always indicate a common ancestor. Unrooted trees show hypothesized relationships among organisms, but not necessarily their evolutionary history.



***Phylogenetic trees**: Both of these phylogenetic trees shows the relationship of the three domains of life (Bacteria, Archaea, and Eukarya), but the (a) rooted tree attempts to identify when various species diverged from a common ancestor, while the (b) unrooted tree does not.*

Drawing Trees and Terminology

In a phylogenetic tree, each branch point represents a single lineage evolving into two distinct ones. A lineage that evolved early from the root of a tree and remains unbranched is called basal taxon. When two lineages stem from the same branch point, they are called sister taxa. A branch with more than two lineages is called a polytomy and serves to illustrate where scientists have not definitively determined all of the evolutionary relationships.



***Rooted phylogenetic trees**: The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where lineages diverged from each other. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.*

It is important to note that the lines making up the tree represent ancestral organisms, not the organisms that are present at the tips of the lines. Sister taxa and polytomy share an ancestor, but the groups of organisms did not split or evolve from each other.; rather they split and evolved from a common ancestor. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other; both have evolved, as represented by the length of the lines extending from the branch point to the tips.

Phylogenetic trees can be drawn in multiple ways, but the order of branches is always the same for all trees based on the same data. Phylogenetic trees can look very different, but still illustrate the same relationships. For example, sister taxa can be rotated around their branch point, but they are still sister taxa. The location of the Animals and Fungi can be exchanged in the rooted tree above (a rotation around their branch point). When branch points are rotated, the taxon order changes but the information in the tree is the same because the sequence of branch points is the same. If you trace the evolutionary path from a common ancestor to an organism at a branch tip, the path does not change even if the branches are rotated. In other words, the evolution of each taxon from a branch point is independent of the other organisms in the tree. Similarly, branches can be drawn at angles to each other or with horizontal/vertical/circumfential bars connecting them (compare trees (a) and (b) above). These geometrical options in drawing phylogenetic trees allow scientists to visualize complicated data to help with interpretations. Scientists often choose options that emphasize the aspects of the evolutionary relationships that they are most interested in illustrating.

Interpreting Rooted Trees

Rooted phylogenetic trees can serve as a pathway to understanding evolutionary history. A pathway can be traced from an ancestor, or even the origin of life, to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the “trunk” of the tree, one can discover that species’ ancestors, as well as where various lineages share a common ancestry. In addition, the tree can be used to study the evolutionary relationships within or between entire groups of organisms.

Many disciplines within biology contribute to understanding how past and present life evolved over time; together, these disciplines contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called systematics. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of organisms. Since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

Key Points

- Rooted trees have a single lineage at the base representing a common ancestor that connects all organisms presented in a phylogenetic diagram.
- Branch points in a phylogenetic tree represent a split where a single lineage evolved into a distinct new one, while basal taxon depict unbranched lineages that diverged early from the root.
- Unrooted trees portray relationships among species, but do not depict their common ancestor.
- Phylogenetic trees are hypotheses and are, therefore, modified as more and better data becomes available.
- Systematics uses data from fossils, the study of bodily structures, molecules used by a species, and DNA analysis to contribute to the building, updating, and maintaining of phylogenetic trees.

Key Terms

- **polytomy**: a section of a phylogeny in which the evolutionary relationships cannot be fully resolved to dichotomies (splits into only two lineages)
- **basal taxon**: a lineage, displayed using a phylogenetic tree, that diverged early from the root and from which no other branches have diverged
- **systematics**: research into the relationships of organisms; the science of systematic classification
- **phylogeny**: the visual representation of the evolutionary history of organisms; based on rigorous analyses

Questions to ponder

- What aspects of organisms provide useful data for their classification?
- Look up a phylogenetic tree in a scientific publication. Are you comfortable interpreting it? What questions do you have about it?

This page titled 4.1: Phylogenetic Trees is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Dawn Sumner.

4.2: Limitations of Phylogenetic Trees

Learning Objectives

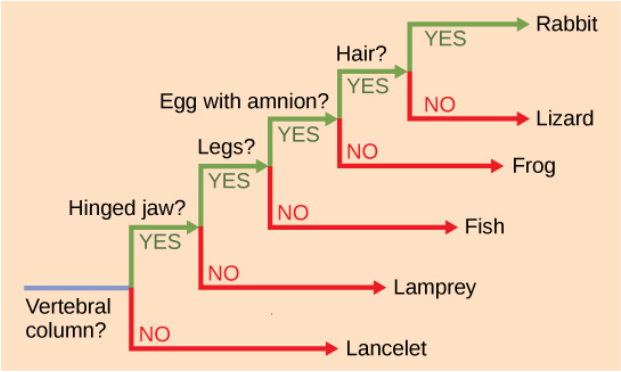
- Identify the limitations of phylogenetic trees as representations of the organization of life
- Construct a simple phylogenetic tree

Limitations of Phylogenetic Trees

Phylogenetic trees represent hypotheses about the evolution of life. They are only as good as the data on which they are based. The data come from our studies of modern organisms and fossils. We do no know everything about modern organisms, and the fossil record includes very few of the organisms that actually lived. Thus, the data that scientists use to make phylogenetic trees will always be incomplete. We will never know enough about the ancestors to all modern organisms to reconstruct the tree of life perfectly. Thus, it is important to understand the strengths and limitations of the data used to make phylogenetic trees.

Morphological Data

Many phylogenetic trees are built using the morphology of organisms or fossils. Closely-related organisms often look alike; they share morphological traits. For example, humans, bonobos, and chimpanzees share more features with each other than they do with mice. While closely related organisms often look similar, it is not always true that lineages that share features are the most closely related. If two closely-related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.



Limitations of phylogenetic trees: This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

Distantly related organisms can also share morphological features. For example, many Bacteria are spherical in shape, as are many Archaea. All bacteria are more distantly related to all Archaea than lizards are to rabbits even though lizards and rabbits look much more different from each other. Thus, morphology is not particularly useful for determining evolutionary relationships among some groups of organisms. In fact, genetic data have shown that very closely related Cyanobacteria (a specific lineage of bacteria that perform oxygenic photosynthesis) can have very different cell shapes, and Cyanobacteria with similar shapes may be only distantly related to each other. Thus, understanding how morphology does or does not relate to evolutionary history is critically important when using morphological data as the basis for phylogenetic trees.

Genetic Data

Many phylogenetic trees are built using genetic data. Genes are the units of organisms that encode the results of evolution, making them particularly useful for building phylogenetic trees. However, different genes evolve in different ways, genes can be swapped among organisms, and genes can be lost by organisms. Thus, the choice of genes to use for a phylogenetic tree needs to reflect the

scientific questions being asked. As an example, genes that encode for antibiotic resistance in bacteria can be shared among bacteria, even between relatively distantly related species. When a scientist makes a phylogenetic tree based on a gene that provides antibiotic resistance, the tree will reflect how that gene evolved, not necessarily how the organisms hosting the gene evolved. As another example, some genes are almost never shared among organisms, such as the genes encoding the machinery to convert DNA into RNA. These genes are critical for the organism to live, and they evolve very slowly. One of these genes, 16S rRNA, is commonly used to build phylogenetic trees showing the evolutionary relationships within Bacteria. These trees are often very reliable in terms of the branching order, but it turns out that there are large numbers of organisms that do not show up in the 16S rRNA data obtained using standard lab techniques. Other techniques have led to the identification of a huge diversity of bacteria (see Hug et al., 2016). As new techniques become available and more data are collected, the complexity of genes as a reflection of evolution is becoming more apparent. And all of the complexities provide information scientists can use to understand the processes and history of evolution.

Branch Length and Time

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time over which evolution occurred. Rather, they reflect the evolutionary difference and the order of divergence among lineages. In other words, a long branch does not typically mean more time passed; nor does a short branch mean less time passed, unless the data are specifically correlated to time with an evolutionary model. A phylogenetic tree may not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. For example, the tree in the diagram above shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember, any phylogenetic tree is an evolutionary hypothesis that represents part of the greater whole. The individual branches do not necessarily evolve at the same rate or in the same way. So, simply because a vertebral column evolved does not mean that invertebrate evolution ceased. It only means that two lineages diverged. Also, groups that are not closely related, but evolve under similar conditions, may appear more similar to each other than to a close relative.

Key Points

- Closely-related species may not always look more alike, while groups that are not closely related yet evolved under similar conditions, may appear more similar to each other.
- In phylogenetic trees, branches do not usually account for length of time. They depict evolutionary order and evolutionary difference.
- Phylogenetic trees do not simply grow in only one direction after two lineages diverge; the evolution of one organism does not necessarily signify the evolutionary end of another.

Questions to ponder

- Choose some organisms that you are familiar with and try to construct a phylogenetic tree showing the relationships among them.
    - What features did you use to construct the tree?
    - What are some of the challenges you had to face?
    - What are some of the uncertainties in how accurately your tree reflects the evolutionary relationships among the organisms?

References

Hug, L.A., Baker, B.J., Anantharaman, K., Brown, C.T., Probst, A.J., Castelle, C.J., Butterfield, C.N., Hernsdorf, A.W., Amano, Y., Ise, K., et al. A new view of the tree of life, Nature Microbiology, 2016, 1:16048. (link)

This page titled 4.2: Limitations of Phylogenetic Trees is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Dawn Sumner.

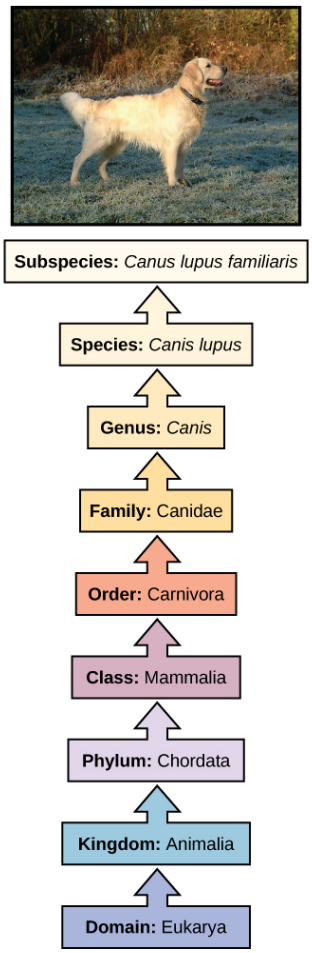
4.3: The Levels of Classification

Learning Objectives

- Describe how taxonomic classification of organisms is accomplished and detail the levels of taxonomic classification from domain to species

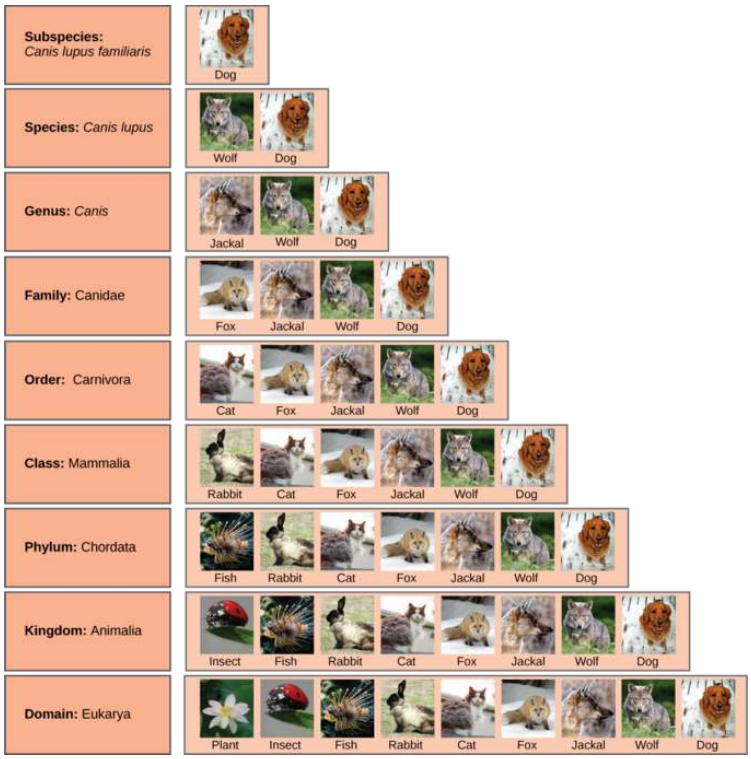
The Levels of Classification

Taxonomy (which literally means “arrangement law”) is the science of classifying organisms to construct internationally-shared classification systems with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then, finally, a single product. This organization from larger to smaller, more-specific categories is called a hierarchical system.



Hierarchical models: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, Canis lupus familiaris, is a subspecies of Canis lupus, which also includes the wolf and dingo.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called domains: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a kingdom. After kingdoms, the subsequent categories of increasing specificity are: phylum, class, order, family, genus, and species.



Levels in taxonomic classification: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies.

The kingdom Animalia stems from the Eukarya domain. The full name of an organism technically has eight terms. For dogs, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species and that genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called binomial nomenclature. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a taxon. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use; in this case, dog. Note that the dog is additionally a subspecies: the "familiaris" in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

Dogs actually share a domain (Eukarya) with the widest morphological diversity of organisms, including plants and butterflies. At each sublevel, the organism are more closely related, so they appear more similar. Historically, scientists classified organisms using physical characteristics, but as DNA technology developed, more precise phylogenies have been determined based on genetic similarity.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. Recall that phylogenetic trees are hypotheses and are modified as more data become available.

Key Points

- Categories within taxonomic classification are arranged in increasing specificity.
- The most general category in taxonomic classification is domain, which is the point of origin for all species; all species belong to one of these domains: Bacteria, Archaea, and Eukarya.
- Within each of the three domains, we find kingdoms, the second category within taxonomic classification, followed by subsequent categories that include phylum, class, order, family, genus, and species.
- At each classification category, organisms become more similar because they are more closely related.

- As scientific technology advances, changes to the taxonomic classification of many species must be altered as inaccuracies in classifications are discovered and corrected.

Key Terms

- **binomial nomenclature**: the scientific system of naming each species of organism with a Latinized name in two parts
- **taxon**: any of the taxonomic categories such as phylum or subspecies
- **Linnaeus**: Swedish botanist, physician and zoologist who laid the foundations for the modern scheme of nomenclature; known as the “father of modern taxonomy”

Source information:

LICENSES AND ATTRIBUTIONS

CC LICENSED CONTENT, SHARED PREVIOUSLY

- Curation and Revision. **Provided by**: Boundless.com. **License**: ***CC BY-SA: Attribution-ShareAlike***

CC LICENSED CONTENT, SPECIFIC ATTRIBUTION

- OpenStax College, Biology. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...ol11448/latest. **License**: ***CC BY: Attribution***
- phylogeny. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/phylogeny. **License**: ***CC BY-SA: Attribution-ShareAlike***
- Boundless. **Provided by**: Boundless Learning. **Located at**: http://www.boundless.com//biology/de...on/basal-taxon. **License**: ***CC BY-SA: Attribution-ShareAlike***
- polytomy. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/polytomy. **License**: ***CC BY-SA: Attribution-ShareAlike***
- systematics. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/systematics. **License**: ***CC BY-SA: Attribution-ShareAlike***
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_01.jpg. **License**: ***CC BY: Attribution***
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_02.jpg. **License**: ***CC BY: Attribution***
- OpenStax College, Biology. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...ol11448/latest. **License**: ***CC BY: Attribution***
- phenotypical. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/phenotypical. **License**: ***CC BY-SA: Attribution-ShareAlike***
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_01.jpg. **License**: *CC BY: Attribution*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_02.jpg. **License**: *CC BY: Attribution*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_03.jpg. **License**: *CC BY: Attribution*
- OpenStax College, Biology. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...ol11448/latest. **License**: *CC BY: Attribution*
- Linnaeus. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/Linnaeus. **License**: *CC BY-SA: Attribution-ShareAlike*
- taxon. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/taxon. **License**: *CC BY-SA: Attribution-ShareAlike*
- binomial nomenclature. **Provided by**: Wiktionary. **Located at**: http://en.wiktionary.org/wiki/binomial_nomenclature. **License**: *CC BY-SA: Attribution-ShareAlike*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_01.jpg. **License**: *CC BY: Attribution*

- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_02.jpg. **License**: *CC BY: Attribution*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_03.jpg. **License**: *CC BY: Attribution*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...e_20_01_05.png. **License**: *CC BY: Attribution*
- OpenStax College, Organizing Life on Earth. October 16, 2013. **Provided by**: OpenStax CNX. **Located at**: http://cnx.org/content/m44588/latest...20_01_04ab.jpg. **License**: *CC BY: Attribution*

This page titled 4.3: The Levels of Classification is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by Boundless (now LumenLearning).

CHAPTER OVERVIEW

5: Structure of life

3.1: Unique Characteristics of Prokaryotic Cells

3.2: Unique Characteristics of Eukaryotic Cells

3.3: Viruses

3.3A: Viruses

3.3B: The Viral Life Cycle

5: Structure of life is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

3.1: Unique Characteristics of Prokaryotic Cells

SKILLS TO DEVELOP

- Explain the distinguishing characteristics of prokaryotic cells
- Describe common cell morphologies and cellular arrangements typical of prokaryotic cells and explain how cells maintain their morphology
- Describe internal and external structures of prokaryotic cells in terms of their physical structure, chemical structure, and function
- Compare the distinguishing characteristics of bacterial and archaeal cells

Cell theory states that the cell is the fundamental unit of life. However, cells vary significantly in size, shape, structure, and function. At the simplest level of construction, all cells possess a few fundamental components. These include cytoplasm (a gel-like substance composed of water and dissolved chemicals needed for growth), which is contained within a plasma membrane (also called a cell membrane or cytoplasmic membrane); one or more chromosomes, which contain the genetic blueprints of the cell; and ribosomes, organelles used for the production of proteins.

Beyond these basic components, cells can vary greatly between organisms, and even within the same multicellular organism. The two largest categories of cells—prokaryotic cells and eukaryotic cells—are defined by major differences in several cell structures. Prokaryotic cells lack a nucleus surrounded by a complex nuclear membrane and generally have a single, circular chromosome located in a nucleoid. Eukaryotic cells have a nucleus surrounded by a complex nuclear membrane that contains multiple, rod-shaped chromosomes.[1]

All plant cells and animal cells are eukaryotic. Some microorganisms are composed of prokaryotic cells, whereas others are composed of eukaryotic cells. Prokaryotic microorganisms are classified within the domains Archaea and Bacteria, whereas eukaryotic organisms are classified within the domain Eukarya.

The structures inside a cell are analogous to the organs inside a human body, with unique structures suited to specific functions. Some of the structures found in prokaryotic cells are similar to those found in some eukaryotic cells; others are unique to prokaryotes. Although there are some exceptions, eukaryotic cells tend to be larger than prokaryotic cells. The comparatively larger size of eukaryotic cells dictates the need to compartmentalize various chemical processes within different areas of the cell, using complex membrane-bound organelles. In contrast, prokaryotic cells generally lack membrane-bound organelles; however, they often contain inclusions that compartmentalize their cytoplasm. Figure 3.1.1 illustrates structures typically associated with prokaryotic cells. These structures are described in more detail in the next section.

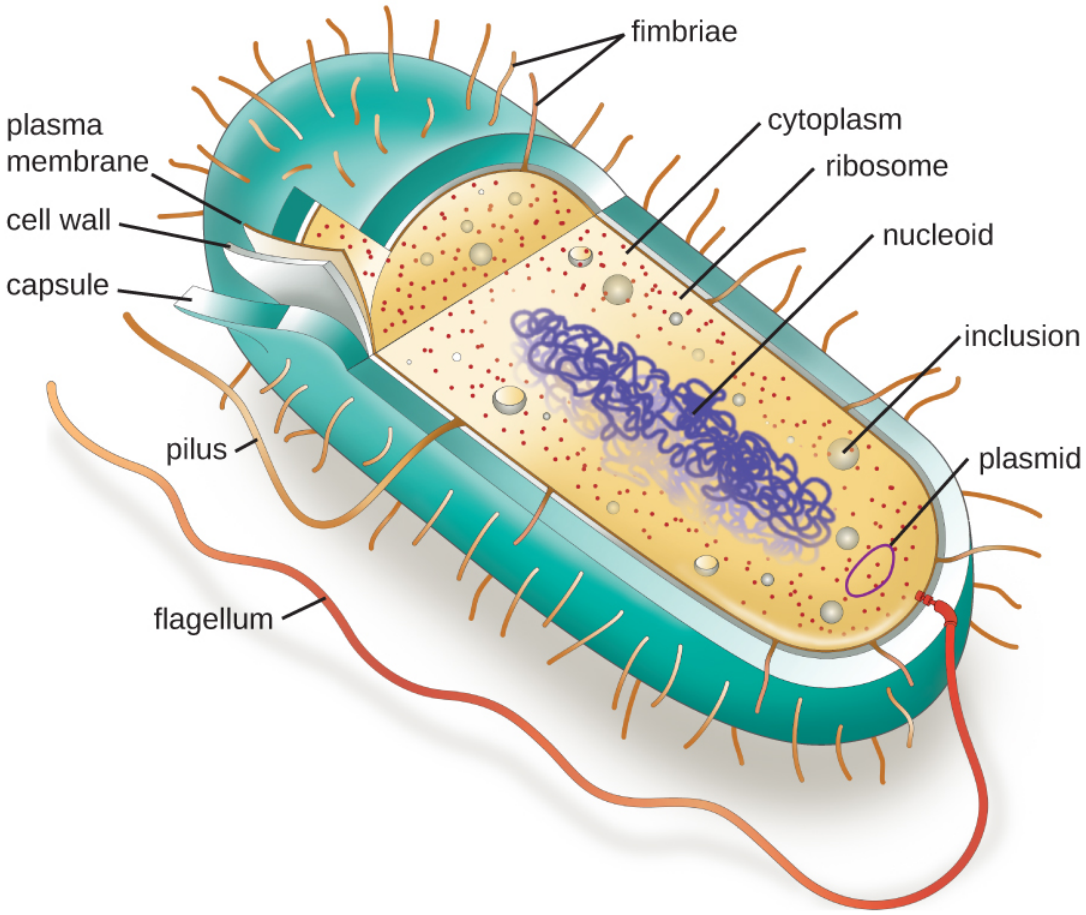
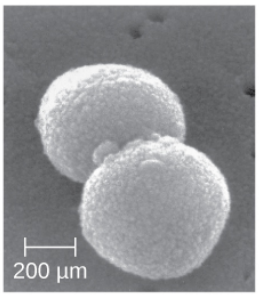
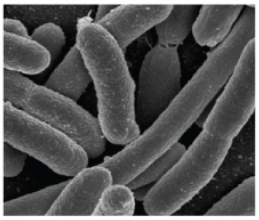
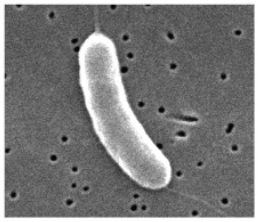
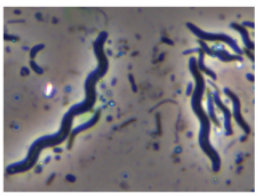
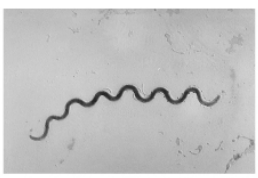


Figure 3.1.1: A typical prokaryotic cell contains a cell membrane, chromosomal DNA that is concentrated in a nucleoid, ribosomes, and a cell wall. Some prokaryotic cells may also possess flagella, pili, fimbriae, and capsules.

Common Cell Morphologies and Arrangements

Individual cells of a particular prokaryotic organism are typically similar in shape, or **cell** morphology. Although thousands of prokaryotic organisms have been identified, only a handful of cell morphologies are commonly seen microscopically. Figure 3.1.2 names and illustrates cell morphologies commonly found in prokaryotic cells. In addition to cellular shape, prokaryotic cells of the same species may group together in certain distinctive arrangements depending on the plane of cell division. Some common arrangements are shown in Figure 3.1.3.

https://geo.libretexts.org/@go/page/6192

Common Prokaryotic Cell Shapes			
Name	**Description**	**Illustration**	**Image**
Coccus (pl. cocci)	Round		
Bacillus (pl. bacilli)	Rod		
Vibrio (pl. vibrios)	Curved rod		
Coccobacillus (pl. coccobacilli)	Short rod		
Spirillum (pl. spirilla)	Spiral		
Spirochete (pl. spirochetes)	Long, loose, helical spiral		

https://geo.libretexts.org/@go/page/6192

Figure 3.1.2***:*** *(credit "Coccus" micrograph: modification of work by Janice Haney Carr, Centers for Disease Control and Prevention; credit "Coccobacillus" micrograph: modification of work by Janice Carr, Centers for Disease Control and Prevention; credit "Spirochete" micrograph: modification of work by Centers for Disease Control and Prevention)*

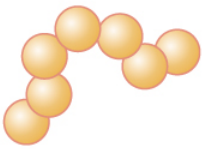
Common Prokaryotic Cell Arrangements		
Name	**Description**	**Illustration**
Coccus (pl. cocci)	Single coccus	
Diplococcus (pl. diplococci)	Pair of two cocci	
Tetrad (pl. tetrads)	Grouping of four cells arranged in a square	
Streptococcus (pl. streptococci)	Chain of cocci	
Staphylococcus (pl. staphylococci)	Cluster of cocci	
Bacillus (pl. bacilli)	Single rod	
Streptobacillus (pl. streptobacilli)	Chain of rods	

Figure 3.1.3: Common cell arrangements.

In most prokaryotic cells, morphology is maintained by the cell wall in combination with cytoskeletal elements. The cell wall is a structure found in most prokaryotes and some eukaryotes; it envelopes the cell membrane, protecting the cell from changes in osmotic pressure (Figure 3.1.4). Osmotic pressure occurs because of differences in the concentration of solutes on opposing sides of a semipermeable membrane. Water is able to pass through a semipermeable membrane, but solutes (dissolved molecules like salts, sugars, and other compounds) cannot. When the concentration of solutes is greater on one side of the membrane, water diffuses across the membrane from the side with the lower concentration (more water) to the side with the higher concentration (less water) until the concentrations on both sides become equal. This diffusion of water is called osmosis, and it can cause extreme osmotic pressure on a cell when its external environment changes.

The external environment of a cell can be described as an isotonic, hypertonic, or hypotonic medium. In an isotonic medium, the solute concentrations inside and outside the cell are approximately equal, so there is no net movement of water across the cell membrane. In a hypertonic medium, the solute concentration outside the cell exceeds that inside the cell, so water diffuses out of the cell and into the external medium. In a hypotonic medium, the solute concentration inside the cell exceeds that outside of the cell, so water will move by osmosis into the cell. This causes the cell to swell and potentially lyse, or burst.

The degree to which a particular cell is able to withstand changes in osmotic pressure is called tonicity. Cells that have a cell wall are better able to withstand subtle changes in osmotic pressure and maintain their shape. In hypertonic environments, cells that lack

a cell wall can become dehydrated, causing crenation, or shriveling of the cell; the plasma membrane contracts and appears scalloped or notched (Figure 3.1.4). By contrast, cells that possess a cell wall undergo plasmolysis rather than crenation. In plasmolysis, the plasma membrane contracts and detaches from the cell wall, and there is a decrease in interior volume, but the cell wall remains intact, thus allowing the cell to maintain some shape and integrity for a period of time (Figure 3.1.5). Likewise, cells that lack a cell wall are more prone to lysis in hypotonic environments. The presence of a cell wall allows the cell to maintain its shape and integrity for a longer time before lysing (Figure 3.1.5).

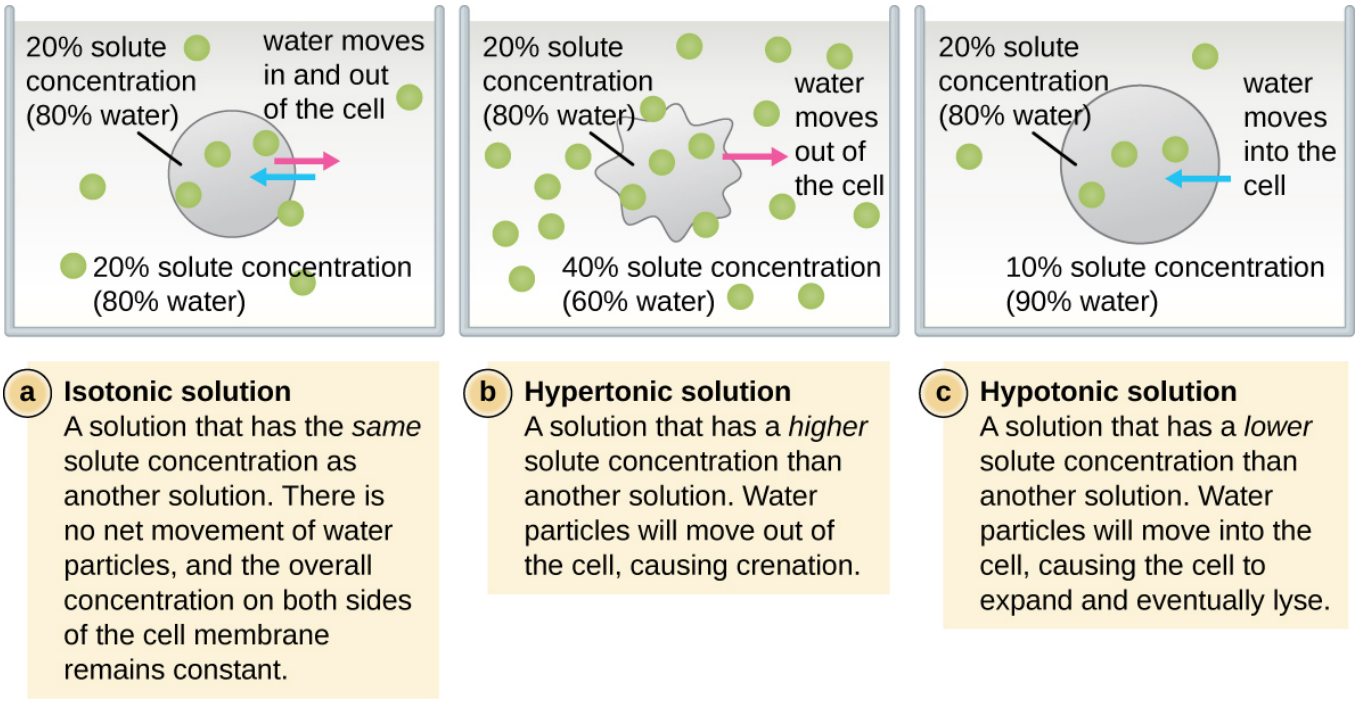


Figure 3.1.4: In cells that lack a cell wall, changes in osmotic pressure can lead to crenation in hypertonic environments or cell lysis in hypotonic environments.

https://geo.libretexts.org/@go/page/6192

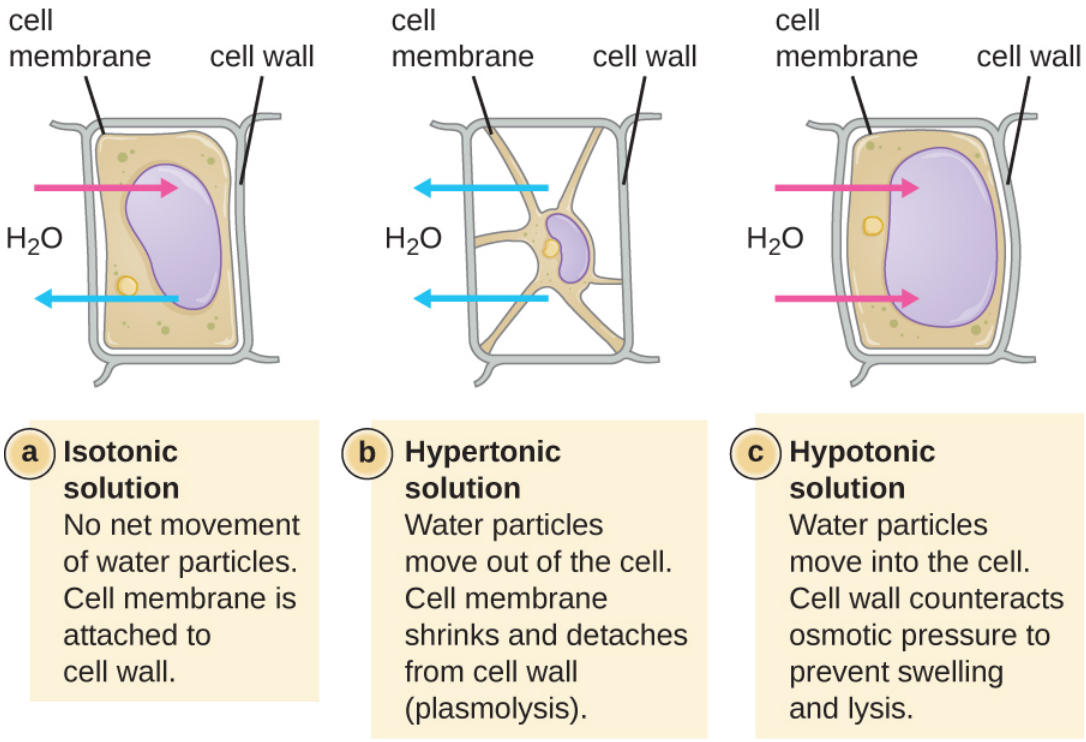


Figure 3.1.5: In prokaryotic cells, the cell wall provides some protection against changes in osmotic pressure, allowing it to maintain its shape longer. The cell membrane is typically attached to the cell wall in an isotonic medium (left). In a hypertonic medium, the cell membrane detaches from the cell wall and contracts (plasmolysis) as water leaves the cell. In a hypotonic medium (right), the cell wall prevents the cell membrane from expanding to the point of bursting, although lysis will eventually occur if too much water is absorbed.

Exercise 3.1.1

1. Explain the difference between cell morphology and arrangement.
2. What advantages do cell walls provide prokaryotic cells?

The Nucleoid

All cellular life has a DNA genome organized into one or more chromosomes. Prokaryotic chromosomes are typically circular, haploid (unpaired), and not bound by a complex nuclear membrane. Prokaryotic DNA and DNA-associated proteins are concentrated within the nucleoid region of the cell (Figure 3.1.6). In general, prokaryotic DNA interacts with nucleoid-associated proteins (NAPs) that assist in the organization and packaging of the chromosome. In bacteria, NAPs function similar to histones, which are the DNA-organizing proteins found in eukaryotic cells. In archaea, the nucleoid is organized by either NAPs or histone-like DNA organizing proteins.

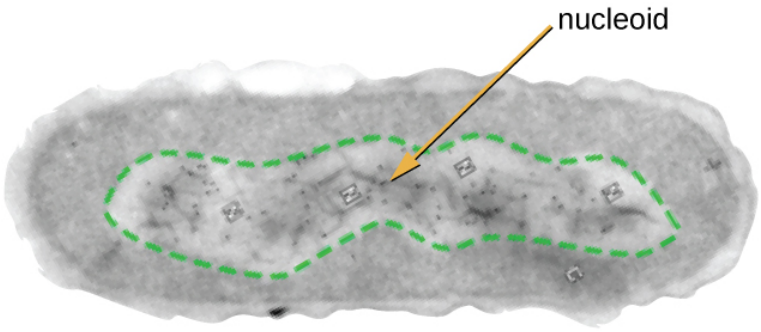


Figure 3.1.6: The nucleoid region (the area enclosed by the green dashed line) is a condensed area of DNA found within prokaryotic cells. Because of the density of the area, it does not readily stain and appears lighter in color when viewed with a transmission electron microscope.

Plasmids

Prokaryotic cells may also contain extrachromosomal DNA, or DNA that is not part of the chromosome. This extrachromosomal DNA is found in plasmid**s**, which are small, circular, double-stranded DNA molecules. Cells that have plasmids often have hundreds of them within a single cell. Plasmids are more commonly found in bacteria; however, plasmids have been found in archaea and eukaryotic organisms. Plasmids often carry genes that confer advantageous traits such as antibiotic resistance; thus, they are important to the survival of the organism. We will discuss plasmids in more detail in Mechanisms of Microbial Genetics.

Ribosomes

All cellular life synthesizes proteins, and organisms in all three domains of life possess ribosomes, structures responsible protein synthesis. However, ribosomes in each of the three domains are structurally different. Ribosomes, themselves, are constructed from proteins, along with ribosomal RNA (rRNA). Prokaryotic ribosomes are found in the cytoplasm. They are called 70S ribosome**s** because they have a size of 70S (Figure 3.1.7), whereas eukaryotic cytoplasmic ribosomes have a size of 80S. (The S stands for Svedberg unit, a measure of sedimentation in an ultracentrifuge, which is based on size, shape, and surface qualities of the structure being analyzed). Although they are the same size, bacterial and archaeal ribosomes have different proteins and rRNA molecules, and the archaeal versions are more similar to their eukaryotic counterparts than to those found in bacteria.

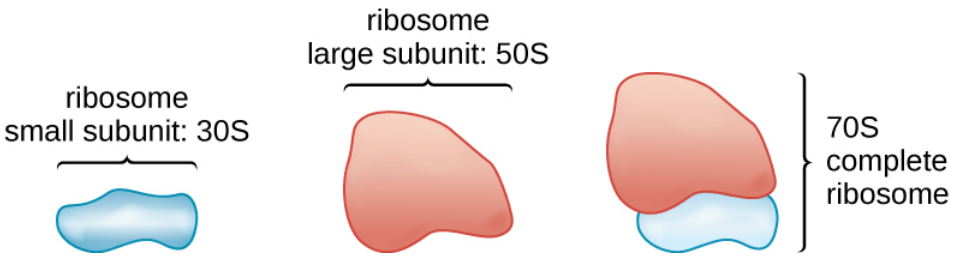


Figure 3.1.7: Prokaryotic ribosomes (70S) are composed of two subunits: the 30S (small subunit) and the 50S (large subunit), each of which are composed of protein and rRNA components.

Inclusions

As single-celled organisms living in unstable environments, some prokaryotic cells have the ability to store excess nutrients within cytoplasmic structures called inclusions. Storing nutrients in a polymerized form is advantageous because it reduces the buildup of osmotic pressure that occurs as a cell accumulates solutes. Various types of inclusions store glycogen and starches, which contain carbon that cells can access for energy. Volutin granules, also called metachromatic granules because of their staining characteristics, are inclusions that store polymerized inorganic phosphate that can be used in metabolism and assist in the formation of biofilms. Microbes known to contain volutin granules include the archaea *Methanosarcina*, the bacterium *Corynebacterium diphtheriae*, and the unicellular eukaryotic alga *Chlamydomonas*. Sulfur granules, another type of inclusion, are found in sulfur bacteria of the genus *Thiobacillus*; these granules store elemental sulfur, which the bacteria use for metabolism.

Occasionally, certain types of inclusions are surrounded by a phospholipid monolayer embedded with protein. Polyhydroxybutyrate (PHB), which can be produced by species of *Bacillus* and *Pseudomonas*, is an example of an inclusion that displays this type of monolayer structure. Industrially, PHB has also been used as a source of biodegradable polymers for bioplastics. Several different types of inclusions are shown in Figure 3.1.8.

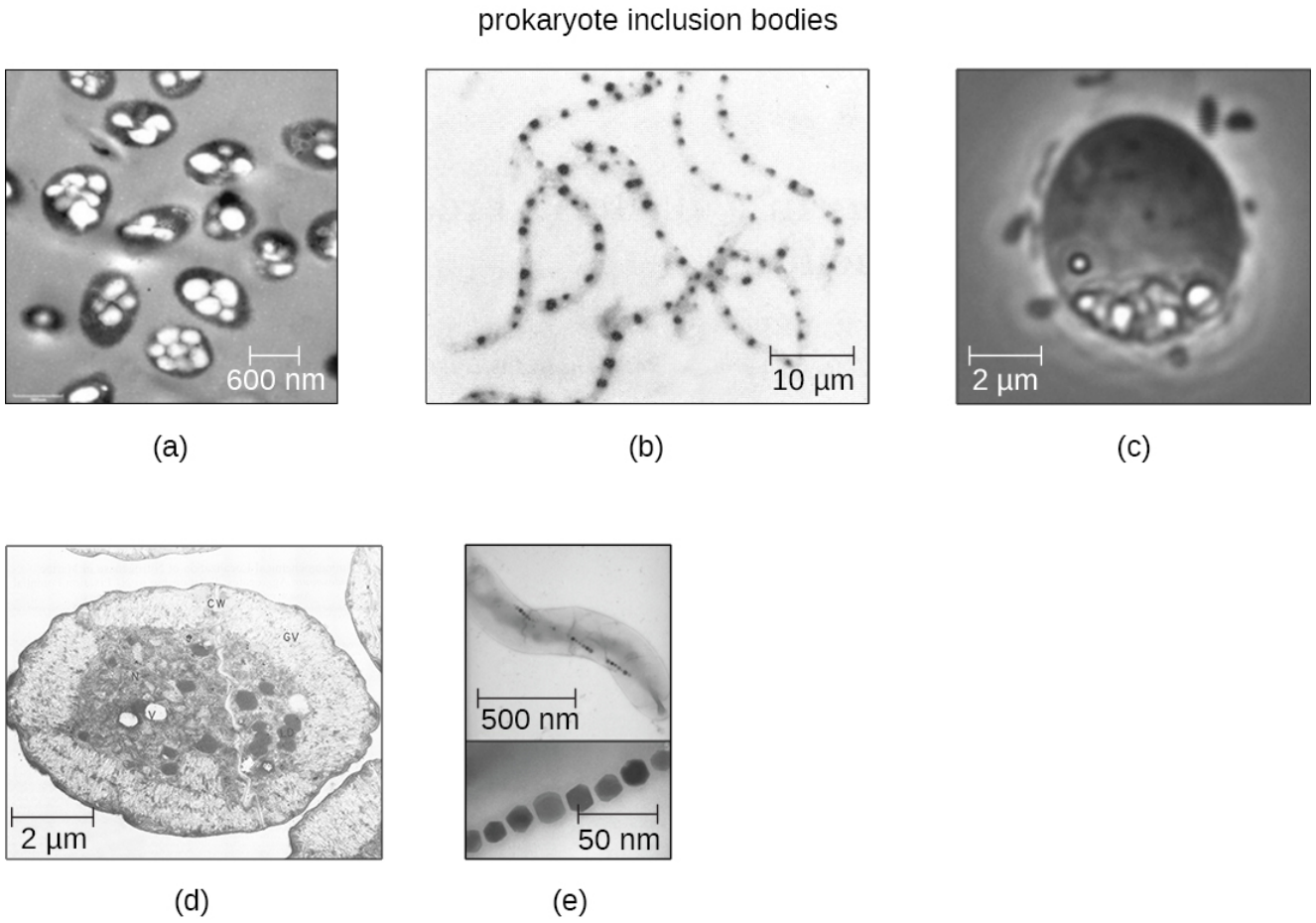


Figure 3.1.8: *Prokaryotic cells may have various types of inclusions. (a) A transmission electron micrograph of polyhydroxybutyrate lipid droplets. (b) A light micrograph of volutin granules. (c) A phase-contrast micrograph of sulfur granules. (d) A transmission electron micrograph of magnetosomes. (e) A transmission electron micrograph of gas vacuoles. (credit b, c, d: modification of work by American Society for Microbiology)*

Some prokaryotic cells have other types of inclusions that serve purposes other than nutrient storage. For example, some prokaryotic cells produce gas vacuoles, accumulations of small, protein-lined vesicles of gas. These gas vacuoles allow the prokaryotic cells that synthesize them to alter their buoyancy so that they can adjust their location in the water column. Magnetotactic bacteria, such as *Magnetospirillum magnetotacticum*, contain magnetosomes, which are inclusions of magnetic iron oxide or iron sulfide surrounded by a lipid layer. These allow cells to align along a magnetic field, aiding their movement (Figure 3.1.8). Cyanobacteria such as *Anabaena cylindrica* and bacteria such as *Halothiobacillus neapolitanus* produce carboxysome inclusions. Carboxysomes are composed of outer shells of thousands of protein subunits. Their interior is filled with ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and carbonic anhydrase. Both of these compounds are used for carbon metabolism. Some prokaryotic cells also possess carboxysomes that sequester functionally related enzymes in one location. These structures are considered proto-organelles because they compartmentalize important compounds or chemical reactions, much like many eukaryotic organelles.

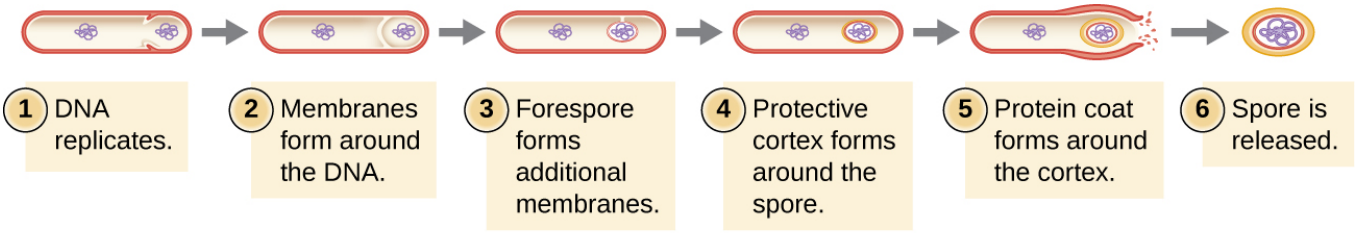
Endospores

Bacterial cells are generally observed as vegetative cells, but some genera of bacteria have the ability to form endospores, structures that essentially protect the bacterial genome in a dormant state when environmental conditions are unfavorable. Endospores (not to be confused with the reproductive spores formed by fungi) allow some bacterial cells to survive long periods without food or water, as well as exposure to chemicals, extreme temperatures, and even radiation. Table 3.1.1 compares the characteristics of vegetative cells and endospores.

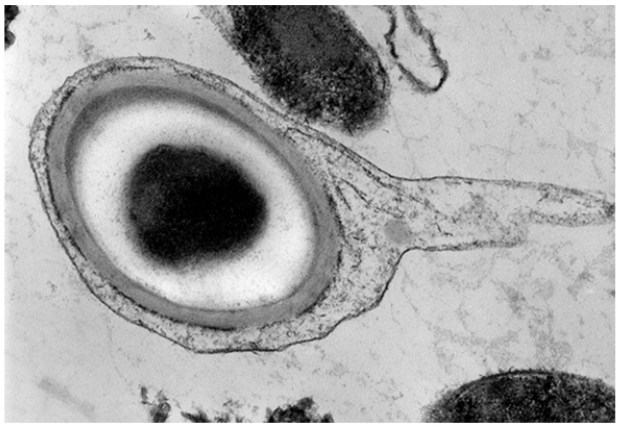
Table 3.1.1***:*** *Characteristics of Vegetative Cells versus Endospores*

Vegetative Cells	Endospores
Sensitive to extreme temperatures and radiation	Resistant to extreme temperatures and radiation
Gram-positive	Do not absorb Gram stain, only special endospore stains (see Staining Microscopic Specimens)
Normal water content and enzymatic activity	Dehydrated; no metabolic activity
Capable of active growth and metabolism	Dormant; no growth or metabolic activity

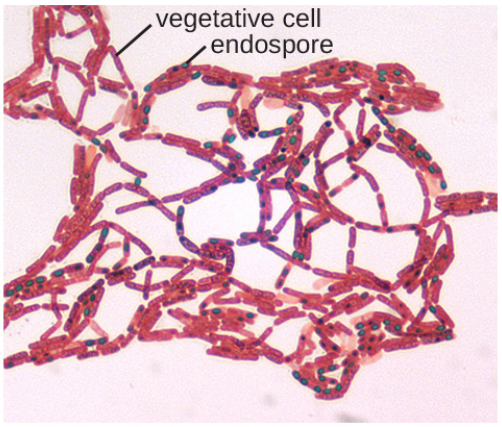
The process by which vegetative cells transform into endospores is called sporulation, and it generally begins when nutrients become depleted or environmental conditions become otherwise unfavorable (Figure 3.1.9). The process begins with the formation of a septum in the vegetative bacterial cell. The septum divides the cell asymmetrically, separating a DNA forespore from the mother cell. The forespore, which will form the core of the endospore, is essentially a copy of the cell's chromosomes, and is separated from the mother cell by a second membrane. A cortex gradually forms around the forespore by laying down layers of calcium and dipicolinic acid between membranes. A protein spore coat then forms around the cortex while the DNA of the mother cell disintegrates. Further maturation of the endospore occurs with the formation of an outermost exosporium. The endospore is released upon disintegration of the mother cell, completing sporulation.



(a)



(b)



(c)

Figure 3.1.9***:*** *(a) Sporulation begins following asymmetric cell division. The forespore becomes surrounded by a double layer of membrane, a cortex, and a protein spore coat, before being released as a mature endospore upon disintegration of the mother cell. (b) An electron micrograph of a Carboxydothermus hydrogenoformans endospore. (c) These Bacillus spp. cells are undergoing sporulation. The endospores have been visualized using Malachite Green spore stain. (credit b: modification of work by Jonathan Eisen)*

Endospores of certain species have been shown to persist in a dormant state for extended periods of time, up to thousands of years.[2] However, when living conditions improve, endospores undergo germination, reentering a vegetative state. After germination, the

cell becomes metabolically active again and is able to carry out all of its normal functions, including growth and cell division.

Not all bacteria have the ability to form endospores; however, there are a number of clinically significant endospore-forming gram-positive bacteria of the genera *Bacillus* and *Clostridium*. These include *B. anthracis*, the causative agent of anthrax, which produces endospores capable of survive for many decades[3]; *C. tetani* (causes tetanus); *C. difficile* (causes pseudomembranous colitis); *C. perfringens* (causes gas gangrene); and *C. botulinum* (causes botulism). Pathogens such as these are particularly difficult to combat because their endospores are so hard to kill. Special sterilization methods for endospore-forming bacteria are discussed in Control of Microbial Growth.

Exercise 3.1.2

1. What is an inclusion?
2. What is the function of an endospore?

Plasma Membrane

Structures that enclose the cytoplasm and internal structures of the cell are known collectively as the cell envelope. In prokaryotic cells, the structures of the cell envelope vary depending on the type of cell and organism. Most (but not all) prokaryotic cells have a cell wall, but the makeup of this cell wall varies. All cells (prokaryotic and eukaryotic) have a plasma membrane (also called cytoplasmic membrane or cell membrane) that exhibits selective permeability, allowing some molecules to enter or leave the cell while restricting the passage of others.

The structure of the plasma membrane is often described in terms of the fluid mosaic model, which refers to the ability of membrane components to move fluidly within the plane of the membrane, as well as the mosaic-like composition of the components, which include a diverse array of lipid and protein components (Figure 3.1.10). The plasma membrane structure of most bacterial and eukaryotic cell types is a bilayer composed mainly of phospholipids formed with ester linkages and proteins. These phospholipids and proteins have the ability to move laterally within the plane of the membranes as well as between the two phospholipid layers.

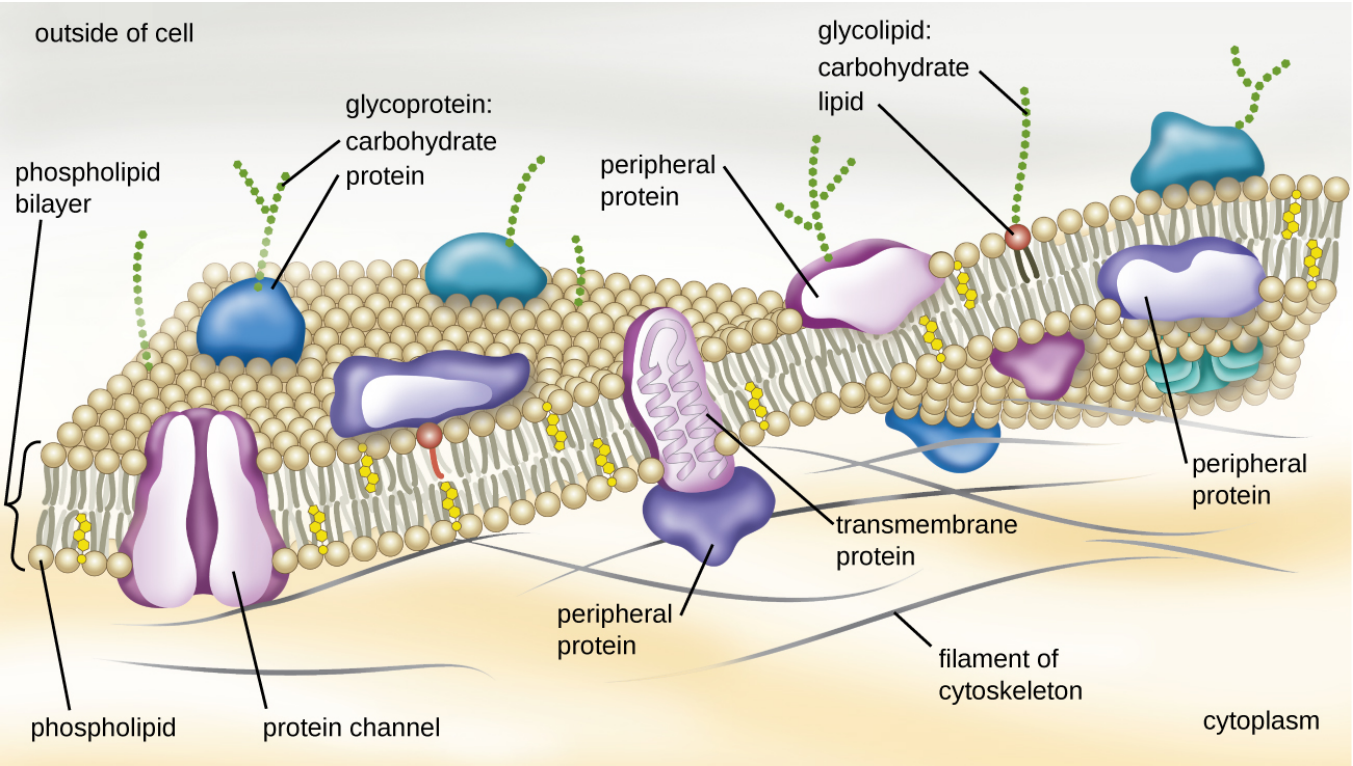


Figure 3.1.10: The bacterial plasma membrane is a phospholipid bilayer with a variety of embedded proteins that perform various functions for the cell. Note the presence of glycoproteins and glycolipids, whose carbohydrate components extend out from the surface of the cell. The abundance and arrangement of these proteins and lipids can vary greatly between species.

Archaeal membranes are fundamentally different from bacterial and eukaryotic membranes in a few significant ways. First, archaeal membrane phospholipids are formed with ether linkages, in contrast to the ester linkages found in bacterial or eukaryotic cell membranes. Second, archaeal phospholipids have branched chains, whereas those of bacterial and eukaryotic cells are straight chained. Finally, although some archaeal membranes can be formed of bilayers like those found in bacteria and eukaryotes, other archaeal plasma membranes are lipid monolayers.

Proteins on the cell's surface are important for a variety of functions, including cell-to-cell communication, and sensing environmental conditions and pathogenic virulence factors. Membrane proteins and phospholipids may have carbohydrates (sugars) associated with them and are called glycoproteins or glycolipids, respectively. These glycoprotein and glycolipid complexes extend out from the surface of the cell, allowing the cell to interact with the external environment (Figure 3.1.10). Glycoproteins and glycolipids in the plasma membrane can vary considerably in chemical composition among archaea, bacteria, and eukaryotes, allowing scientists to use them to characterize unique species.

Plasma membranes from different cells types also contain unique phospholipids, which contain fatty acids. As described in Using Biochemistry to Identify Microorganisms, phospholipid-derived fatty acid analysis (PLFA) profiles can be used to identify unique types of cells based on differences in fatty acids. Archaea, bacteria, and eukaryotes each have a unique PFLA profile.

Membrane Transport Mechanisms

One of the most important functions of the plasma membrane is to control the transport of molecules into and out of the cell. Internal conditions must be maintained within a certain range despite any changes in the external environment. The transport of substances across the plasma membrane allows cells to do so.

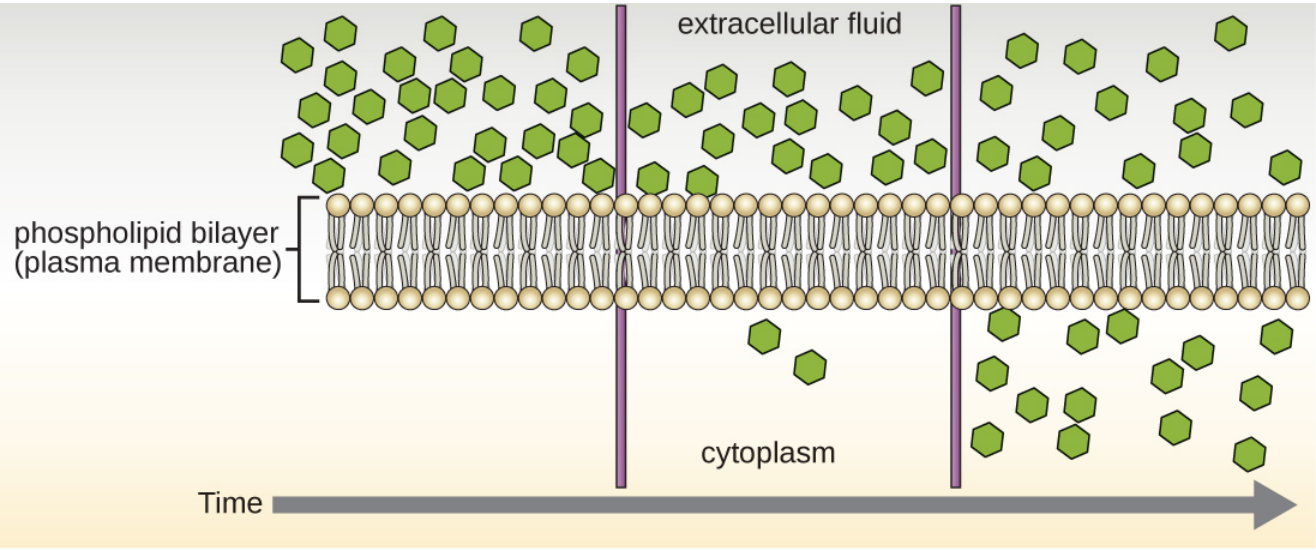


Figure 3.1.11: Simple diffusion down a concentration gradient directly across the phospholipid bilayer. (credit: modification of work by Mariana Ruiz Villareal)

Cells use various modes of transport across the plasma membrane. For example, molecules moving from a higher concentration to a lower concentration with the concentration gradient are transported by simple diffusion, also known as passive transport (Figure 3.1.11). Some small molecules, like carbon dioxide, may cross the membrane bilayer directly by simple diffusion. However, charged molecules, as well as large molecules, need the help of carriers or channels in the membrane. These structures ferry molecules across the membrane, a process known as facilitated diffusion (Figure 3.1.12).

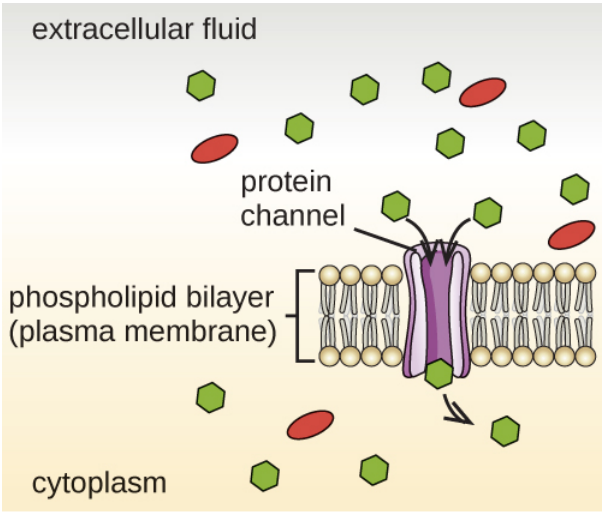


Figure 3.1.12: *Facilitated diffusion down a concentration gradient through a membrane protein. (credit: modification of work by Mariana Ruiz Villareal)*

Active transport occurs when cells move molecules across their membrane *against* concentration gradients (Figure 3.1.13). A major difference between passive and active transport is that active transport requires adenosine triphosphate (ATP) or other forms of energy to move molecules "uphill." Therefore, active transport structures are often called "pumps."

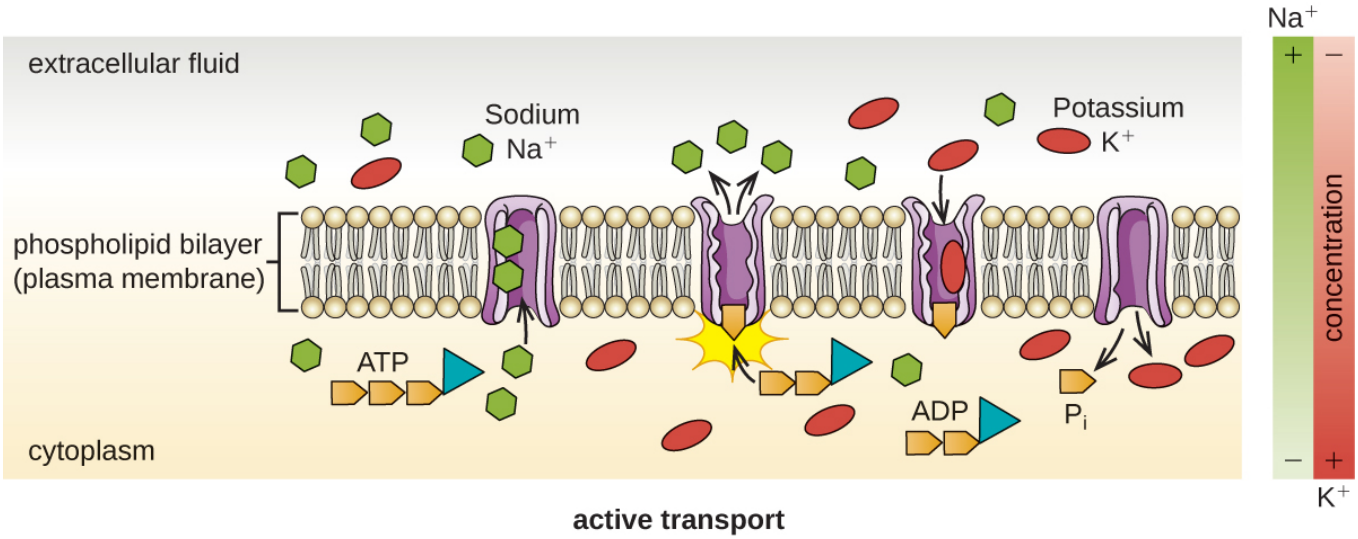


Figure 3.1.13: *Active transport against a concentration gradient via a membrane pump that requires energy. (credit: modification of work by Mariana Ruiz Villareal)*

Group translocation also transports substances into bacterial cells. In this case, as a molecule moves into a cell against its concentration gradient, it is chemically modified so that it does not require transport against an unfavorable concentration gradient. A common example of this is the bacterial phosphotransferase system, a series of carriers that phosphorylates (i.e., adds phosphate ions to) glucose or other sugars upon entry into cells. Since the phosphorylation of sugars is required during the early stages of sugar metabolism, the phosphotransferase system is considered to be an energy neutral system.

Photosynthetic Membrane Structures

Some prokaryotic cells, namely cyanobacteria and photosynthetic bacteria, have membrane structures that enable them to perform photosynthesis. These structures consist of an infolding of the plasma membrane that encloses photosynthetic pigments such as green chlorophylls and bacteriochlorophylls. In cyanobacteria, these membrane structures are called thylakoids; in photosynthetic bacteria, they are called chromatophores, lamellae, or chlorosomes.

Cell Wall

The primary function of the cell wall is to protect the cell from harsh conditions in the outside environment. When present, there are notable similarities and differences among the cell walls of archaea, bacteria, and eukaryotes.

The major component of bacterial cell walls is called peptidoglycan (or murein); it is only found in bacteria. Structurally, peptidoglycan resembles a layer of meshwork or fabric (Figure 3.1.14). Each layer is composed of long chains of alternating molecules of N-acetylglucosamine (NAG) and N-acetylmuramic acid (NAM). The structure of the long chains has significant two-dimensional tensile strength due to the formation of peptide bridges that connect NAG and NAM within each peptidoglycan layer. In gram-negative bacteria, tetrapeptide chains extending from each NAM unit are directly cross-linked, whereas in gram-positive bacteria, these tetrapeptide chains are linked by pentaglycine cross-bridges. Peptidoglycan subunits are made inside of the bacterial cell and then exported and assembled in layers, giving the cell its shape.

Since peptidoglycan is unique to bacteria, many antibiotic drugs are designed to interfere with peptidoglycan synthesis, weakening the cell wall and making bacterial cells more susceptible to the effects of osmotic pressure (see Mechanisms of Antibacterial Drugs). In addition, certain cells of the human immune system are able "recognize" bacterial pathogens by detecting peptidoglycan on the surface of a bacterial cell; these cells then engulf and destroy the bacterial cell, using enzymes such as lysozyme, which breaks down and digests the peptidoglycan in their cell walls (see Pathogen Recognition and Phagocytosis).

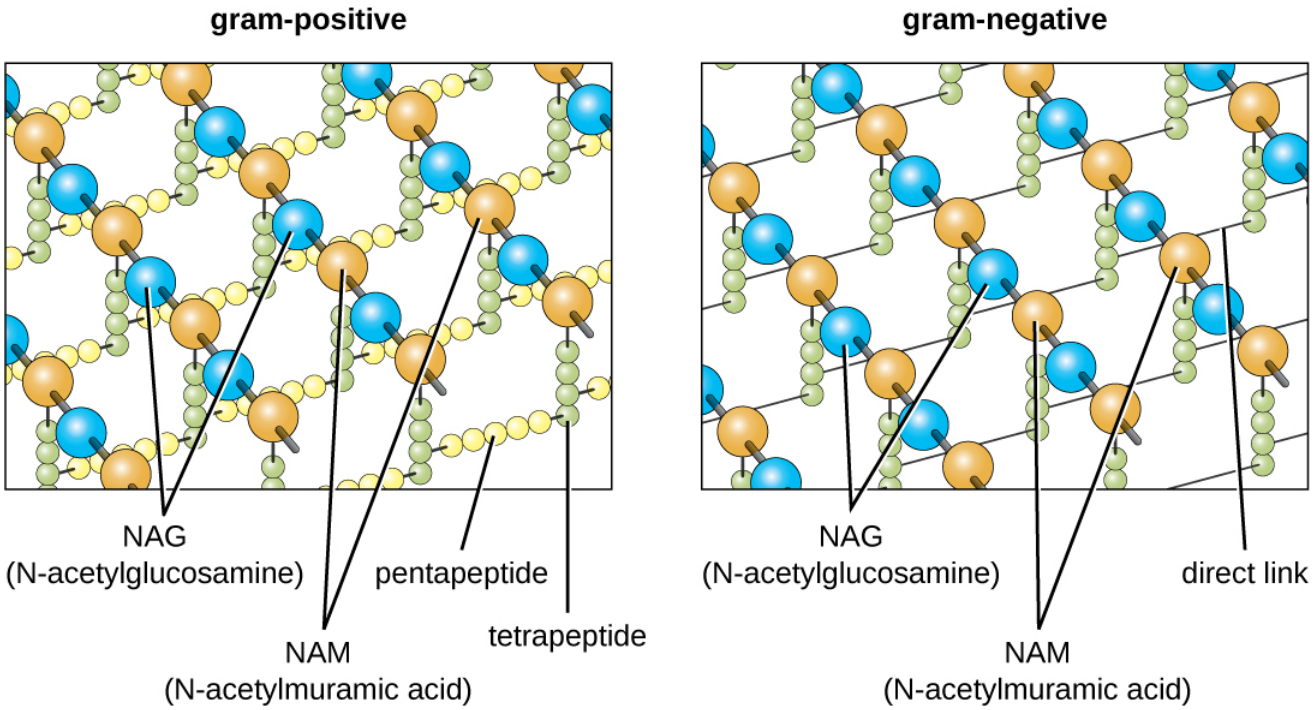


Figure 3.1.14: Peptidoglycan is composed of polymers of alternating NAM and NAG subunits, which are cross-linked by peptide bridges linking NAM subunits from various glycan chains. This provides the cell wall with tensile strength in two dimensions.

The Gram staining protocol (see Staining Microscopic Specimens) is used to differentiate two common types of cell wall structures (Figure 3.1.15). Gram-positive cells have a cell wall consisting of many layers of peptidoglycan totaling 30–100 nm in thickness. These peptidoglycan layers are commonly embedded with teichoic acids (TAs), carbohydrate chains that extend through and beyond the peptidoglycan layer.[4] TA is thought to stabilize peptidoglycan by increasing its rigidity. TA also plays a role in the ability of pathogenic gram-positive bacteria such as *Streptococcus* to bind to certain proteins on the surface of host cells, enhancing their ability to cause infection. In addition to peptidoglycan and TAs, bacteria of the family Mycobacteriaceae have an external layer of waxy mycolic acids in their cell wall; as described in Staining Microscopic Specimens, these bacteria are referred to as acid-fast, since acid-fast stains must be used to penetrate the mycolic acid layer for purposes of microscopy (Figure 3.1.16).

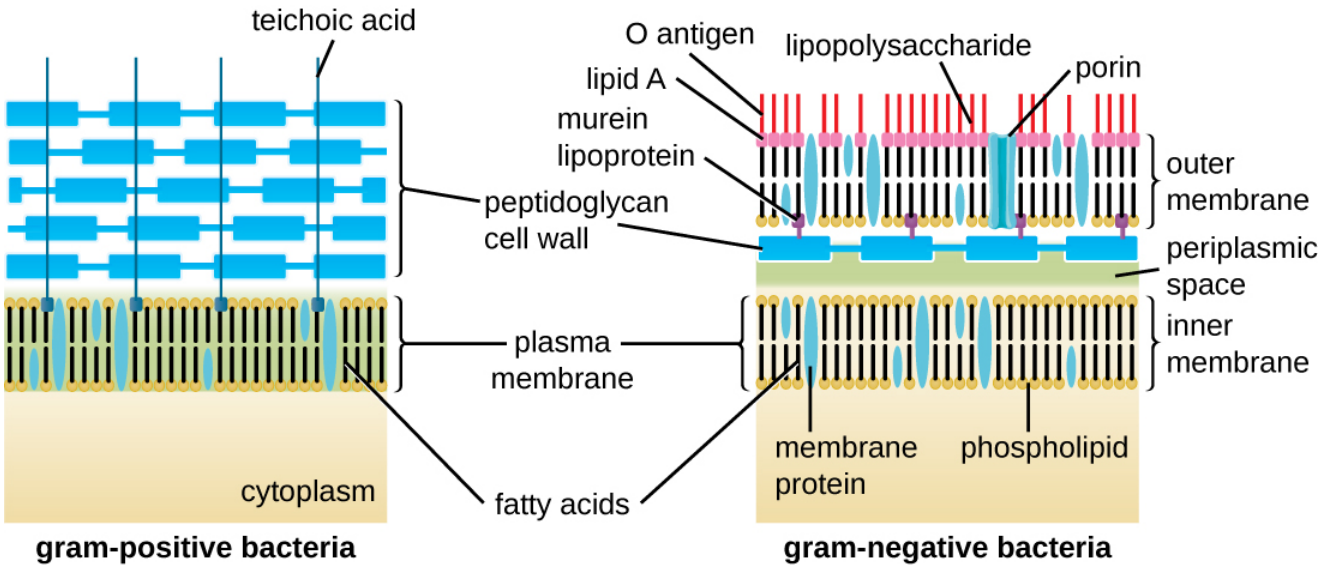


Figure 3.1.15: Bacteria contain two common cell wall structural types. Gram-positive cell walls are structurally simple, containing a thick layer of peptidoglycan with embedded teichoic acid external to the plasma membrane.[5] Gram-negative cell walls are structurally more complex, containing three layers: the inner membrane, a thin layer of peptidoglycan, and an outer membrane containing lipopolysaccharide. (credit: modification of work by "Franciscosp2"/Wikimedia Commons)

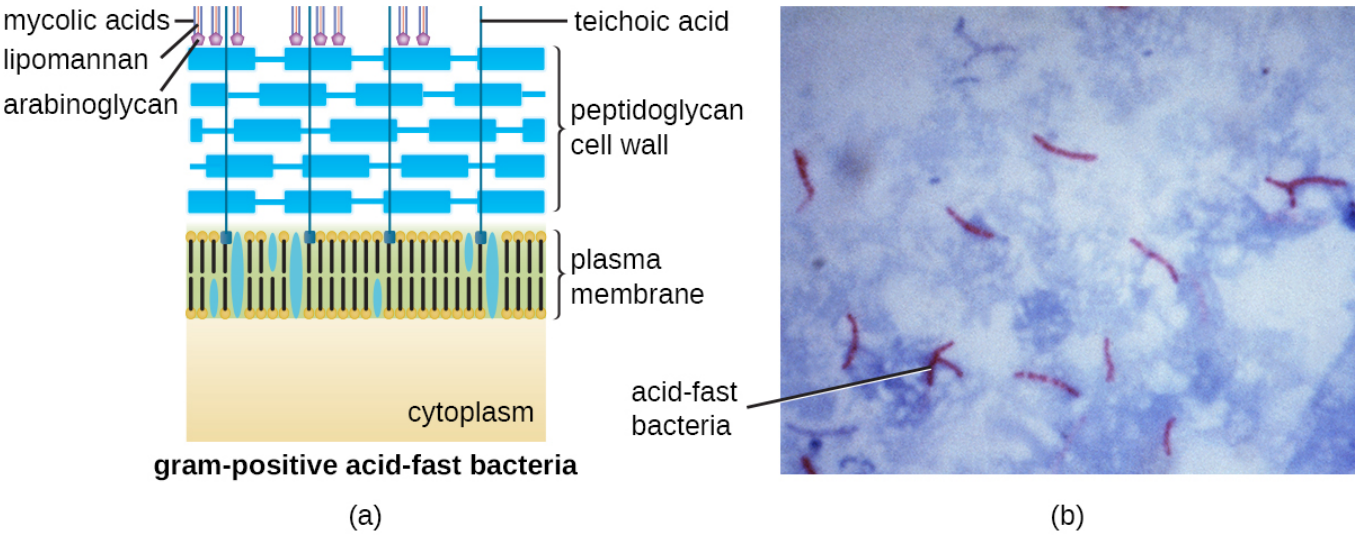


Figure 3.1.16: (a) Some gram-positive bacteria, including members of the Mycobacteriaceae, produce waxy mycolic acids found exterior to their structurally-distinct peptidoglycan. (b) The acid-fast staining protocol detects the presence of cell walls that are rich in mycolic acid. Acid-fast cells are stained red by carbolfuschin. (credit a: modification of work by "Franciscosp2"/Wikimedia Commons; credit b: modification of work by Centers for Disease Control and Prevention)

Gram-negative cells have a much thinner layer of peptidoglycan (no more than about 4 nm thick[6]) than gram-positive cells, and the overall structure of their cell envelope is more complex. In gram-negative cells, a gel-like matrix occupies the periplasmic space between the cell wall and the plasma membrane, and there is a second lipid bilayer called the outer membrane, which is external to the peptidoglycan layer (Figure 3.1.15). This outer membrane is attached to the peptidoglycan by murein lipoprotein. The outer leaflet of the outer membrane contains the molecule lipopolysaccharide (LPS), which functions as an endotoxin in infections involving gram-negative bacteria, contributing to symptoms such as fever, hemorrhaging, and septic shock. Each LPS molecule is composed of Lipid A, a core polysaccharide, and an O side chain that is composed of sugar-like molecules that comprise the external face of the LPS (Figure 3.1.17). The composition of the O side chain varies between different species and strains of bacteria. Parts of the O side chain called antigens can be detected using serological or immunological tests to identify specific pathogenic strains like *Escherichia coli* O157:H7, a deadly strain of bacteria that causes bloody diarrhea and kidney failure.

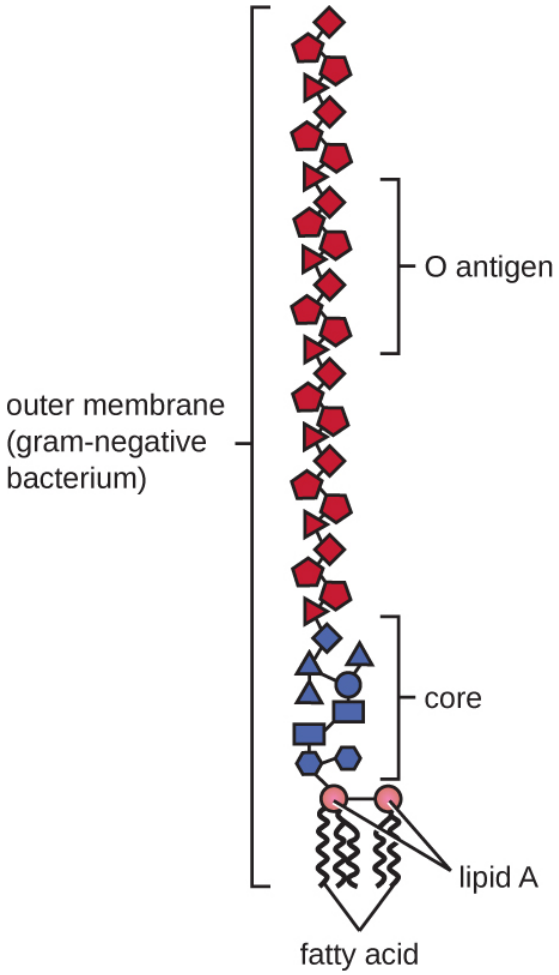


Figure 3.1.17: The outer membrane of a gram-negative bacterial cell contains lipopolysaccharide (LPS), a toxin composed of Lipid A embedded in the outer membrane, a core polysaccharide, and the O side chain.

Archaeal cell wall structure differs from that of bacteria in several significant ways. First, archaeal cell walls do not contain peptidoglycan; instead, they contain a similar polymer called pseudopeptidoglycan (pseudomurein) in which NAM is replaced with a different subunit. Other archaea may have a layer of glycoproteins or polysaccharides that serves as the cell wall instead of pseudopeptidoglycan. Last, as is the case with some bacterial species, there are a few archaea that appear to lack cell walls entirely.

Glycocalyces and S-Layers

Although most prokaryotic cells have cell walls, some may have additional cell envelope structures exterior to the cell wall, such as glycocalyces and S-layers. A glycocalyx is a sugar coat, of which there are two important types: capsules and slime layers. A capsule is an organized layer located outside of the cell wall and usually composed of polysaccharides or proteins (Figure 3.1.18). A slime layer is a less tightly organized layer that is only loosely attached to the cell wall and can be more easily washed off. Slime layers may be composed of polysaccharides, glycoproteins, or glycolipids.

Glycocalyces allows cells to adhere to surfaces, aiding in the formation of biofilms (colonies of microbes that form in layers on surfaces). In nature, most microbes live in mixed communities within biofilms, partly because the biofilm affords them some level of protection. Biofilms generally hold water like a sponge, preventing desiccation. They also protect cells from predation and hinder the action of antibiotics and disinfectants. All of these properties are advantageous to the microbes living in a biofilm, but they present challenges in a clinical setting, where the goal is often to eliminate microbes.

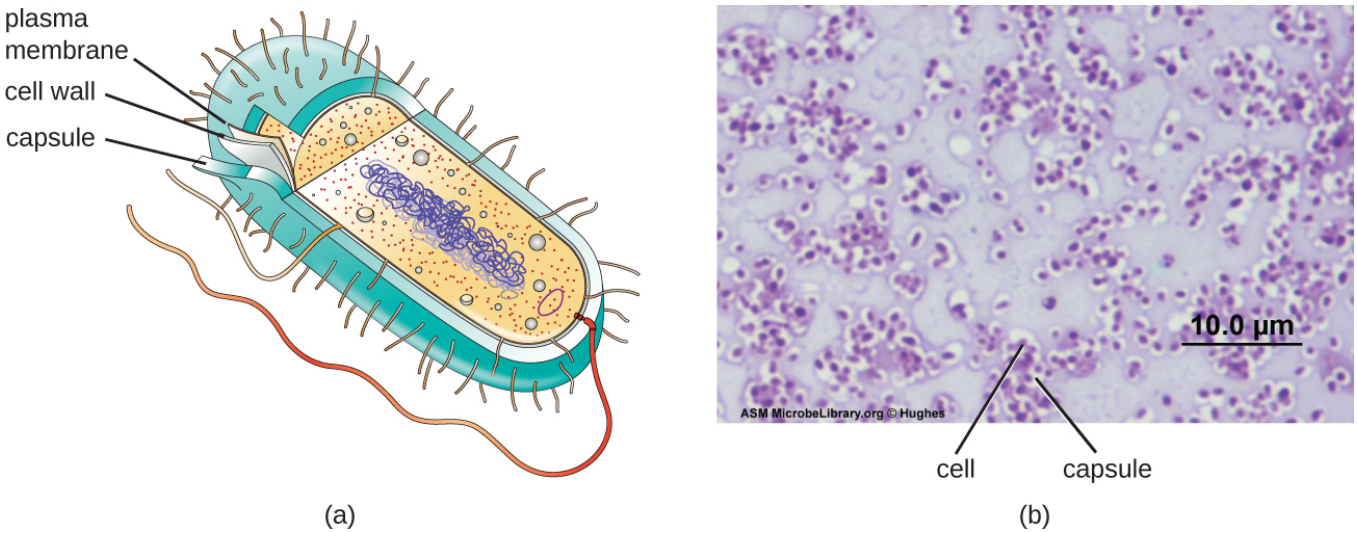


Figure 3.1.18: (a) Capsules are a type of glycocalyx composed of an organized layer of polysaccharides. (b) A capsule stain of Pseudomonas aeruginosa, a bacterial pathogen capable of causing many different types of infections in humans. (credit b: modification of work by American Society for Microbiology)

The ability to produce a capsule can contribute to a microbe's pathogenicity (ability to cause disease) because the capsule can make it more difficult for phagocytic cells (such as white blood cells) to engulf and kill the microorganism. *Streptococcus pneumoniae*, for example, produces a capsule that is well known to aid in this bacterium's pathogenicity. As explained in Staining Microscopic specimens, capsules are difficult to stain for microscopy; negative staining techniques are typically used.

An S-layer is another type of cell envelope structure; it is composed of a mixture of structural proteins and glycoproteins. In bacteria, S-layers are found outside the cell wall, but in some archaea, the S-layer serves *as* the cell wall. The exact function of S-layers is not entirely understood, and they are difficult to study; but available evidence suggests that they may play a variety of functions in different prokaryotic cells, such as helping the cell withstand osmotic pressure and, for certain pathogens, interacting with the host immune system.

PART 3

After diagnosing Barbara with pneumonia, the PA writes her a prescription for amoxicillin, a commonly-prescribed type of penicillin derivative. More than a week later, despite taking the full course as directed, Barbara still feels weak and is not fully recovered, although she is still able to get through her daily activities. She returns to the health center for a follow-up visit.

Many types of bacteria, fungi, and viruses can cause pneumonia. Amoxicillin targets the peptidoglycan of bacterial cell walls. Since the amoxicillin has not resolved Barbara's symptoms, the PA concludes that the causative agent probably lacks peptidoglycan, meaning that the pathogen could be a virus, a fungus, or a bacterium that lacks peptidoglycan. Another possibility is that the pathogen is a bacterium containing peptidoglycan but has developed resistance to amoxicillin.

Exercise 3.1.3

1. How can the PA definitively identify the cause of Barbara's pneumonia?
2. What form of treatment should the PA prescribe, given that the amoxicillin was ineffective?

Filamentous Appendages

Many bacterial cells have protein appendages embedded within their cell envelopes that extend outward, allowing interaction with the environment. These appendages can attach to other surfaces, transfer DNA, or provide movement. Filamentous appendages include fimbriae, pili, and flagella.

Fimbriae and Pili

Fimbriae and pili are structurally similar and, because differentiation between the two is problematic, these terms are often used interchangeably.[7] [8] The term fimbriae commonly refers to short bristle-like proteins projecting from the cell surface by the hundreds. Fimbriae enable a cell to attach to surfaces and to other cells. For pathogenic bacteria, adherence to host cells is important for colonization, infectivity, and virulence. Adherence to surfaces is also important in biofilm formation.

The term pili (singular: pilus) commonly refers to longer, less numerous protein appendages that aid in attachment to surfaces (Figure 3.1.19). A specific type of pilus, called the F pilus or sex pilus, is important in the transfer of DNA between bacterial cells, which occurs between members of the same generation when two cells physically transfer or exchange parts of their respective genomes (see How Asexual Prokaryotes Achieve Genetic Diversity).

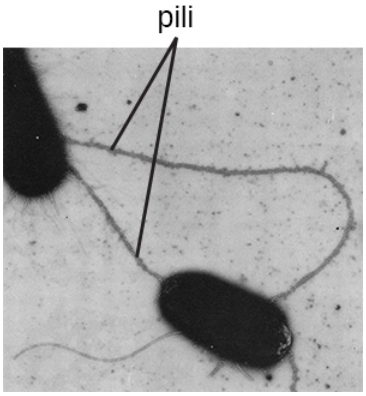


Figure 3.1.19: Bacteria may produce two different types of protein appendages that aid in surface attachment. Fimbriae typically are more numerous and shorter, whereas pili (shown here) are longer and less numerous per cell. (credit: modification of work by American Society for Microbiology)

Group A Strep

Before the structure and function of the various components of the bacterial cell envelope were well understood, scientists were already using cell envelope characteristics to classify bacteria. In 1933, Rebecca Lancefield proposed a method for serotyping various β-hemolytic strains of *Streptococcus* species using an agglutination assay, a technique using the clumping of bacteria to detect specific cell-surface antigens. In doing so, Lancefield discovered that one group of *S. pyogenes*, found in Group A, was associated with a variety of human diseases. She determined that various strains of Group A strep could be distinguished from each other based on variations in specific cell surface proteins that she named M proteins.

Today, more than 80 different strains of Group A strep have been identified based on M proteins. Various strains of Group A strep are associated with a wide variety of human infections, including streptococcal pharyngitis (strep throat), impetigo, toxic shock syndrome, scarlet fever, rheumatic fever, and necrotizing fasciitis. The M protein is an important virulence factor for Group A strep, helping these strains evade the immune system. Changes in M proteins appear to alter the infectivity of a particular strain of Group A strep.

Flagella

Flagella are structures used by cells to move in aqueous environments. Bacterial flagella act like propellers. They are stiff spiral filaments composed of flagellin protein subunits that extend outward from the cell and spin in solution. The basal body is the motor for the flagellum and is embedded in the plasma membrane (Figure 3.1.20). A hook region connects the basal body to the filament. Gram-positive and gram-negative bacteria have different basal body configurations due to differences in cell wall structure.

Different types of motile bacteria exhibit different arrangements of flagella (Figure 3.1.21). A bacterium with a singular flagellum, typically located at one end of the cell (polar), is said to have a monotrichous flagellum. An example of a monotrichously flagellated bacterial pathogen is *Vibrio cholerae*, the gram-negative bacterium that causes cholera. Cells with amphitrichous flagella have a flagellum or tufts of flagella at each end. An example is *Spirillum minor*, the cause of spirillary (Asian) rat-bite fever or sodoku. Cells with lophotrichous flagella have a tuft at one end of the cell. The gram-negative bacillus *Pseudomonas aeruginosa*, an opportunistic pathogen known for causing many infections, including “swimmer’s ear” and burn wound infections,

has lophotrichous flagella. Flagella that cover the entire surface of a bacterial cell are called peritrichous flagella. The gram-negative bacterium *E. coli* shows a peritrichous arrangement of flagella.

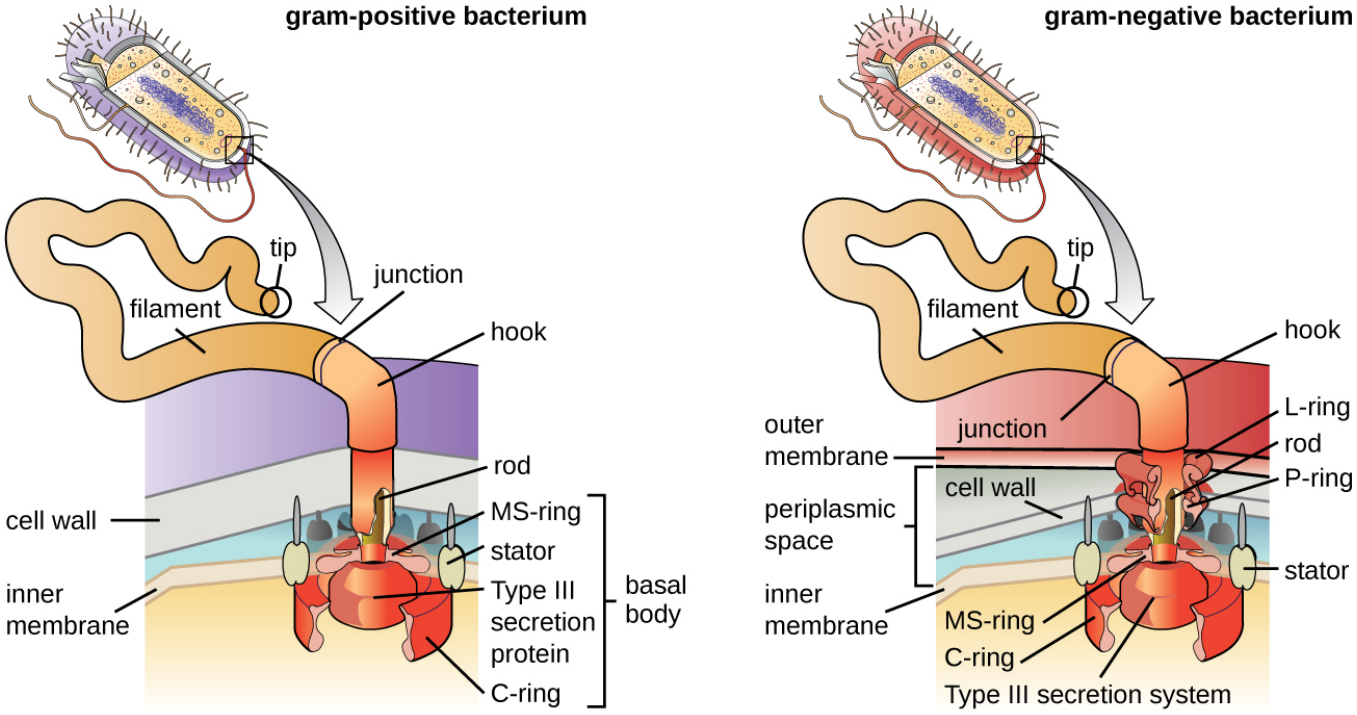


Figure 3.1.20: The basic structure of a bacterial flagellum consists of a basal body, hook, and filament. The basal body composition and arrangement differ between gram-positive and gram-negative bacteria. (credit: modification of work by "LadyofHats"/Mariana Ruiz Villareal)

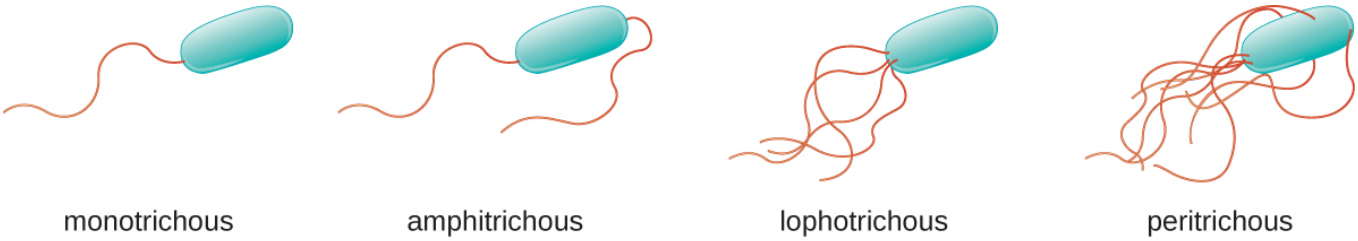


Figure 3.1.21: Flagellated bacteria may exhibit multiple arrangements of their flagella. Common arrangements include monotrichous, amphitrichous, lophotrichous, or peritrichous.

Directional movement depends on the configuration of the flagella. Bacteria can move in response to a variety of environmental signals, including light (phototaxis), magnetic fields (magnetotaxis) using magnetosomes, and, most commonly, chemical gradients (chemotaxis). Purposeful movement toward a chemical attractant, like a food source, or away from a repellent, like a poisonous chemical, is achieved by increasing the length of runs and decreasing the length of tumbles. When running, flagella rotate in a counterclockwise direction, allowing the bacterial cell to move forward. In a peritrichous bacterium, the flagella are all bundled together in a very streamlined way (Figure 3.1.22), allowing for efficient movement. When tumbling, flagella are splayed out while rotating in a clockwise direction, creating a looping motion and preventing meaningful forward movement but reorienting the cell toward the direction of the attractant. When an attractant exists, runs and tumbles still occur; however, the length of runs is longer, while the length of the tumbles is reduced, allowing overall movement toward the higher concentration of the attractant. When no chemical gradient exists, the lengths of runs and tumbles are more equal, and overall movement is more random (Figure 3.1.23).

https://geo.libretexts.org/@go/page/6192

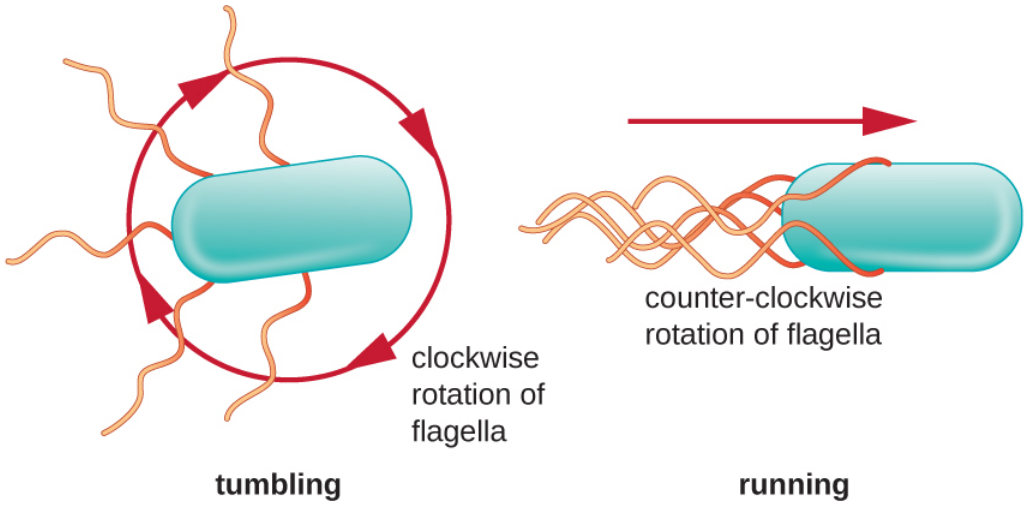


Figure 3.1.22: Bacteria achieve directional movement by changing the rotation of their flagella. In a cell with peritrichous flagella, the flagella bundle when they rotate in a counterclockwise direction, resulting in a run. However, when the flagella rotate in a clockwise direction, the flagella are no longer bundled, resulting in tumbles.

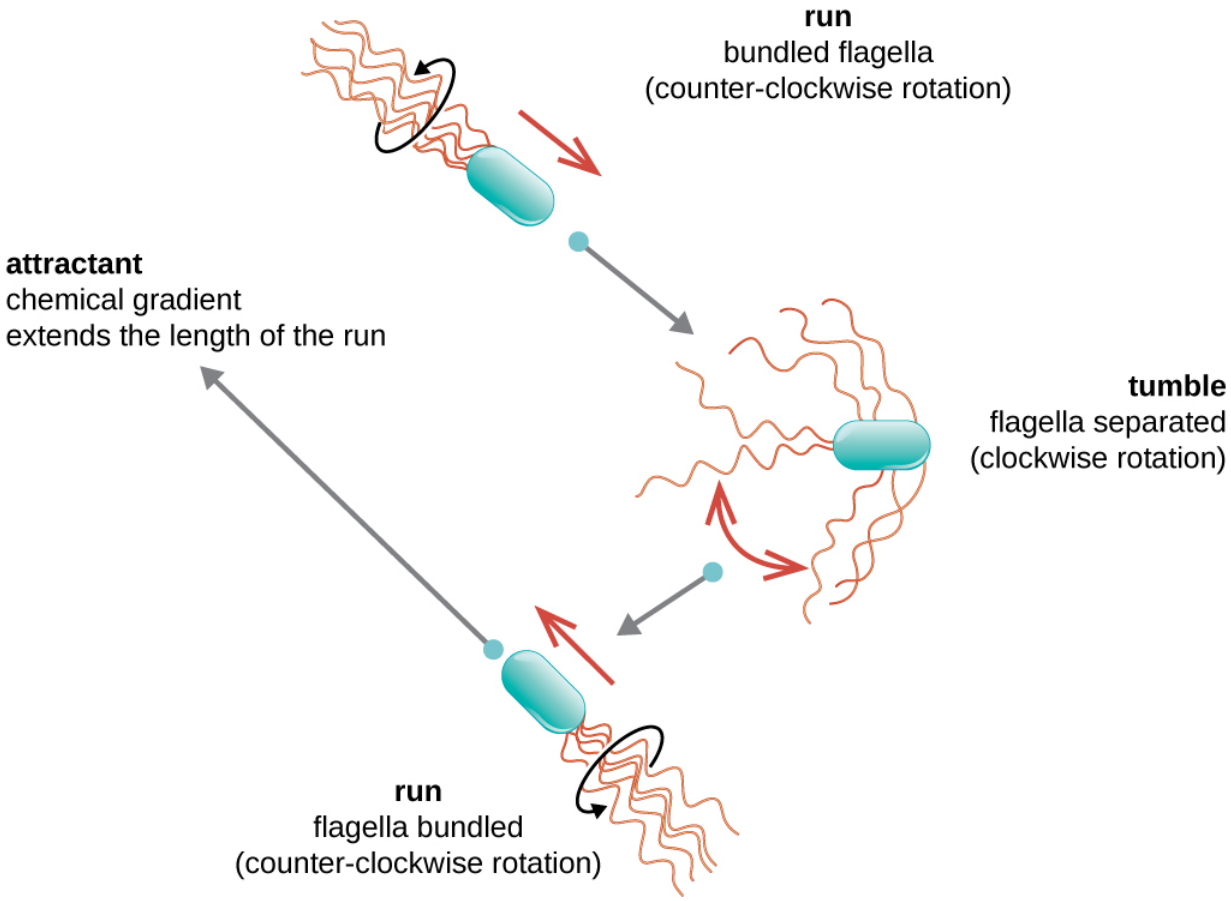


Figure 3.1.23: Without a chemical gradient, flagellar rotation cycles between counterclockwise (run) and clockwise (tumble) with no overall directional movement. However, when a chemical gradient of an attractant exists, the length of runs is extended, while the length of tumbles is decreased. This leads to chemotaxis: an overall directional movement toward the higher concentration of the attractant.

Exercise 3.1.4

1. What is the peptidoglycan layer and how does it differ between gram-positive and gram-negative bacteria?
2. Compare and contrast monotrichous, amphitrichous, lophotrichous, and peritrichous flagella.

https://geo.libretexts.org/@go/page/6192

Summary

- Prokaryotic cells differ from eukaryotic cells in that their genetic material is contained in a **nucleoid** rather than a membrane-bound nucleus. In addition, prokaryotic cells generally lack membrane-bound organelles.
- Prokaryotic cells of the same species typically share a similar **cell morphology** and **cellular arrangement**.
- Most prokaryotic cells have a **cell wall** that helps the organism maintain cellular morphology and protects it against changes in osmotic pressure.
- Outside of the nucleoid, prokaryotic cells may contain extrachromosomal DNA in **plasmids**.
- Prokaryotic **ribosomes** that are found in the cytoplasm have a size of 70S.
- Some prokaryotic cells have **inclusions** that store nutrients or chemicals for other uses.
- Some prokaryotic cells are able to form **endospores** through **sporulation** to survive in a dormant state when conditions are unfavorable. Endospores can **germinate**, transforming back into **vegetative cells** when conditions improve.
- In prokaryotic cells, the **cell envelope** includes a **plasma membrane** and usually a cell wall.
- Bacterial membranes are composed of phospholipids with integral or peripheral proteins. The fatty acid components of these phospholipids are ester-linked and are often used to identify specific types of bacteria. The proteins serve a variety of functions, including transport, cell-to-cell communication, and sensing environmental conditions. Archaeal membranes are distinct in that they are composed of fatty acids that are ether-linked to phospholipids.
- Some molecules can move across the bacterial membrane by simple diffusion, but most large molecules must be actively transported through membrane structures using cellular energy.
- Prokaryotic cell walls may be composed of **peptidoglycan** (bacteria) or **pseudopeptidoglycan** (archaea).
- Gram-positive bacterial cells are characterized by a thick **peptidoglycan** layer, whereas gram-negative bacterial cells are characterized by a thin peptidoglycan layer surrounded by an outer membrane.
- Some prokaryotic cells produce **glycocalyx** coatings, such as **capsules** and **slime layers**, that aid in attachment to surfaces and/or evasion of the host immune system.
- Some prokaryotic cells have **fimbriae** or **pili**, filamentous appendages that aid in attachment to surfaces. Pili are also used in the transfer of genetic material between cells.
- Some prokaryotic cells use one or more **flagella** to move through water. **Peritrichous** bacteria, which have numerous flagella, use **runs** and **tumbles** to move purposefully in the direction of a chemical attractant.

Footnotes

1. 1 Y.-H.M. Chan, W.F. Marshall. “Scaling Properties of Cell and Organelle Size.” *Organogenesis* 6 no. 2 (2010):88–96.
2. 2 F. Rothfuss, M Bender, R Conrad. “Survival and Activity of Bacteria in a Deep, Aged Lake Sediment (Lake Constance).” *Microbial Ecology* 33 no. 1 (1997):69–77.
3. 3 R. Sinclair et al. “Persistence of Category A Select Agents in the Environment.” *Applied and Environmental Microbiology* 74 no. 3 (2008):555–563.
4. 4 T.J. Silhavy, D. Kahne, S. Walker. “The Bacterial Cell Envelope.” *Cold Spring Harbor Perspectives in Biology* 2 no. 5 (2010):a000414.
5. 5 B. Zuber et al. “Granular Layer in the Periplasmic Space of Gram-Positive Bacteria and Fine Structures of *Enterococcus gallinarum* and *Streptococcus gordonii* Septa Revealed by Cryo-Electron Microscopy of Vitreous Sections.” *Journal of Bacteriology* 188 no. 18 (2006):6652–6660
6. 6 L. Gana, S. Chena, G.J. Jensena. “Molecular Organization of Gram-Negative Peptidoglycan.” *Proceedings of the National Academy of Sciences of the United States of America* 105 no. 48 (2008):18953–18957.
7. 7 J.A. Garnetta et al. “Structural Insights Into the Biogenesis and Biofilm Formation by the *Escherichia coli* Common Pilus.” *Proceedings of the National Academy of Sciences of the United States of America* 109 no. 10 (2012):3950–3955.
8. 8 T. Proft, E.N. Baker. “Pili in Gram-Negative and Gram-Positive Bacteria—Structure, Assembly and Their Role in Disease.” *Cellular and Molecular Life Sciences* 66 (2009):613.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 3.1: Unique Characteristics of Prokaryotic Cells is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

3.2: Unique Characteristics of Eukaryotic Cells

SKILLS TO DEVELOP

- Explain the distinguishing characteristics of eukaryotic cells
- Describe internal and external structures of prokaryotic cells in terms of their physical structure, chemical structure, and function
- Identify and describe structures and organelles unique to eukaryotic cells
- Compare and contrast similar structures found in prokaryotic and eukaryotic cells

Eukaryotic organisms include protozoans, algae, fungi, plants, and animals. Some eukaryotic cells are independent, single-celled microorganisms, whereas others are part of multicellular organisms. The cells of eukaryotic organisms have several distinguishing characteristics. Above all, eukaryotic cells are defined by the presence of a nucleus surrounded by a complex nuclear membrane. Also, eukaryotic cells are characterized by the presence of membrane-bound organelles in the cytoplasm. Organelles such as mitochondria, the endoplasmic reticulum (ER), Golgi apparatus, lysosomes, and peroxisomes are held in place by the cytoskeleton, an internal network that supports transport of intracellular components and helps maintain cell shape (Figure 3.2.1). The genome of eukaryotic cells is packaged in multiple, rod-shaped chromosomes as opposed to the single, circular-shaped chromosome that characterizes most prokaryotic cells. Table 3.2.1 compares the characteristics of eukaryotic cell structures with those of bacteria and archaea.

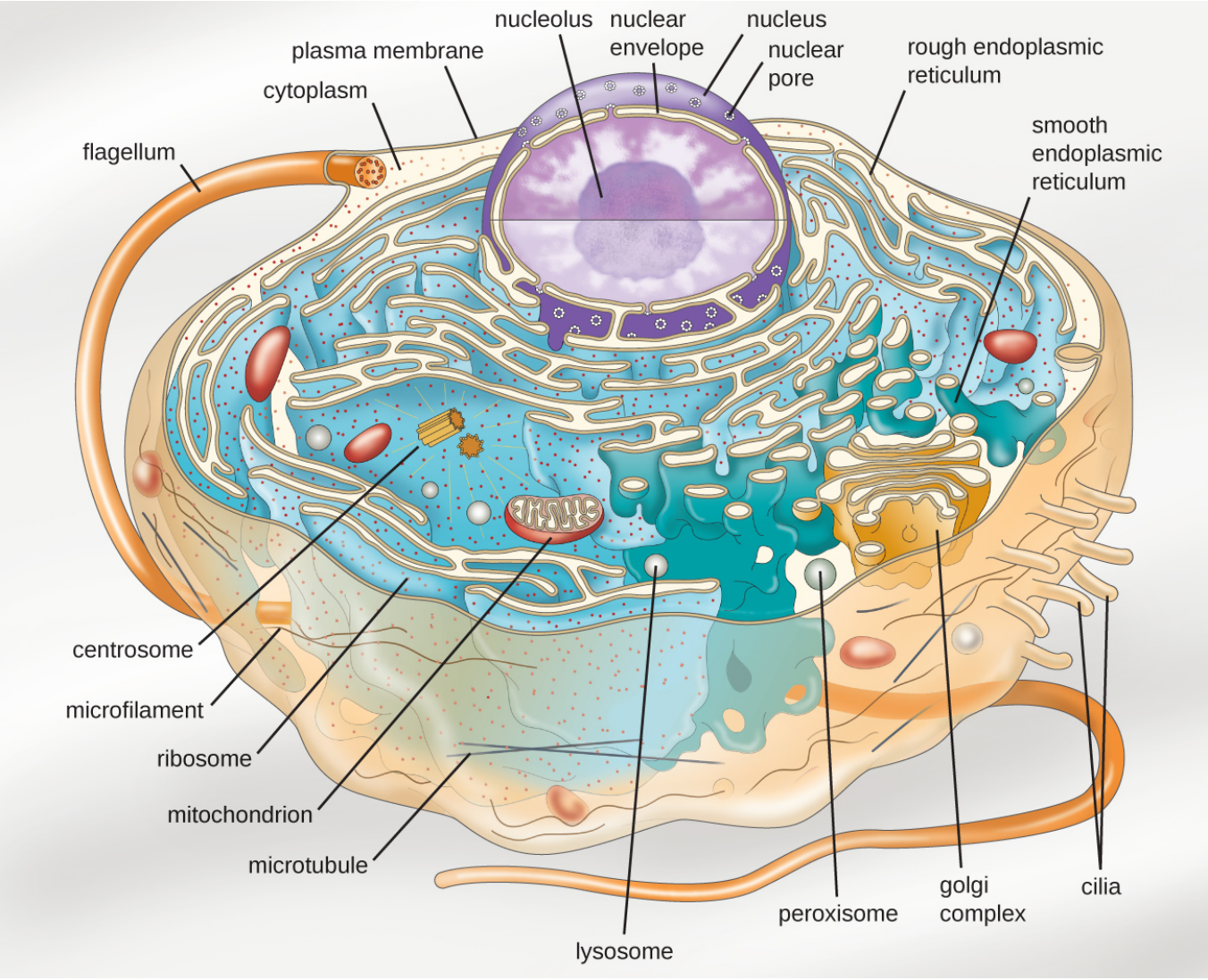


Figure 3.2.1: An illustration of a generalized, single-celled eukaryotic organism. Note that cells of eukaryotic organisms vary greatly in terms of structure and function, and a particular cell may not have all of the structures shown here.

Table 3.2.1***:*** *Summary of Cell Structures.*

https://geo.libretexts.org/@go/page/6193

Cell Structure	Prokaryotes		Eukaryotes
	Bacteria	Archaea	
Size	~0.5–1 μM	~0.5–1 μM	~5–20 μM
Surface area-to-volume ratio	High	High	Low
Nucleus	No	No	Yes
Genome characteristics	• Single chromosome • Circular • Haploid • Lacks histones	• Single chromosome • Circular • Haploid • Contains histones	• Multiple chromosomes • Linear • Haploid or diploid • Contains histones
Cell division	Binary fission	Binary fission	Mitosis, meiosis
Membrane lipid composition	• Ester-linked • Straight-chain fatty acids • Bilayer	• Ether-linked • Branched isoprenoids • Bilayer or monolayer	• Ester-linked • Straight-chain fatty acids • Sterols • Bilayer
Cell wall composition	• Peptidoglycan, or • None	• Pseudopeptidoglycan, or • Glycopeptide, or • Polysaccharide, or • Protein (S-layer), or • None	• Cellulose (plants, some algae) • Chitin (molluscs, insects, crustaceans, and fungi) • Silica (some algae) • Most others lack cell walls
Motility structures	Rigid spiral flagella composed of flagellin	Rigid spiral flagella composed of archaeal flagellins	Flexible flagella and cilia composed of microtubules
Membrane-bound organelles	No	No	Yes
Endomembrane system	No	No	Yes (ER, Golgi, lysosomes)
Ribosomes	70S	70S	• 80S in cytoplasm and rough ER • 70S in mitochondria, chloroplasts

Cell Morphologies

Eukaryotic cells display a wide variety of different cell morphologies. Possible shapes include spheroid, ovoid, cuboidal, cylindrical, flat, lenticular, fusiform, discoidal, crescent, ring stellate, and polygonal (Figure 3.2.2). Some eukaryotic cells are irregular in shape, and some are capable of changing shape. The shape of a particular type of eukaryotic cell may be influenced by factors such as its primary function, the organization of its cytoskeleton, the viscosity of its cytoplasm, the rigidity of its cell membrane or cell wall (if it has one), and the physical pressure exerted on it by the surrounding environment and/or adjoining cells.

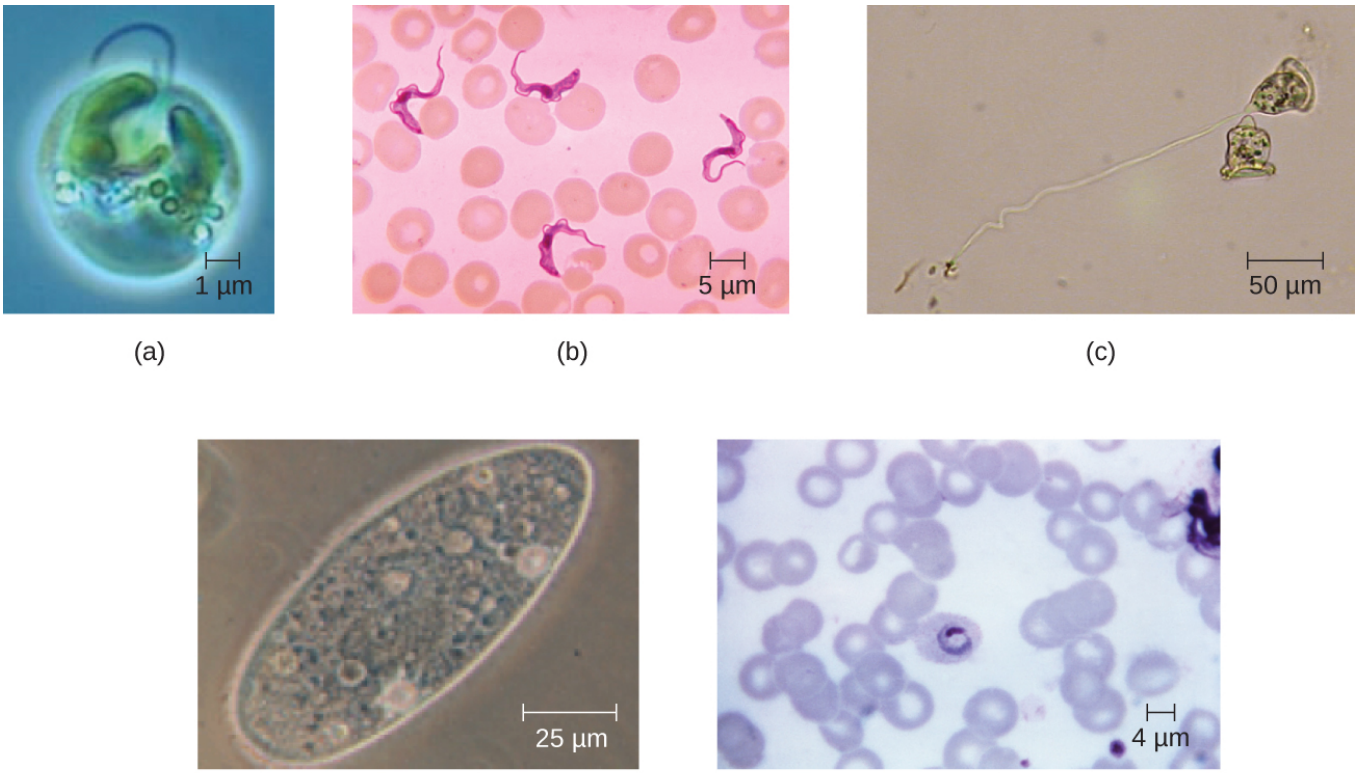


Figure 3.2.2: Eukaryotic cells come in a variety of cell shapes. (a) Spheroid Chromulina alga. (b) Fusiform shaped Trypanosoma. (c) Bell-shaped Vorticella. (d) Ovoid Paramecium. (e) Ring-shaped Plasmodium ovale. (credit a: modification of work by NOAA; credit b, e: modification of work by Centers for Disease Control and Prevention).

Exercise 3.2.1

Identify two differences between eukaryotic and prokaryotic cell.

Nucleus

Unlike prokaryotic cells, in which DNA is loosely contained in the nucleoid region, eukaryotic cells possess a nucleus, which is surrounded by a complex nuclear membrane that houses the DNA genome (Figure 3.2.3). By containing the cell's DNA, the nucleus ultimately controls all activities of the cell and also serves an essential role in reproduction and heredity. Eukaryotic cells typically have their DNA organized into multiple linear chromosomes. The DNA within the nucleus is highly organized and condensed to fit inside the nucleus, which is accomplished by wrapping the DNA around proteins called histones.

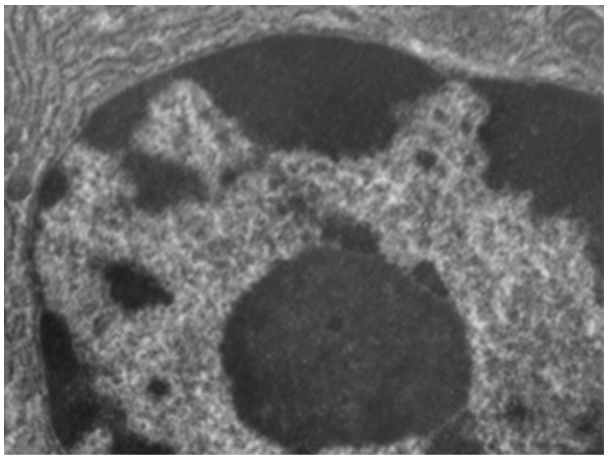


Figure 3.2.3: Eukaryotic cells have a well-defined nucleus. The nucleus of this mammalian lung cell is the large, dark, oval-shaped structure in the lower half of the image.

Although most eukaryotic cells have only one nucleus, exceptions exist. For example, protozoans of the genus *Paramecium* typically have two complete nuclei: a small nucleus that is used for reproduction (micronucleus) and a large nucleus that directs cellular metabolism (macronucleus). Additionally, some fungi transiently form cells with two nuclei, called heterokaryotic cells, during sexual reproduction. Cells whose nuclei divide, but whose cytoplasm does not, are called coenocytes.

The nucleus is bound by a complex nuclear membrane, often called the nuclear envelope, that consists of two distinct lipid bilayers that are contiguous with each other (Figure 3.2.4). Despite these connections between the inner and outer membranes, each membrane contains unique lipids and proteins on its inner and outer surfaces. The nuclear envelope contains nuclear pores, which are large, rosette-shaped protein complexes that control the movement of materials into and out of the nucleus. The overall shape of the nucleus is determined by the nuclear lamina, a meshwork of intermediate filaments found just inside the nuclear envelope membranes. Outside the nucleus, additional intermediate filaments form a looser mesh and serve to anchor the nucleus in position within the cell.

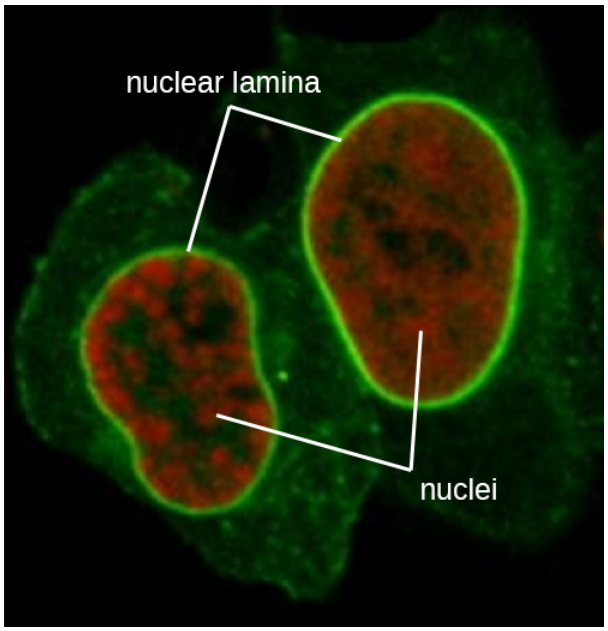


Figure 3.2.4: In this fluorescent microscope image, all the intermediate filaments have been stained with a bright green fluorescent stain. The nuclear lamina is the intense bright green ring around the faint red nuclei.

Nucleolus

The nucleolus is a dense region within the nucleus where ribosomal RNA (rRNA) biosynthesis occurs. In addition, the nucleolus is also the site where assembly of ribosomes begins. Preribosomal complexes are assembled from rRNA and proteins in the

nucleolus; they are then transported out to the cytoplasm, where ribosome assembly is completed (Figure 3.2.5).

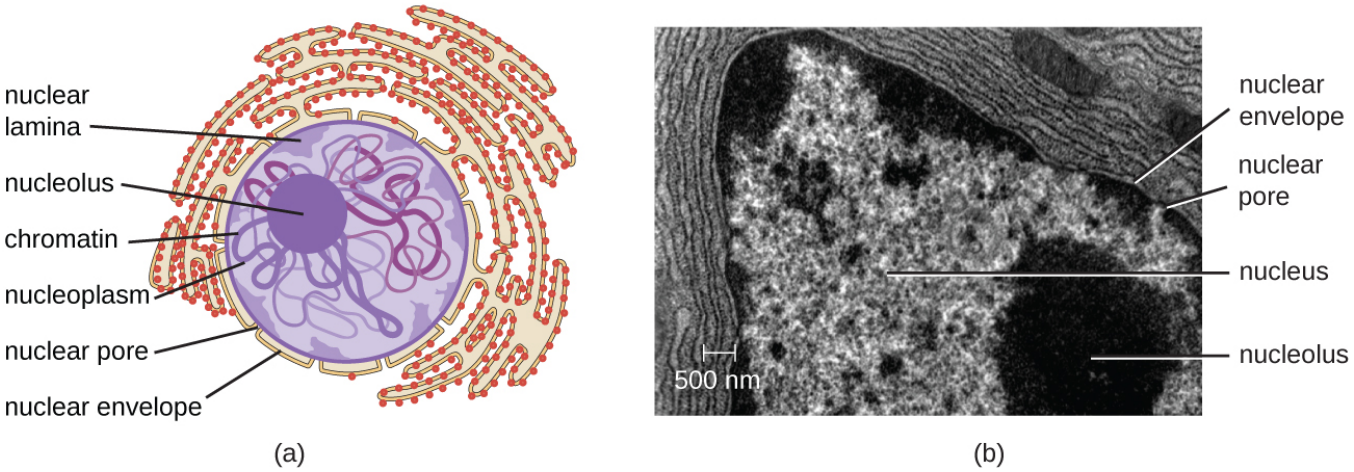


Figure 3.2.5: (a) The nucleolus is the dark, dense area within the nucleus. It is the site of rRNA synthesis and preribosomal assembly. (b) Electron micrograph showing the nucleolus.

Ribosomes

Ribosomes found in eukaryotic organelles such as mitochondria or chloroplasts have 70S ribosomes—the same size as prokaryotic ribosomes. However, nonorganelle-associated ribosomes in eukaryotic cells are 80S ribosomes, composed of a 40S small subunit and a 60S large subunit. In terms of size and composition, this makes them distinct from the ribosomes of prokaryotic cells.

The two types of nonorganelle-associated eukaryotic ribosomes are defined by their location in the cell: free ribosomesand membrane-bound ribosomes. Free ribosomes are found in the cytoplasm and serve to synthesize water-soluble proteins; membrane-bound ribosomes are found attached to the rough endoplasmic reticulum and make proteins for insertion into the cell membrane or proteins destined for export from the cell.

The differences between eukaryotic and prokaryotic ribosomes are clinically relevant because certain antibiotic drugs are designed to target one or the other. For example, cycloheximide targets eukaryotic action, whereas chloramphenicol targets prokaryotic ribosomes.[1] Since human cells are eukaryotic, they generally are not harmed by antibiotics that destroy the prokaryotic ribosomes in bacteria. However, sometimes negative side effects may occur because mitochondria in human cells contain prokaryotic ribosomes.

Endomembrane System

The endomembrane system, unique to eukaryotic cells, is a series of membranous tubules, sacs, and flattened disks that synthesize many cell components and move materials around within the cell (Figure 3.2.6). Because of their larger cell size, eukaryotic cells require this system to transport materials that cannot be dispersed by diffusion alone. The endomembrane system comprises several organelles and connections between them, including the endoplasmic reticulum, Golgi apparatus, lysosomes, and vesicles.

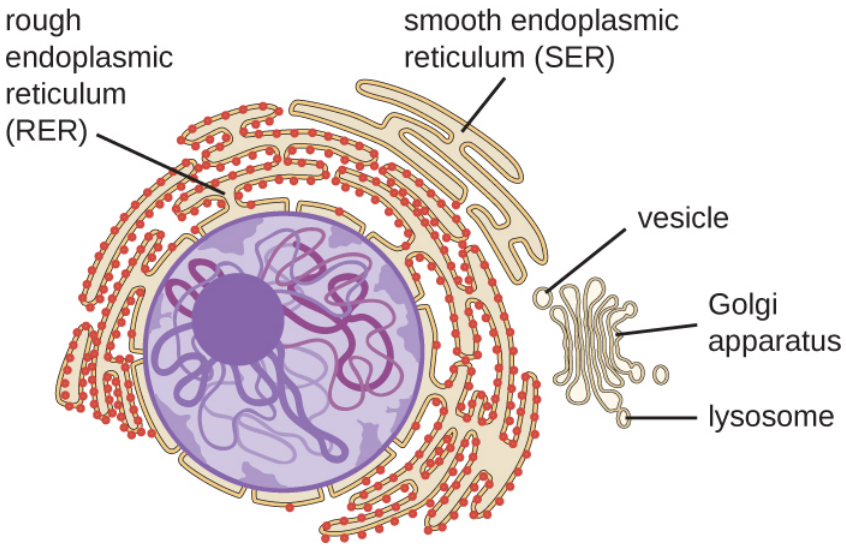


Figure 3.2.6: The endomembrane system is composed of a series of membranous intracellular structures that facilitate movement of materials throughout the cell and to the cell membrane.

Endoplasmic Reticulum

The endoplasmic reticulum (ER) is an interconnected array of tubules and cisternae (flattened sacs) with a single lipid bilayer (Figure 3.2.7). The spaces inside of the cisternae are called lumen of the ER. There are two types of ER, rough endoplasmic reticulum (RER) and smooth endoplasmic reticulum (SER). These two different types of ER are sites for the synthesis of distinctly different types of molecules. RER is studded with ribosomes bound on the cytoplasmic side of the membrane. These ribosomes make proteins destined for the plasma membrane (Figure Runaway argument for \eatSpaces?). Following synthesis, these proteins are inserted into the membrane of the RER. Small sacs of the RER containing these newly synthesized proteins then bud off as transport vesicles and move either to the Golgi apparatus for further processing, directly to the plasma membrane, to the membrane of another organelle, or out of the cell. Transport vesicles are single-lipid, bilayer, membranous spheres with hollow interiors that carry molecules. SER does not have ribosomes and, therefore, appears “smooth.” It is involved in biosynthesis of lipids, carbohydrate metabolism, and detoxification of toxic compounds within the cell.

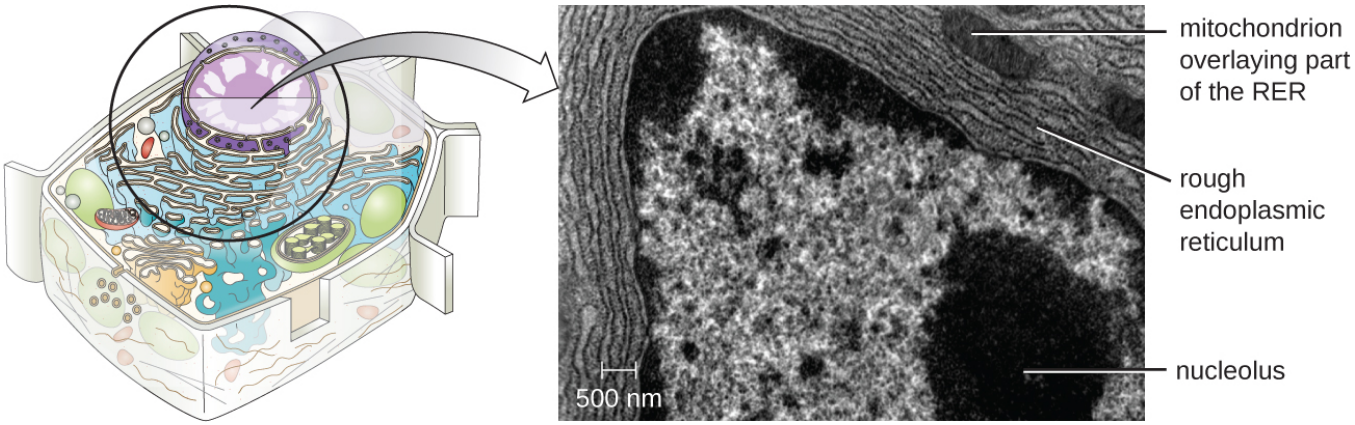


Figure 3.2.7: The rough endoplasmic reticulum is studded with ribosomes for the synthesis of membrane proteins (which give it its rough appearance).

Golgi Apparatus

The Golgi apparatus was discovered within the endomembrane system in 1898 by Italian scientist Camillo Golgi (1843–1926), who developed a novel staining technique that showed stacked membrane structures within the cells of *Plasmodium*, the causative agent of malaria. The Golgi apparatus is composed of a series of membranous disks called dictyosomes, each having a single lipid bilayer, that are stacked together (Figure 3.2.8).

Enzymes in the Golgi apparatus modify lipids and proteins transported from the ER to the Golgi, often adding carbohydrate components to them, producing glycolipids, glycoproteins, or proteoglycans. Glycolipids and glycoproteins are often inserted into the plasma membrane and are important for signal recognition by other cells or infectious particles. Different types of cells can be distinguished from one another by the structure and arrangement of the glycolipids and glycoproteins contained in their plasma membranes. These glycolipids and glycoproteins commonly also serve as cell surface receptors.

Transport vesicles leaving the ER fuse with a Golgi apparatus on its receiving, or *cis*, face. The proteins are processed within the Golgi apparatus, and then additional transport vesicles containing the modified proteins and lipids pinch off from the Golgi apparatus on its outgoing, or *trans*, face. These outgoing vesicles move to and fuse with the plasma membrane or the membrane of other organelles.

Exocytosis is the process by which secretory vesicles (spherical membranous sacs) release their contents to the cell's exterior (Figure 3.2.8). All cells have constitutive secretory pathways in which secretory vesicles transport soluble proteins that are released from the cell continually (constitutively). Certain specialized cells also have regulated secretory pathways, which are used to store soluble proteins in secretory vesicles. Regulated secretion involves substances that are only released in response to certain events or signals. For example, certain cells of the human immune system (e.g., mast cells) secrete histamine in response to the presence of foreign objects or pathogens in the body. Histamine is a compound that triggers various mechanisms used by the immune system to eliminate pathogens.

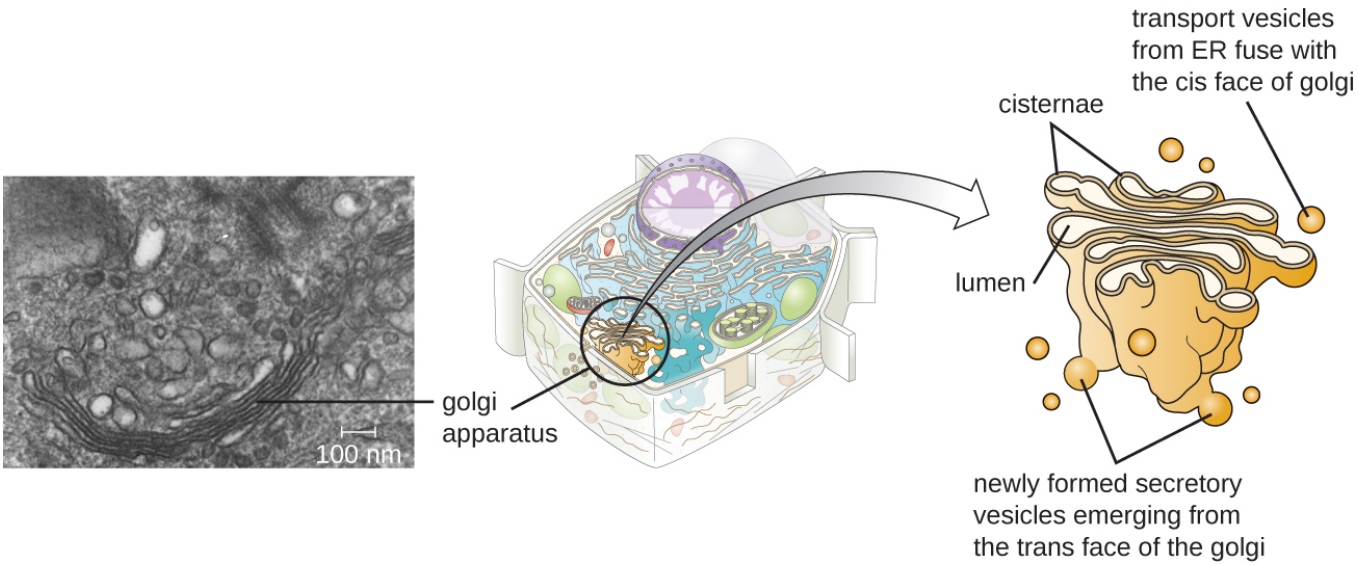


Figure 3.2.8: A transmission electron micrograph (left) of a Golgi apparatus in a white blood cell. The illustration (right) shows the cup-shaped, stacked disks and several transport vesicles. The Golgi apparatus modifies lipids and proteins, producing glycolipids and glycoproteins, respectively, which are commonly inserted into the plasma membrane.

Lysosomes

In the 1960s, Belgian scientist Christian de Duve (1917–2013) discovered lysosomes, membrane-bound organelles of the endomembrane system that contain digestive enzymes. Certain types of eukaryotic cells use lysosomes to break down various particles, such as food, damaged organelles or cellular debris, microorganisms, or immune complexes. Compartmentalization of the digestive enzymes within the lysosome allows the cell to efficiently digest matter without harming the cytoplasmic components of the cell.

Exercise 3.2.2

Name the components of the endomembrane system and describe the function of each component.

Peroxisomes

Christian de Duve is also credited with the discovery of peroxisomes, membrane-bound organelles that are not part of the endomembrane system (Figure 3.2.9). Peroxisomes form independently in the cytoplasm from the synthesis of peroxin proteins by free ribosomes and the incorporation of these peroxin proteins into existing peroxisomes. Growing peroxisomes then divide by a process similar to binary fission.

Peroxisomes were first named for their ability to produce hydrogen peroxide, a highly reactive molecule that helps to break down molecules such as uric acid, amino acids, and fatty acids. Peroxisomes also possess the enzyme catalase, which can degrade hydrogen peroxide. Along with the SER, peroxisomes also play a role in lipid biosynthesis. Like lysosomes, the compartmentalization of these degradative molecules within an organelle helps protect the cytoplasmic contents from unwanted damage.

The peroxisomes of certain organisms are specialized to meet their particular functional needs. For example, glyoxysomes are modified peroxisomes of yeasts and plant cells that perform several metabolic functions, including the production of sugar molecules. Similarly, glycosomes are modified peroxisomes made by certain trypanosomes, the pathogenic protozoans that cause Chagas disease and African sleeping sickness.

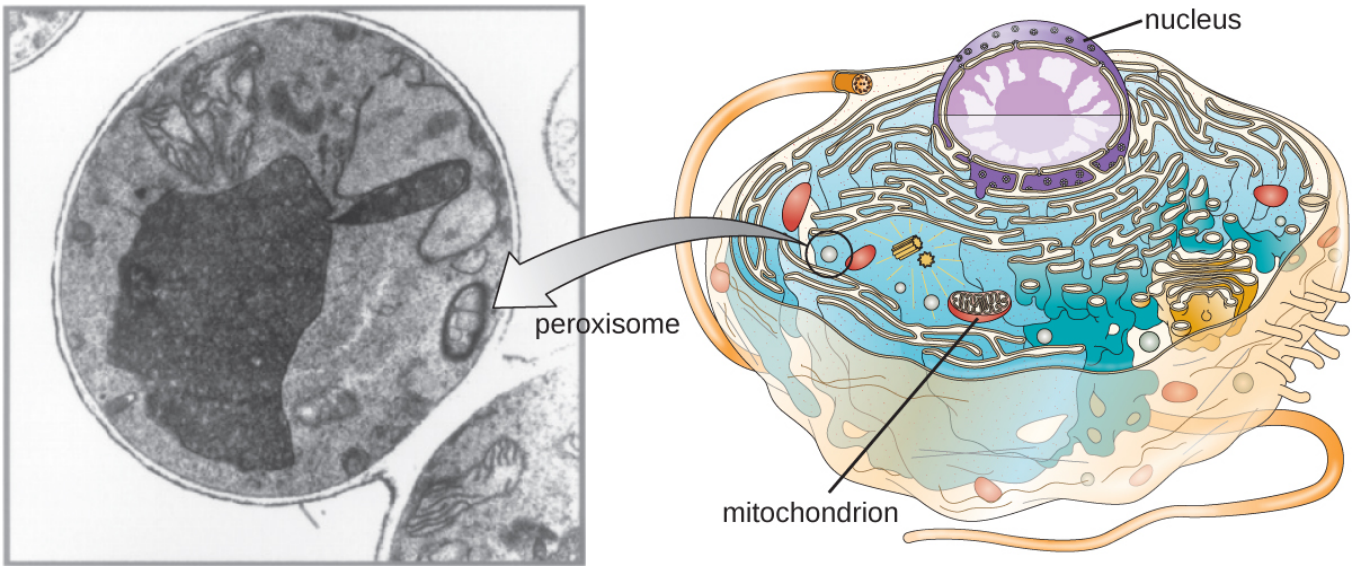


Figure 3.2.9: A transmission electron micrograph (left) of a cell containing a peroxisome. The illustration (right) shows the location of peroxisomes in a cell. These eukaryotic structures play a role in lipid biosynthesis and breaking down various molecules. They may also have other specialized functions depending on the cell type. (credit “micrograph”: modification of work by American Society for Microbiology).

Cytoskeleton

Eukaryotic cells have an internal cytoskeleton made of microfilaments, intermediate filaments, and microtubules. This matrix of fibers and tubes provides structural support as well as a network over which materials can be transported within the cell and on which organelles can be anchored (Figure 3.2.10). For example, the process of exocytosis involves the movement of a vesicle via the cytoskeletal network to the plasma membrane, where it can release its contents.

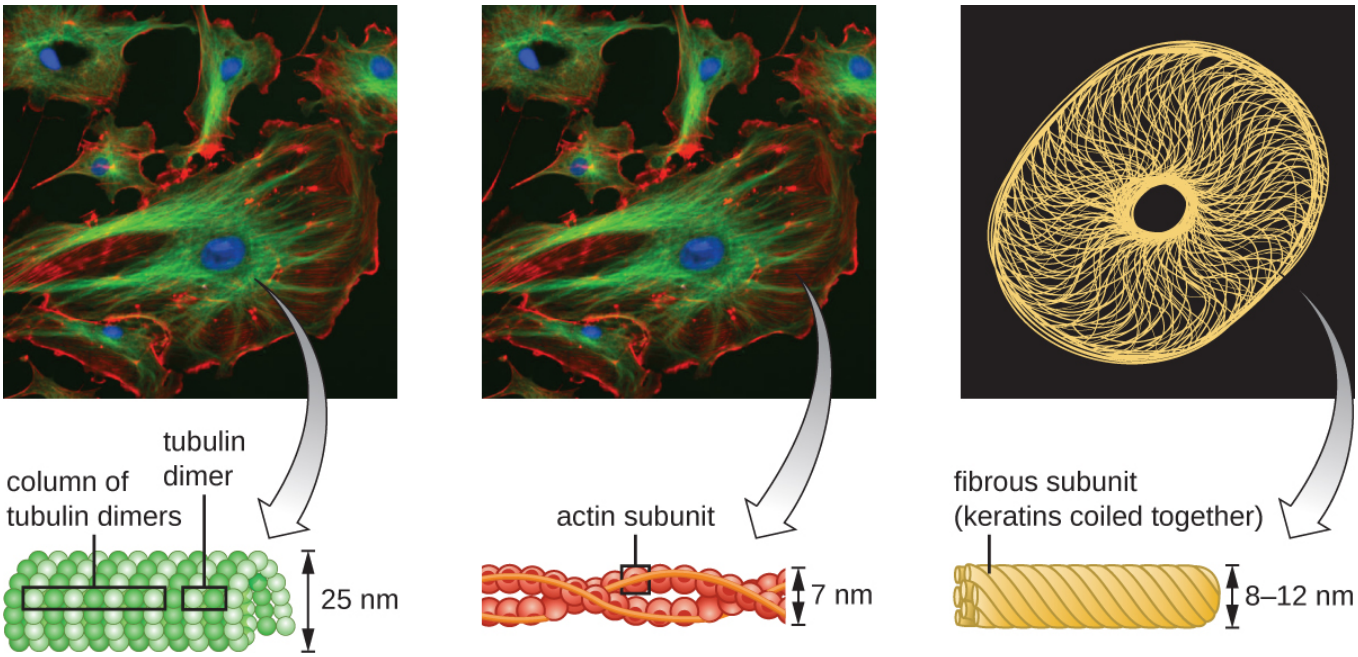


Figure 3.2.10: The cytoskeleton is a network of microfilaments, intermediate filaments, and microtubules found throughout the cytoplasm of a eukaryotic cell. In these fluorescently labeled animal cells, the microtubules are green, the actin microfilaments are red, the nucleus is blue, and keratin (a type of intermediate filament) is yellow.

Microfilaments are composed of two intertwined strands of actin, each composed of actin monomers forming filamentous cables 6 nm in diameter[2] (Figure 3.2.11). The actin filaments work together with motor proteins, like myosin, to effect muscle contraction in animals or the amoeboid movement of some eukaryotic microbes. In ameboid organisms, actin can be found in two forms: a stiffer, polymerized, gel form and a more fluid, unpolymerized soluble form. Actin in the gel form creates stability in the ectoplasm, the gel-like area of cytoplasm just inside the plasma membrane of ameboid protozoans.

Temporary extensions of the cytoplasmic membrane called pseudopodia (meaning “false feet”) are produced through the forward flow of soluble actin filaments into the pseudopodia, followed by the gel-sol cycling of the actin filaments, resulting in cell motility. Once the cytoplasm extends outward, forming a pseudopodium, the remaining cytoplasm flows up to join the leading edge, thereby creating forward locomotion. Beyond amoeboid movement, microfilaments are also involved in a variety of other processes in eukaryotic cells, including cytoplasmic streaming (the movement or circulation of cytoplasm within the cell), cleavage furrow formation during cell division, and muscle movement in animals (Figure 3.2.11). These functions are the result of the dynamic nature of microfilaments, which can polymerize and depolymerize relatively easily in response to cellular signals, and their interactions with molecular motors in different types of eukaryotic cells.

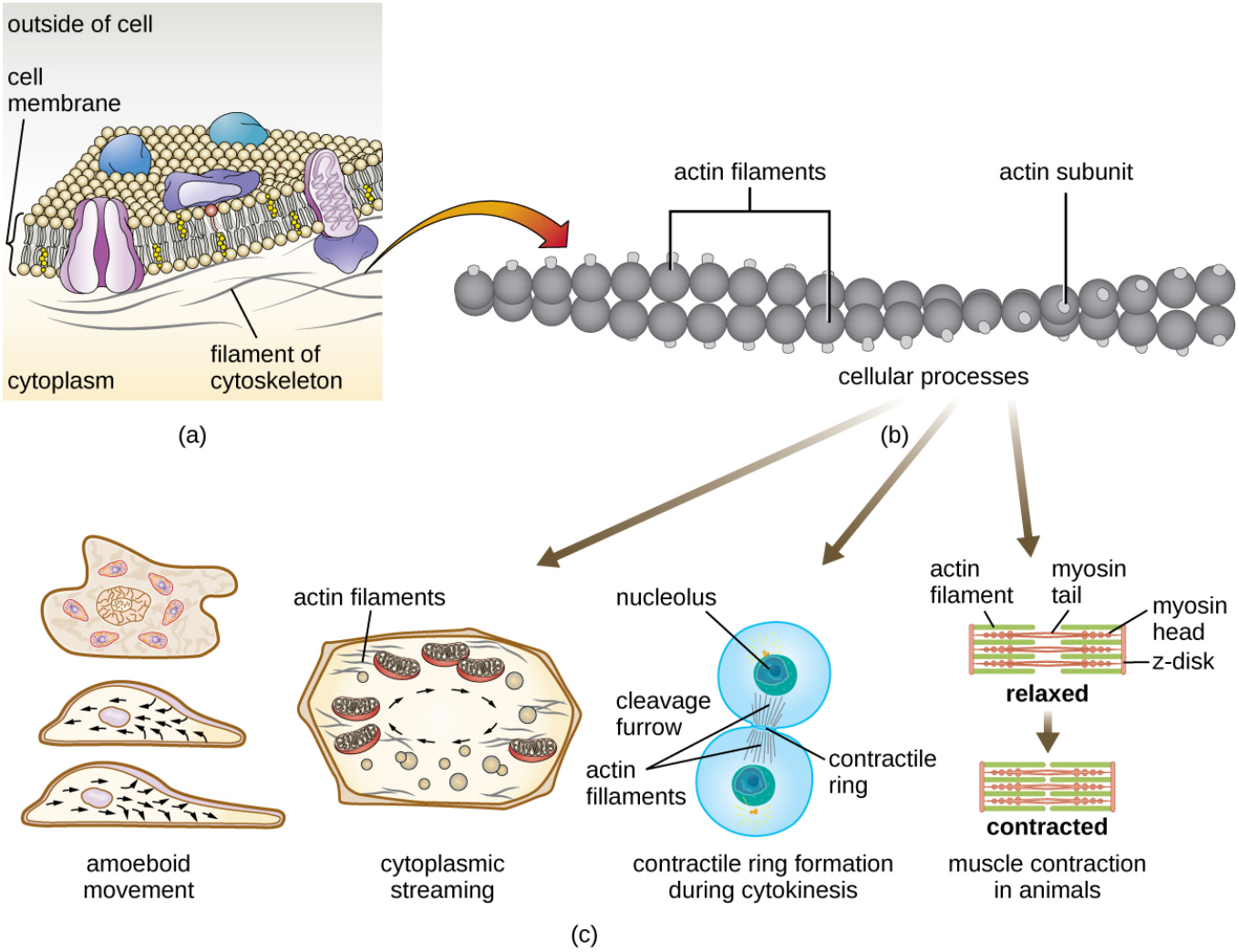


Figure 3.2.11: (a) A microfilament is composed of a pair of actin filaments. (b) Each actin filament is a string of polymerized actin monomers. (c) The dynamic nature of actin, due to its polymerization and depolymerization and its association with myosin, allows microfilaments to be involved in a variety of cellular processes, including ameboid movement, cytoplasmic streaming, contractile ring formation during cell division, and muscle contraction in animals.

Intermediate filaments (Figure 3.2.12) are a diverse group of cytoskeletal filaments that act as cables within the cell. They are termed “intermediate” because their 10-nm diameter is thicker than that of actin but thinner than that of microtubules.[3]They are composed of several strands of polymerized subunits that, in turn, are made up of a wide variety of monomers. Intermediate filaments tend to be more permanent in the cell and maintain the position of the nucleus. They also form the nuclear lamina (lining or layer) just inside the nuclear envelope. Additionally, intermediate filaments play a role in anchoring cells together in animal tissues. The intermediate filament protein desmin is found in desmosomes, the protein structures that join muscle cells together and help them resist external physical forces. The intermediate filament protein keratin is a structural protein found in hair, skin, and nails.

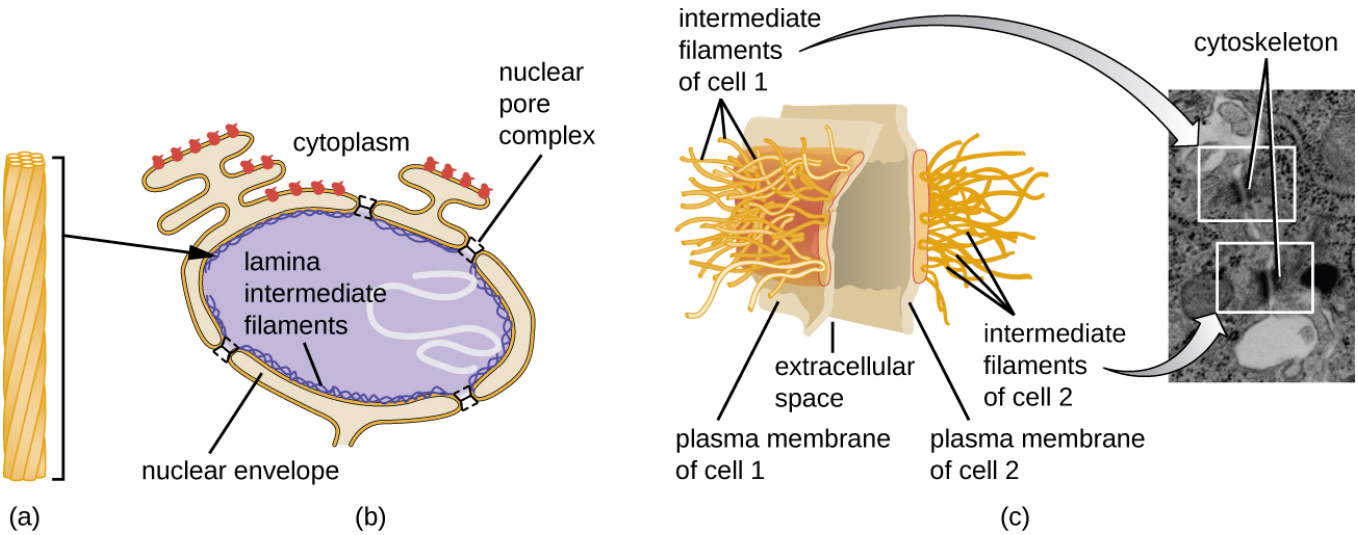


Figure 3.2.12: (a) Intermediate filaments are composed of multiple strands of polymerized subunits. They are more permanent than other cytoskeletal structures and serve a variety of functions. (b) Intermediate filaments form much of the nuclear lamina. (c) Intermediate filaments form the desmosomes between cells in some animal tissues. (credit c "illustration": modification of work by Mariana Ruiz Villareal)

Microtubules (Figure 3.2.13) are a third type of cytoskeletal fiber composed of tubulin dimers (α tubulin and β tubulin). These form hollow tubes 23 nm in diameter that are used as girders within the cytoskeleton.[4] Like microfilaments, microtubules are dynamic and have the ability to rapidly assemble and disassemble. Microtubules also work with motor proteins (such as dynein and kinesin) to move organelles and vesicles around within the cytoplasm. Additionally, microtubules are the main components of eukaryotic flagella and cilia, composing both the filament and the basal body components (Figure 3.2.20).

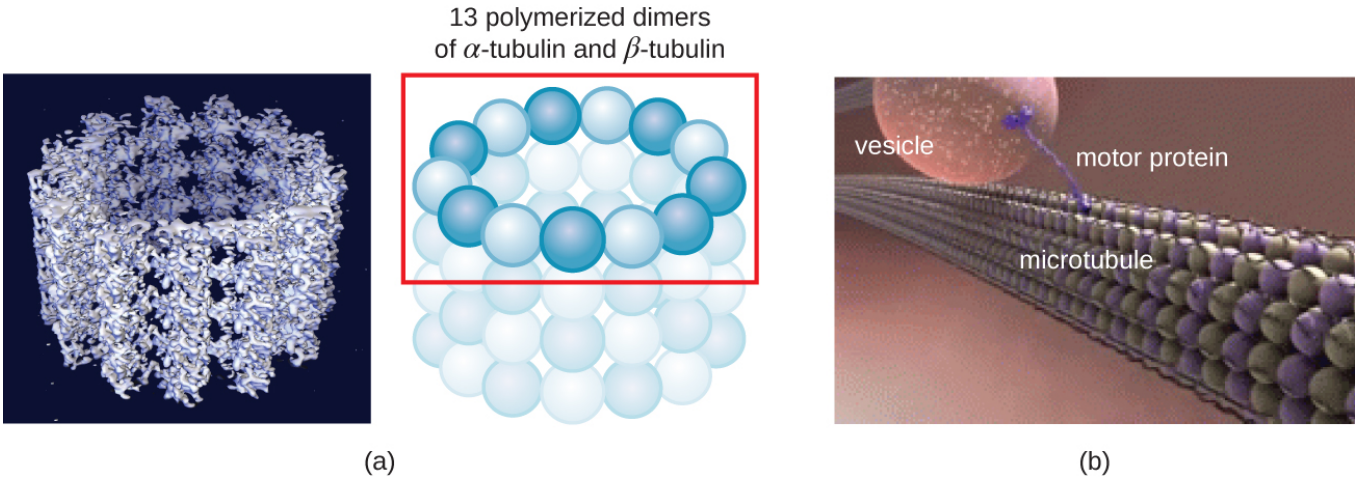


Figure 3.2.13: (a) Microtubules are hollow structures composed of polymerized tubulin dimers. (b) They are involved in several cellular processes, including the movement of organelles throughout the cytoplasm. Motor proteins carry organelles along microtubule tracks that crisscross the entire cell. (credit b: modification of work by National Institute on Aging)

In addition, microtubules are involved in cell division, forming the mitotic spindle that serves to separate chromosomes during mitosis and meiosis. The mitotic spindle is produced by two centrosomes, which are essentially microtubule-organizing centers, at opposite ends of the cell. Each centrosome is composed of a pair of centrioles positioned at right angles to each other, and each centriole is an array of nine parallel microtubules arranged in triplets (Figure 3.2.14).

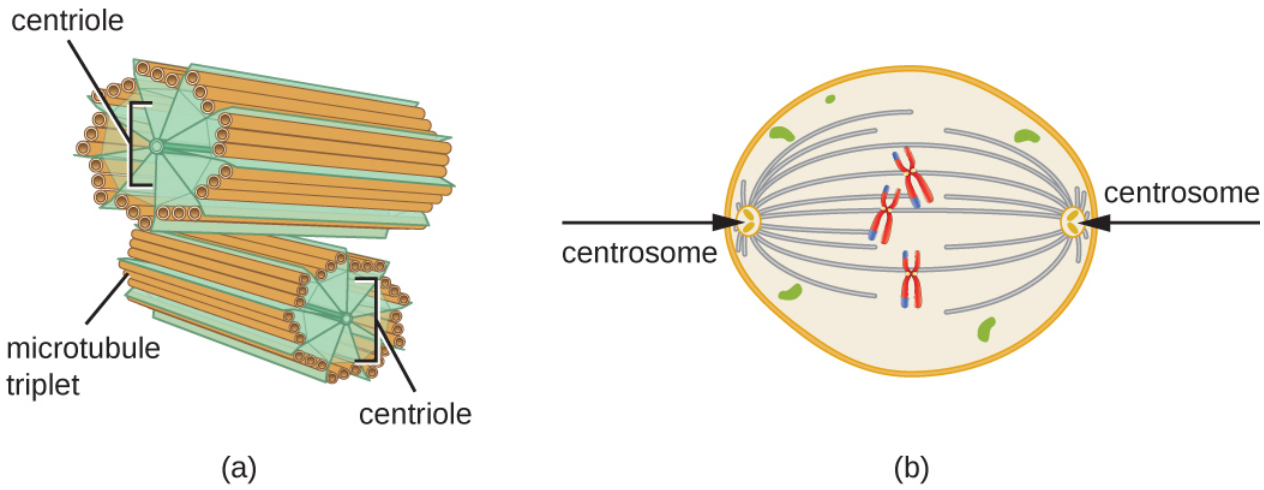


Figure 3.2.14***:*** *(a) A centrosome is composed of two centrioles positioned at right angles to each other. Each centriole is composed of nine triplets of microtubules held together by accessory proteins. (b) In animal cells, the centrosomes (arrows) serve as microtubule-organizing centers of the mitotic spindle during mitosis.*

Exercise 3.2.3

Compare and contrast the three types of cytoskeletal structures described in this section.

Mitochondria

The large, complex organelles in which aerobic cellular respiration occurs in eukaryotic cells are called mitochondria(Figure 3.2.15). The term “mitochondrion” was first coined by German microbiologist Carl Benda in 1898 and was later connected with the process of respiration by Otto Warburg in 1913. Scientists during the 1960s discovered that mitochondria have their own genome and 70S ribosomes. The mitochondrial genome was found to be bacterial, when it was sequenced in 1976. These findings ultimately supported the endosymbiotic theory proposed by Lynn Margulis, which states that mitochondria originally arose through an endosymbiotic event in which a bacterium capable of aerobic cellular respiration was taken up by phagocytosis into a host cell and remained as a viable intracellular component.

Each mitochondrion has two lipid membranes. The outer membrane is a remnant of the original host cell’s membrane structures. The inner membrane was derived from the bacterial plasma membrane. The electron transport chain for aerobic respiration uses integral proteins embedded in the inner membrane. The mitochondrial matrix, corresponding to the location of the original bacterium’s cytoplasm, is the current location of many metabolic enzymes. It also contains mitochondrial DNA and 70S ribosomes. Invaginations of the inner membrane, called cristae, evolved to increase surface area for the location of biochemical reactions. The folding patterns of the cristae differ among various types of eukaryotic cells and are used to distinguish different eukaryotic organisms from each other.

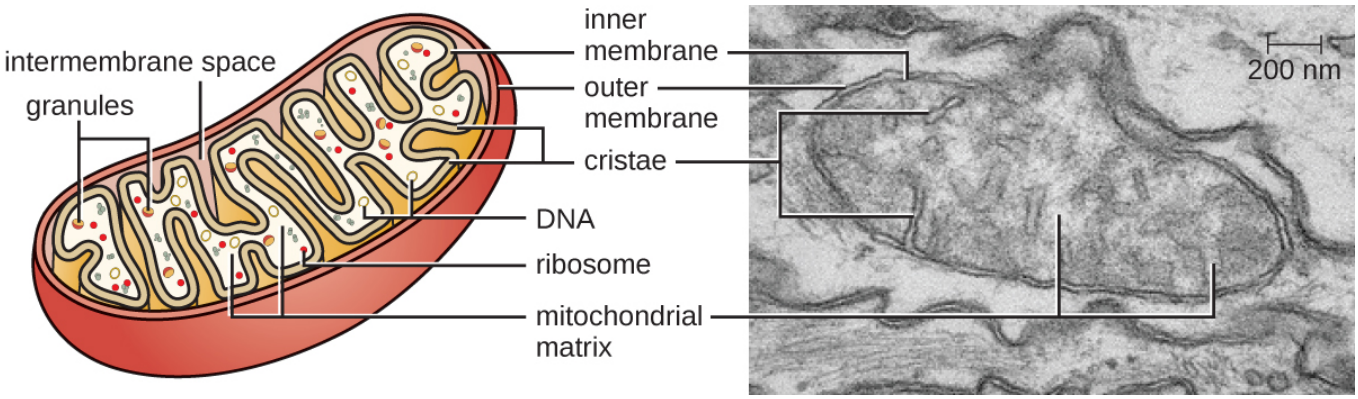


Figure 3.2.15***:*** *Each mitochondrion is surrounded by two membranes, the inner of which is extensively folded into cristae and is the site of the intermembrane space. The mitochondrial matrix contains the mitochondrial DNA, ribosomes, and metabolic enzymes. The transmission electron micrograph of a mitochondrion, on the right, shows both membranes, including cristae and the mitochondrial matrix. (credit "micrograph": modification of work by Matthew Britton; scale-bar data from Matt Russell)*

Chloroplasts

Plant cells and algal cells contain chloroplasts, the organelles in which photosynthesis occurs (Figure 3.2.16). All chloroplasts have at least three membrane systems: the outer membrane, the inner membrane, and the thylakoid membrane system. Inside the outer and inner membranes is the chloroplast stroma, a gel-like fluid that makes up much of a chloroplast's volume, and in which the thylakoid system floats. The thylakoid system is a highly dynamic collection of folded membrane sacs. It is where the green photosynthetic pigment chlorophyll is found and the light reactions of photosynthesis occur. In most plant chloroplasts, the thylakoids are arranged in stacks called grana (singular: granum), whereas in some algal chloroplasts, the thylakoids are free floating.

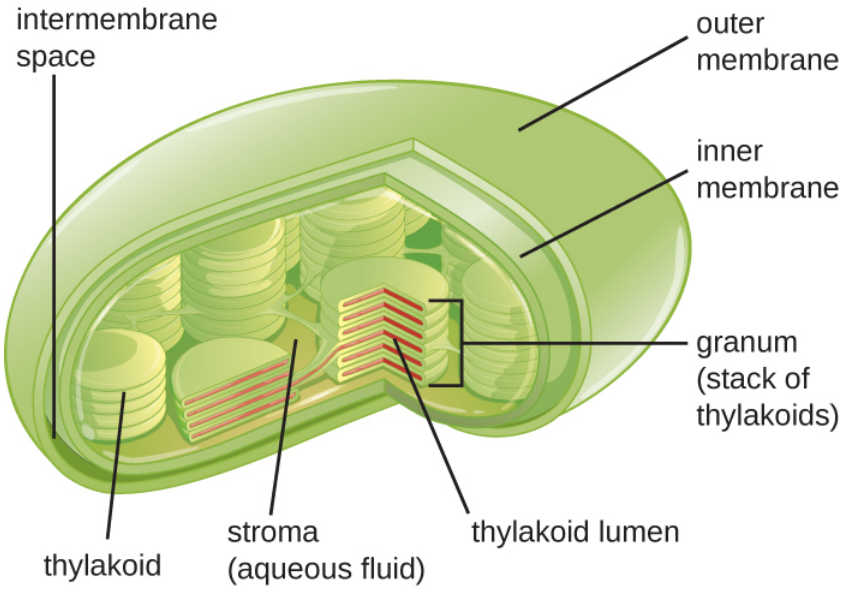


Figure 3.2.16***:*** *Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.*

Other organelles similar to mitochondria have arisen in other types of eukaryotes, but their roles differ. Hydrogenosomes are found in some anaerobic eukaryotes and serve as the location of anaerobic hydrogen production. Hydrogenosomes typically lack their own DNA and ribosomes. Kinetoplasts are a variation of the mitochondria found in some eukaryotic pathogens. In these organisms,

each cell has a single, long, branched mitochondrion in which kinetoplast DNA, organized as multiple circular pieces of DNA, is found concentrated at one pole of the cell.

MITOCHONDRIA-RELATED ORGANELLES IN PROTOZOAN PARASITES

Many protozoans, including several protozoan parasites that cause infections in humans, can be identified by their unusual appearance. Distinguishing features may include complex cell morphologies, the presence of unique organelles, or the absence of common organelles. The protozoan parasites *Giardia lamblia* and *Trichomonas vaginalis* are two examples.

G. lamblia, a frequent cause of diarrhea in humans and many other animals, is an anaerobic parasite that possesses two nuclei and several flagella. Its Golgi apparatus and endoplasmic reticulum are greatly reduced, and it lacks mitochondria completely. However, it does have organelles known as mitosomes, double-membrane-bound organelles that appear to be severely reduced mitochondria. This has led scientists to believe that *G. lamblia*'s ancestors once possessed mitochondria that evolved to become mitosomes. *T. vaginalis*, which causes the sexually transmitted infection vaginitis, is another protozoan parasite that lacks conventional mitochondria. Instead, it possesses hydrogenosomes, mitochondrial-related, double-membrane-bound organelles that produce molecular hydrogen used in cellular metabolism. Scientists believe that hydrogenosomes, like mitosomes, also evolved from mitochondria.[5]

Plasma Membrane

The plasma membrane of eukaryotic cells is similar in structure to the prokaryotic plasma membrane in that it is composed mainly of phospholipids forming a bilayer with embedded peripheral and integral proteins (Figure 3.2.17). These membrane components move within the plane of the membrane according to the fluid mosaic model. However, unlike the prokaryotic membrane, eukaryotic membranes contain sterols, including cholesterol, that alter membrane fluidity. Additionally, many eukaryotic cells contain some specialized lipids, including sphingolipids, which are thought to play a role in maintaining membrane stability as well as being involved in signal transduction pathways and cell-to-cell communication.

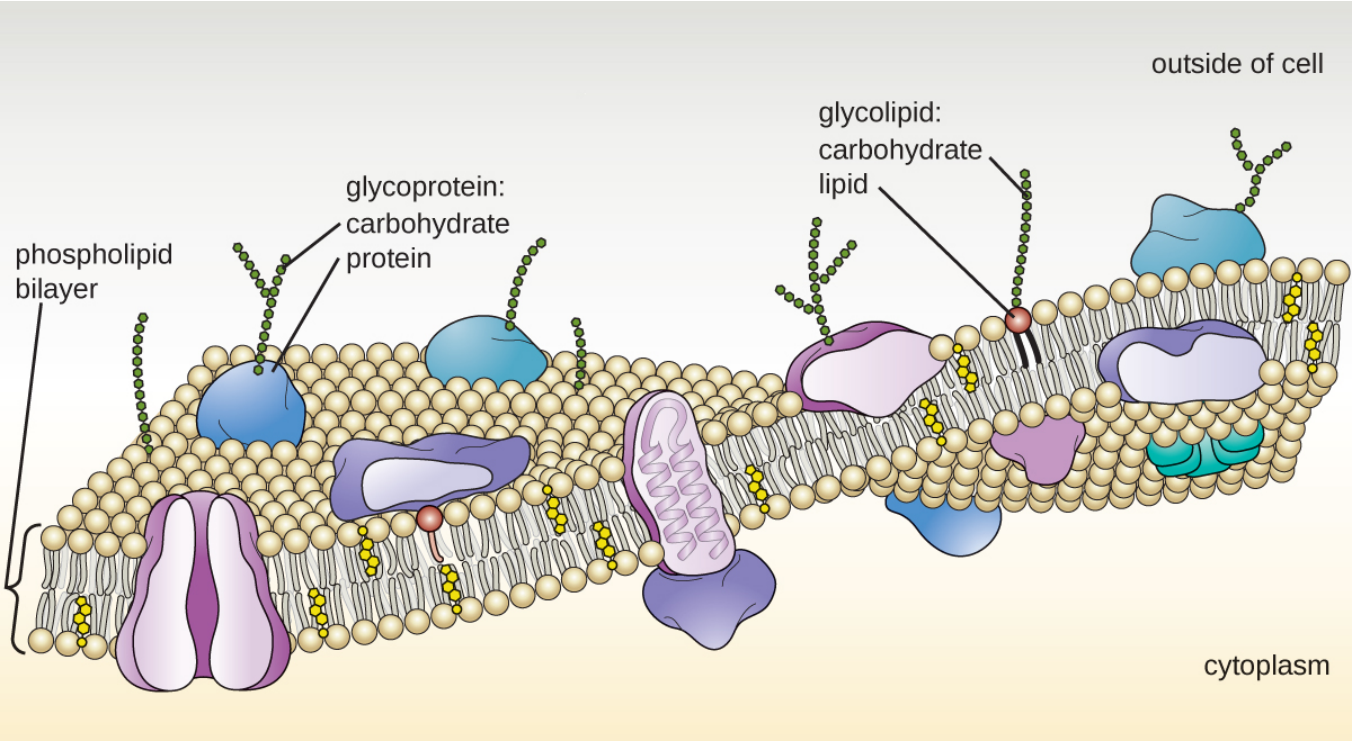


Figure 3.2.17: The eukaryotic plasma membrane is composed of a lipid bilayer with many embedded or associated proteins. It contains cholesterol for the maintenance of membrane, as well as glycoproteins and glycolipids that are important in the recognition other cells or pathogens.

Membrane Transport Mechanisms

The processes of simple diffusion, facilitated diffusion, and active transport are used in both eukaryotic and prokaryotic cells. However, eukaryotic cells also have the unique ability to perform various types of endocytosis, the uptake of matter through plasma membrane invagination and vacuole/vesicle formation (Figure 3.2.18). A type of endocytosis involving the engulfment of large particles through membrane invagination is called phagocytosis, which means “cell eating.” In phagocytosis, particles (or other cells) are enclosed in a pocket within the membrane, which then pinches off from the membrane to form a vacuole that completely surrounds the particle. Another type of endocytosis is called pinocytosis, which means “cell drinking.” In pinocytosis, small, dissolved materials and liquids are taken into the cell through small vesicles. Saprophytic fungi, for example, obtain their nutrients from dead and decaying matter largely through pinocytosis.

Receptor-mediated endocytosis is a type of endocytosis that is initiated by specific molecules called ligands when they bind to cell surface receptors on the membrane. Receptor-mediated endocytosis is the mechanism that peptide and amine-derived hormones use to enter cells and is also used by various viruses and bacteria for entry into host cells.

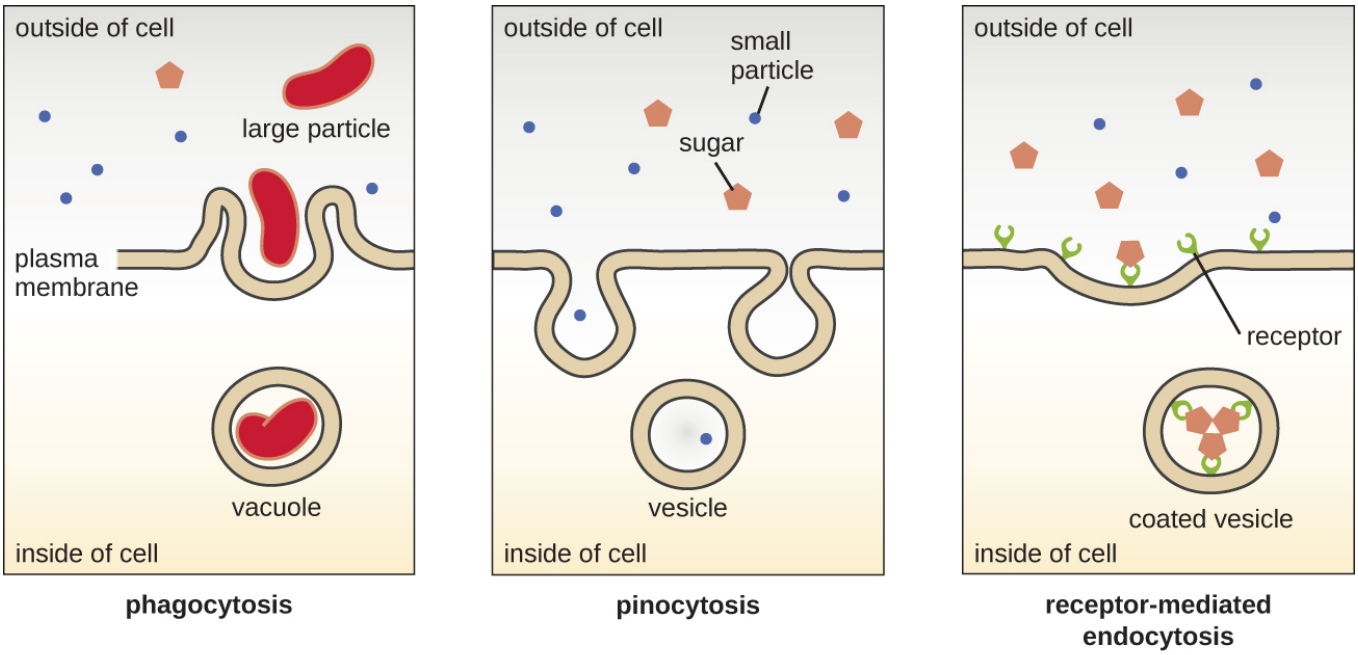


Figure 3.2.18: Three variations of endocytosis are shown. (a) In phagocytosis, the cell membrane surrounds the particle and pinches off to form an intracellular vacuole. (b) In pinocytosis, the cell membrane surrounds a small volume of fluid and pinches off, forming a vesicle. (c) In receptor-mediated endocytosis, the uptake of substances is targeted to a specific substance (a ligand) that binds at the receptor on the external cell membrane. (credit: modification of work by Mariana Ruiz Villarreal)

The process by which secretory vesicles release their contents to the cell's exterior is called exocytosis. Vesicles move toward the plasma membrane and then meld with the membrane, ejecting their contents out of the cell. Exocytosis is used by cells to remove waste products and may also be used to release chemical signals that can be taken up by other cells.

Cell Wall

In addition to a plasma membrane, some eukaryotic cells have a cell wall. Cells of fungi, algae, plants, and even some protists have cell walls. Depending upon the type of eukaryotic cell, cell walls can be made of a wide range of materials, including cellulose (fungi and plants); biogenic silica, calcium carbonate, agar, and carrageenan (protists and algae); or chitin (fungi). In general, all cell walls provide structural stability for the cell and protection from environmental stresses such as desiccation, changes in osmotic pressure, and traumatic injury.[6]

Extracellular Matrix

Cells of animals and some protozoans do not have cell walls to help maintain shape and provide structural stability. Instead, these types of eukaryotic cells produce an extracellular matrix for this purpose. They secrete a sticky mass of carbohydrates and proteins into the spaces between adjacent cells (Figure 3.2.19). Some protein components assemble into a basement membrane to which the remaining extracellular matrix components adhere. Proteoglycans typically form the bulky mass of the extracellular matrix while fibrous proteins, like collagen, provide strength. Both proteoglycans and collagen are attached to fibronectin proteins, which, in turn, are attached to integrin proteins. These integrin proteins interact with transmembrane proteins in the plasma membranes of eukaryotic cells that lack cell walls.

In animal cells, the extracellular matrix allows cells within tissues to withstand external stresses and transmits signals from the outside of the cell to the inside. The amount of extracellular matrix is quite extensive in various types of connective tissues, and variations in the extracellular matrix can give different types of tissues their distinct properties. In addition, a host cell's extracellular matrix is often the site where microbial pathogens attach themselves to establish infection. For example, *Streptococcus pyogenes*, the bacterium that causes strep throat and various other infections, binds to fibronectin in the extracellular matrix of the cells lining the oropharynx (upper region of the throat).

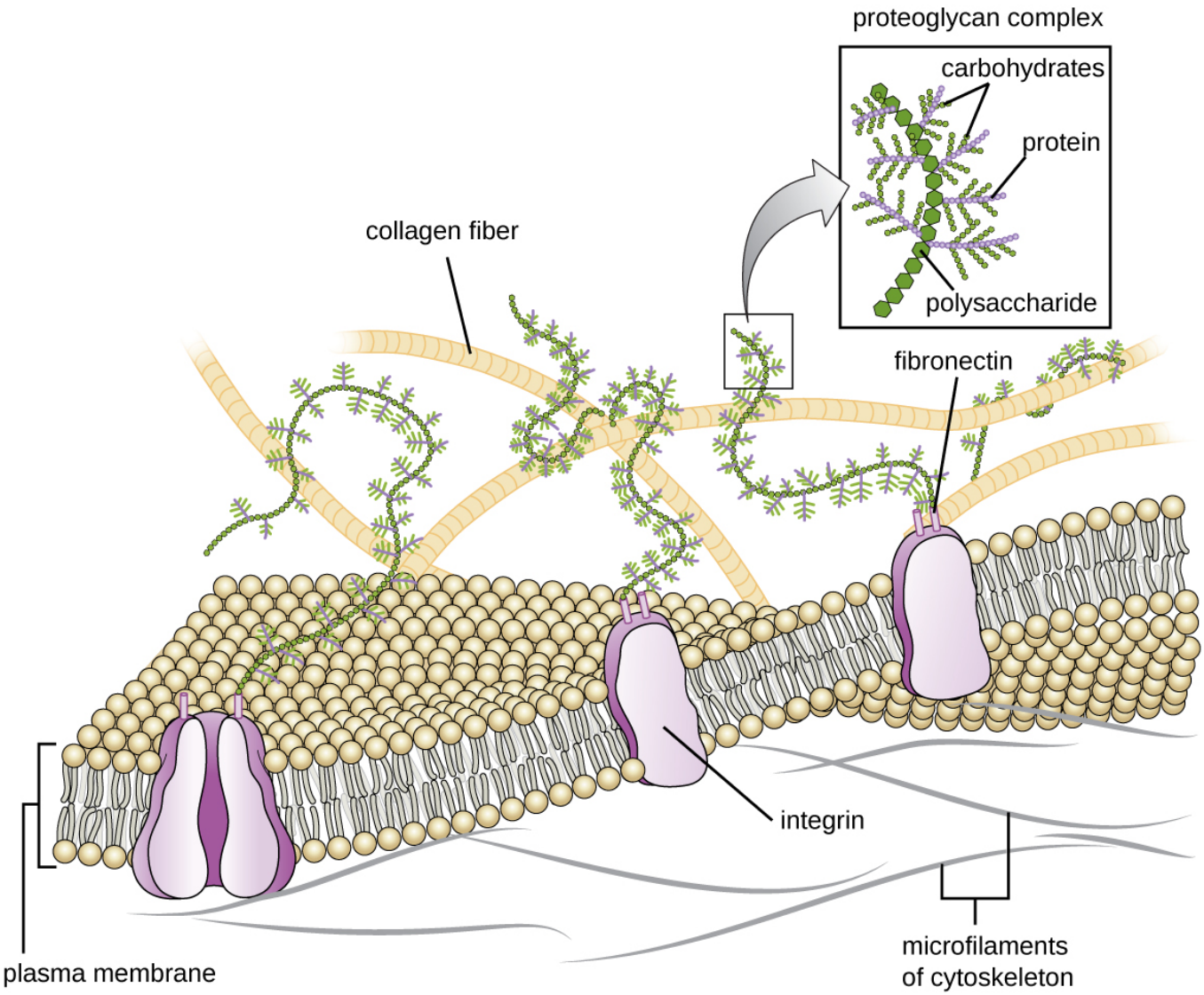


Figure 3.2.19: The extracellular matrix is composed of protein and carbohydrate components. It protects cells from physical stresses and transmits signals arriving at the outside edges of the tissue to cells deeper within the tissue.

Flagella and Cilia

Some eukaryotic cells use flagella for locomotion; however, eukaryotic flagella are structurally distinct from those found in prokaryotic cells. Whereas the prokaryotic flagellum is a stiff, rotating structure, a eukaryotic flagellum is more like a flexible whip composed of nine parallel pairs of microtubules surrounding a central pair of microtubules. This arrangement is referred to as a 9+2 array (Figure 3.2.20). The parallel microtubules use dynein motor proteins to move relative to each other, causing the flagellum to bend.

Cilia (singular: **cilium**) are a similar external structure found in some eukaryotic cells. Unique to eukaryotes, cilia are shorter than flagella and often cover the entire surface of a cell; however, they are structurally similar to flagella (a 9+2 array of microtubules) and use the same mechanism for movement. A structure called a basal body is found at the base of each cilium and flagellum. The basal body, which attaches the cilium or flagellum to the cell, is composed of an array of triplet microtubules similar to that of a centriole but embedded in the plasma membrane. Because of their shorter length, cilia use a rapid, flexible, waving motion. In addition to motility, cilia may have other functions such as sweeping particles past or into cells. For example, ciliated protozoans use the sweeping of cilia to move food particles into their mouthparts, and ciliated cells in the mammalian respiratory tract beat in synchrony to sweep mucus and debris up and out of the lungs (Figure 3.2.20).

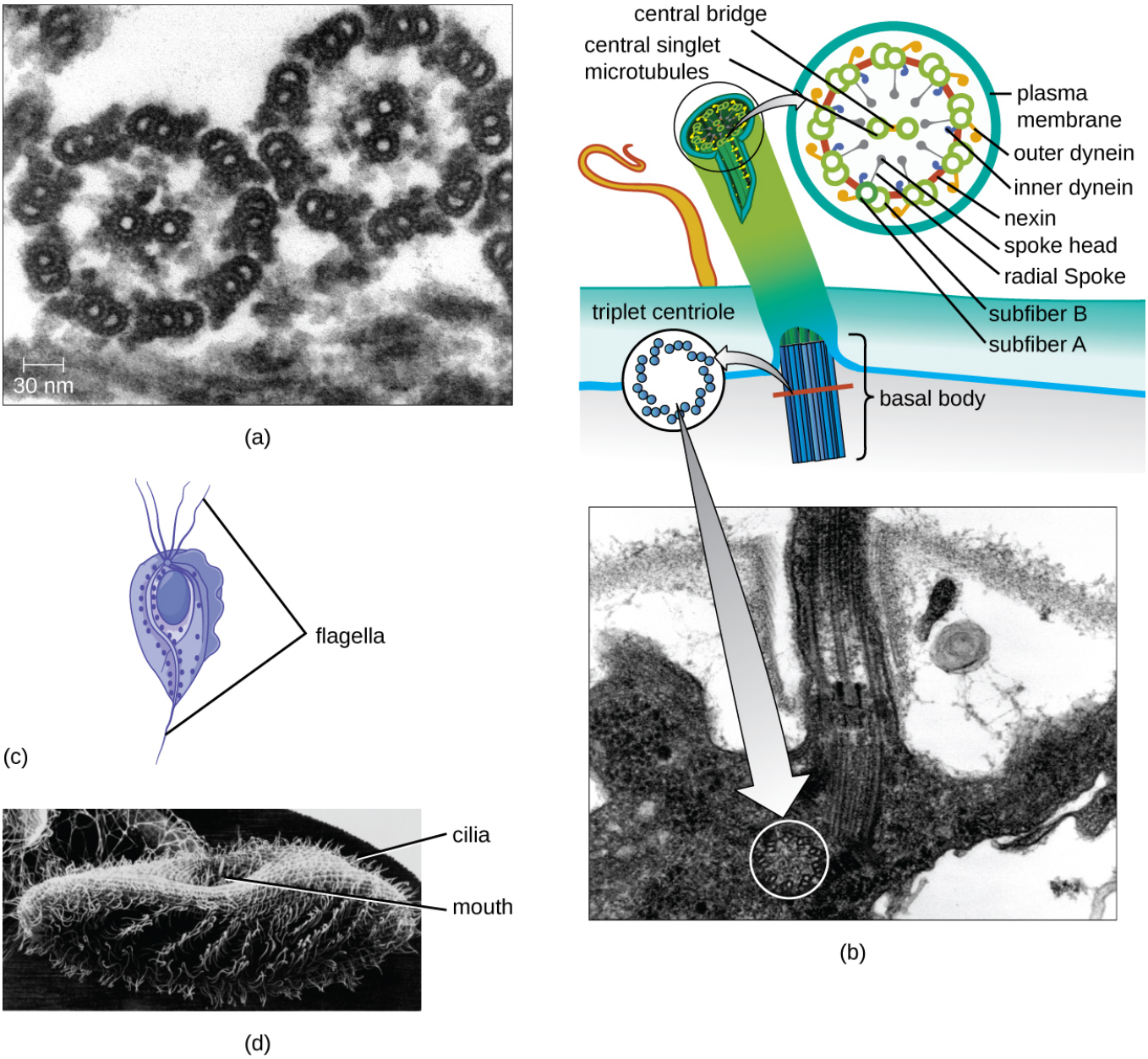


Figure 3.2.20: (a) Eukaryotic flagella and cilia are composed of a 9+2 array of microtubules, as seen in this transmission electron micrograph cross-section. (b) The sliding of these microtubules relative to each other causes a flagellum to bend. (c) An illustration of Trichomonas vaginalis, a flagellated protozoan parasite that causes vaginitis. (d) Many protozoans, like this Paramecium, have numerous cilia that aid in locomotion as well as in feeding. Note the mouth opening shown here. (credit d: modification of work by University of Vermont/National Institutes of Health)

Exercise 3.2.4

1. Explain how the cellular envelope of eukaryotic cells compares to that of prokaryotic cells.
2. Explain the difference between eukaryotic and prokaryotic flagella.

Resolution

Since amoxicillin has not resolved Barbara's case of pneumonia, the PA prescribes another antibiotic, azithromycin, which targets bacterial ribosomes rather than peptidoglycan. After taking the azithromycin as directed, Barbara's symptoms resolve and she finally begins to feel like herself again. Presuming no drug resistance to amoxicillin was involved, and given the

effectiveness of azithromycin, the causative agent of Barbara's pneumonia is most likely *Mycoplasma pneumoniae*. Even though this bacterium is a prokaryotic cell, it is not inhibited by amoxicillin because it does not have a cell wall and, therefore, does not make peptidoglycan.

Key Concepts and Summary

- Eukaryotic cells are defined by the presence of a **nucleus** containing the DNA genome and bound by a **nuclear membrane** (or **nuclear envelope**) composed of two lipid bilayers that regulate transport of materials into and out of the nucleus through nuclear pores.
- Eukaryotic cell morphologies vary greatly and may be maintained by various structures, including the cytoskeleton, the cell membrane, and/or the cell wall
- The **nucleolus**, located in the nucleus of eukaryotic cells, is the site of ribosomal synthesis and the first stages of ribosome assembly.
- Eukaryotic cells contain **80S ribosomes** in the rough endoplasmic reticulum (**membrane bound-ribosomes**) and cytoplasm (**free ribosomes**). They contain 70s ribosomes in mitochondria and chloroplasts.
- Eukaryotic cells have evolved an **endomembrane** system, containing membrane-bound organelles involved in transport. These include vesicles, the endoplasmic reticulum, and the Golgi apparatus.
- The **smooth endoplasmic reticulum** plays a role in lipid biosynthesis, carbohydrate metabolism, and detoxification of toxic compounds. The **rough endoplasmic reticulum** contains membrane-bound 80S ribosomes that synthesize proteins destined for the cell membrane
- The **Golgi apparatus** processes proteins and lipids, typically through the addition of sugar molecules, producing glycoproteins or glycolipids, components of the plasma membrane that are used in cell-to-cell communication.
- **Lysosomes** contain digestive enzymes that break down small particles ingested by **endocytosis**, large particles or cells ingested by **phagocytosis**, and damaged intracellular components.
- The **cytoskeleton**, composed of **microfilaments**, **intermediate filaments**, and **microtubules**, provides structural support in eukaryotic cells and serves as a network for transport of intracellular materials.
- **Centrosomes** are microtubule-organizing centers important in the formation of the mitotic spindle in mitosis.
- **Mitochondria** are the site of cellular respiration. They have two membranes: an outer membrane and an inner membrane with cristae. The mitochondrial matrix, within the inner membrane, contains the mitochondrial DNA, 70S ribosomes, and metabolic enzymes.
- The plasma membrane of eukaryotic cells is structurally similar to that found in prokaryotic cells, and membrane components move according to the fluid mosaic model. However, eukaryotic membranes contain sterols, which alter membrane fluidity, as well as glycoproteins and glycolipids, which help the cell recognize other cells and infectious particles.
- In addition to active transport and passive transport, eukaryotic cell membranes can take material into the cell via **endocytosis**, or expel matter from the cell via **exocytosis.**
- Cells of fungi, algae, plants, and some protists have a **cell wall,** whereas cells of animals and some protozoans have a sticky **extracellular matrix** that provides structural support and mediates cellular signaling.
- Eukaryotic flagella are structurally distinct from prokaryotic flagella but serve a similar purpose (locomotion). **Cilia**are structurally similar to eukaryotic flagella, but shorter; they may be used for locomotion, feeding, or movement of extracellular particles.

Footnotes

1. 1 A.E. Barnhill, M.T. Brewer, S.A. Carlson. "Adverse Effects of Antimicrobials via Predictable or Idiosyncratic Inhibition of Host Mitochondrial Components." *Antimicrobial Agents and Chemotherapy* 56 no. 8 (2012):4046–4051.
2. 2 Fuchs E, Cleveland DW. "A Structural Scaffolding of Intermediate Filaments in Health and Disease." *Science* 279 no. 5350 (1998):514–519.
3. 3 E. Fuchs, D.W. Cleveland. "A Structural Scaffolding of Intermediate Filaments in Health and Disease." *Science* 279 no. 5350 (1998):514–519.
4. 4 E. Fuchs, D.W. Cleveland. "A Structural Scaffolding of Intermediate Filaments in Health and Disease." *Science* 279 no. 5350 (1998):514–519.

5. 5 N. Yarlett, J.H.P. Hackstein. “Hydrogenosomes: One Organelle, Multiple Origins.” *BioScience* 55 no. 8 (2005):657–658.
6. 6 M. Dudzick. “Protists.” OpenStax CNX. November 27, 2013. http://cnx.org/contents/f7048bb6-e46...ef291cf7049c@1

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 3.2: Unique Characteristics of Eukaryotic Cells is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

3.3: Viruses

Viral structure and reproduction are different than for cellular life.

3.3: Viruses is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

3.3A: Viruses

Skills to Develop

- Describe the general characteristics of viruses as pathogens
- Describe viral genomes
- Describe the general characteristics of viral life cycles
- Differentiate among bacteriophages, plant viruses, and animal viruses
- Describe the characteristics used to identify viruses as obligate intracellular parasites

Clinical Focus - PART 1

David, a 45-year-old journalist, has just returned to the U.S. from travels in Russia, China, and Africa. He is not feeling well, so he goes to his general practitioner complaining of weakness in his arms and legs, fever, headache, noticeable agitation, and minor discomfort. He thinks it may be related to a dog bite he suffered while interviewing a Chinese farmer. He is experiencing some prickling and itching sensations at the site of the bite wound, but he tells the doctor that the dog seemed healthy and that he had not been concerned until now. The doctor ordered a culture and sensitivity test to rule out bacterial infection of the wound, and the results came back negative for any possible pathogenic bacteria.

Exercise 3.3*A*.1

1. Based on this information, what additional tests should be performed on the patient?
2. What type of treatment should the doctor recommend?

Despite their small size, which prevented them from being seen with light microscopes, the discovery of a filterable component smaller than a bacterium that causes tobacco mosaic disease (TMD) dates back to 1892.[1] At that time, Dmitri Ivanovski, a Russian botanist, discovered the source of TMD by using a porcelain filtering device first invented by Charles Chamberland and Louis Pasteur in Paris in 1884. Porcelain Chamberland filters have a pore size of 0.1 µm, which is small enough to remove all bacteria ≥0.2 µm from any liquids passed through the device. An extract obtained from TMD-infected tobacco plants was made to determine the cause of the disease. Initially, the source of the disease was thought to be bacterial. It was surprising to everyone when Ivanovski, using a Chamberland filter, found that the cause of TMD was not removed after passing the extract through the porcelain filter. So if a bacterium was not the cause of TMD, what could be causing the disease? Ivanovski concluded the cause of TMD must be an extremely small bacterium or bacterial spore. Other scientists, including Martinus Beijerinck, continued investigating the cause of TMD. It was Beijerinck, in 1899, who eventually concluded the causative agent was not a bacterium but, instead, possibly a chemical, like a biological poison we would describe today as a toxin. As a result, the word *virus*, Latin for poison, was used to describe the cause of TMD a few years after Ivanovski's initial discovery. Even though he was not able to see the virus that caused TMD, and did not realize the cause was not a bacterium, Ivanovski is credited as the original discoverer of viruses and a founder of the field of virology.

Today, we can see viruses using electron microscopes (Figure 3.3*A*.1) and we know much more about them. Viruses are distinct biological entities; however, their evolutionary origin is still a matter of speculation. In terms of taxonomy, they are not included in the tree of life because they are acellular (not consisting of cells). In order to survive and reproduce, viruses must infect a cellular host, making them obligate intracellular parasites. The genome of a virus enters a host cell and directs the production of the viral components, proteins and nucleic acids, needed to form new virus particles called virion**s**. New virions are made in the host cell by assembly of viral components. The new virions transport the viral genome to another host cell to carry out another round of infection. Table 3.3*A*.1 summarizes the properties of viruses.

Table 3.3*A*.1***:*** *P*roperties of viruses.

https://geo.libretexts.org/@go/page/6195

Characteristics of Viruses
Infectious, acellular pathogens
Obligate intracellular parasites with host and cell-type specificity
DNA or RNA genome (never both)
Genome is surrounded by a protein capsid and, in some cases, a phospholipid membrane studded with viral glycoproteins
Lack genes for many products needed for successful reproduction, requiring exploitation of host-cell genomes to reproduce

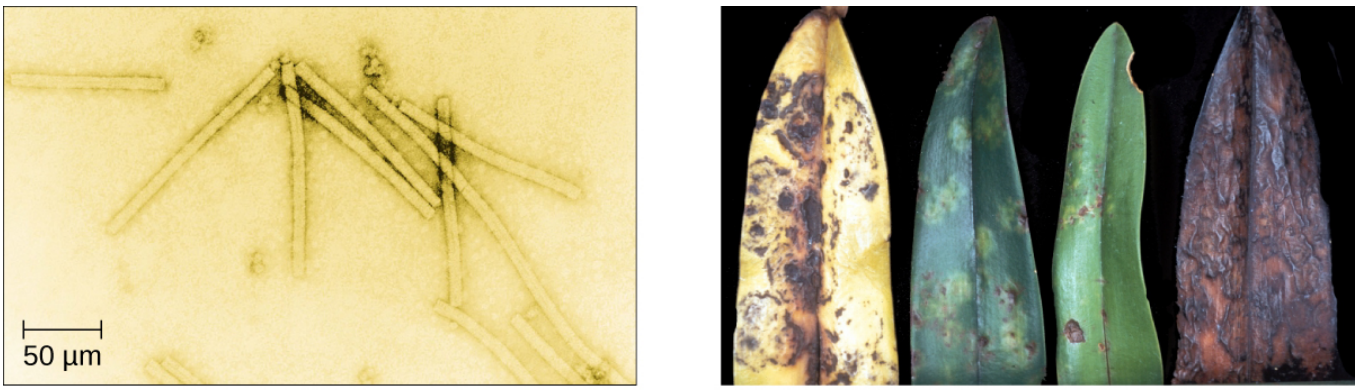


Figure 3.3A.1: *(a) Tobacco mosaic virus (TMV) viewed with transmission electron microscope. (b) Plants infected with tobacco mosaic disease (TMD), caused by TMV. (credit a: modification of work by USDA Agricultural Research Service—scale-bar data from Matt Russell; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State University)*

Exercise 3.3A.2

Why was the first virus investigated mistaken for a toxin?

Hosts and Viral Transmission

Viruses can infect every type of host cell, including those of plants, animals, fungi, protists, bacteria, and archaea. Most viruses will only be able to infect the cells of one or a few species of organism. This is called the host range. However, having a wide host range is not common and viruses will typically only infect specific hosts and only specific cell types within those hosts. The viruses that infect bacteria are called bacteriophage**s**, or simply phages. The word *phage* comes from the Greek word for devour. Other viruses are just identified by their host group, such as animal or plant viruses. Once a cell is infected, the effects of the virus can vary depending on the type of virus. Viruses may cause abnormal growth of the cell or cell death, alter the cell's genome, or cause little noticeable effect in the cell.

Viruses can be transmitted through direct contact, indirect contact with fomites, or through a vector: an animal that transmits a pathogen from one host to another. Arthropods such as mosquitoes, ticks, and flies, are typical vectors for viral diseases, and they may act as mechanical vector**s** or biological vector**s**. Mechanical transmission occurs when the arthropod carries a viral pathogen on the outside of its body and transmits it to a new host by physical contact. Biological transmission occurs when the arthropod carries the viral pathogen inside its body and transmits it to the new host through biting.

In humans, a wide variety of viruses are capable of causing various infections and diseases. Some of the deadliest emerging pathogens in humans are viruses, yet we have few treatments or drugs to deal with viral infections, making them difficult to eradicate.

Viruses that can be transmitted from an animal host to a human host can cause zoonoses. For example, the avian influenza virus originates in birds, but can cause disease in humans. Reverse zoonoses are caused by infection of an animal by a virus that originated in a human.

FIGHTING BACTERIA WITH VIRUSES

The emergence of superbugs, or multidrug resistant bacteria, has become a major challenge for pharmaceutical companies and a serious health-care problem. According to a 2013 report by the US Centers for Disease Control and Prevention (CDC), more than 2 million people are infected with drug-resistant bacteria in the US annually, resulting in at least 23,000 deaths.[2] The continued use and overuse of antibiotics will likely lead to the evolution of even more drug-resistant strains.

One potential solution is the use of phage therapy, a procedure that uses bacteria-killing viruses (bacteriophages) to treat bacterial infections. Phage therapy is not a new idea. The discovery of bacteriophages dates back to the early 20th century, and phage therapy was first used in Europe in 1915 by the English bacteriologist Frederick Twort.[3] However, the subsequent discovery of penicillin and other antibiotics led to the near abandonment of this form of therapy, except in the former Soviet Union and a few countries in Eastern Europe. Interest in phage therapy outside of the countries of the former Soviet Union is only recently re-emerging because of the rise in antibiotic-resistant bacteria.[4]

Phage therapy has some advantages over antibiotics in that phages kill only one specific bacterium, whereas antibiotics kill not only the pathogen but also beneficial bacteria of the normal microbiota. Development of new antibiotics is also expensive for drug companies and for patients, especially for those who live in countries with high poverty rates.

Phages have also been used to prevent food spoilage. In 2006, the US Food and Drug Administration approved the use of a solution containing six bacteriophages that can be sprayed on lunch meats such as bologna, ham, and turkey to kill *Listeria monocytogenes*, a bacterium responsible for listeriosis, a form of food poisoning. Some consumers have concerns about the use of phages on foods, however, especially given the rising popularity of organic products. Foods that have been treated with phages must declare "bacteriophage preparation" in the list of ingredients or include a label declaring that the meat has been "treated with antimicrobial solution to reduce microorganisms."[5]

Exercise 3.3A.3

1. Why do humans not have to be concerned about the presence of bacteriophages in their food?
2. What are three ways that viruses can be transmitted between hosts?

Viral Structures

In general, virions (viral particles) are small and cannot be observed using a regular light microscope. They are much smaller than prokaryotic and eukaryotic cells; this is an adaptation allowing viruses to infect these larger cells (see Figure 3.3A.2). The size of a virion can range from 20 nm for small viruses up to 900 nm for typical, large viruses (see Figure 3.3A.3). Recent discoveries, however, have identified new giant viral species, such as *Pandoravirus salinus* and *Pithovirus sibericum*, with sizes approaching that of a bacterial cell.[6]

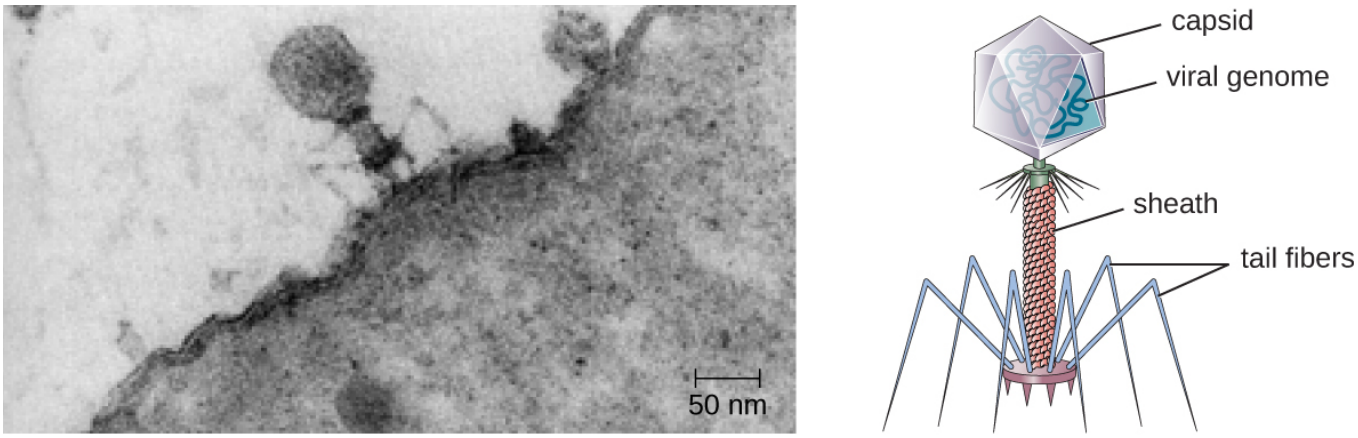


Figure 3.3A.2: (a) In this transmission electron micrograph, a bacteriophage (a virus that infects bacteria) is dwarfed by the bacterial cell it infects. (b) An illustration of the bacteriophage in the micrograph. (credit a: modification of work by U.S. Department of Energy, Office of Science, LBL, PBD)

In 1935, after the development of the electron microscope, Wendell Stanley was the first scientist to crystallize the structure of the tobacco mosaic virus and discovered that it is composed of RNA and protein. In 1943, he isolated *Influenza B virus*, which contributed to the development of an influenza (flu) vaccine. Stanley's discoveries unlocked the mystery of the nature of viruses that had been puzzling scientists for over 40 years and his contributions to the field of virology led to him being awarded the Nobel Prize in 1946.

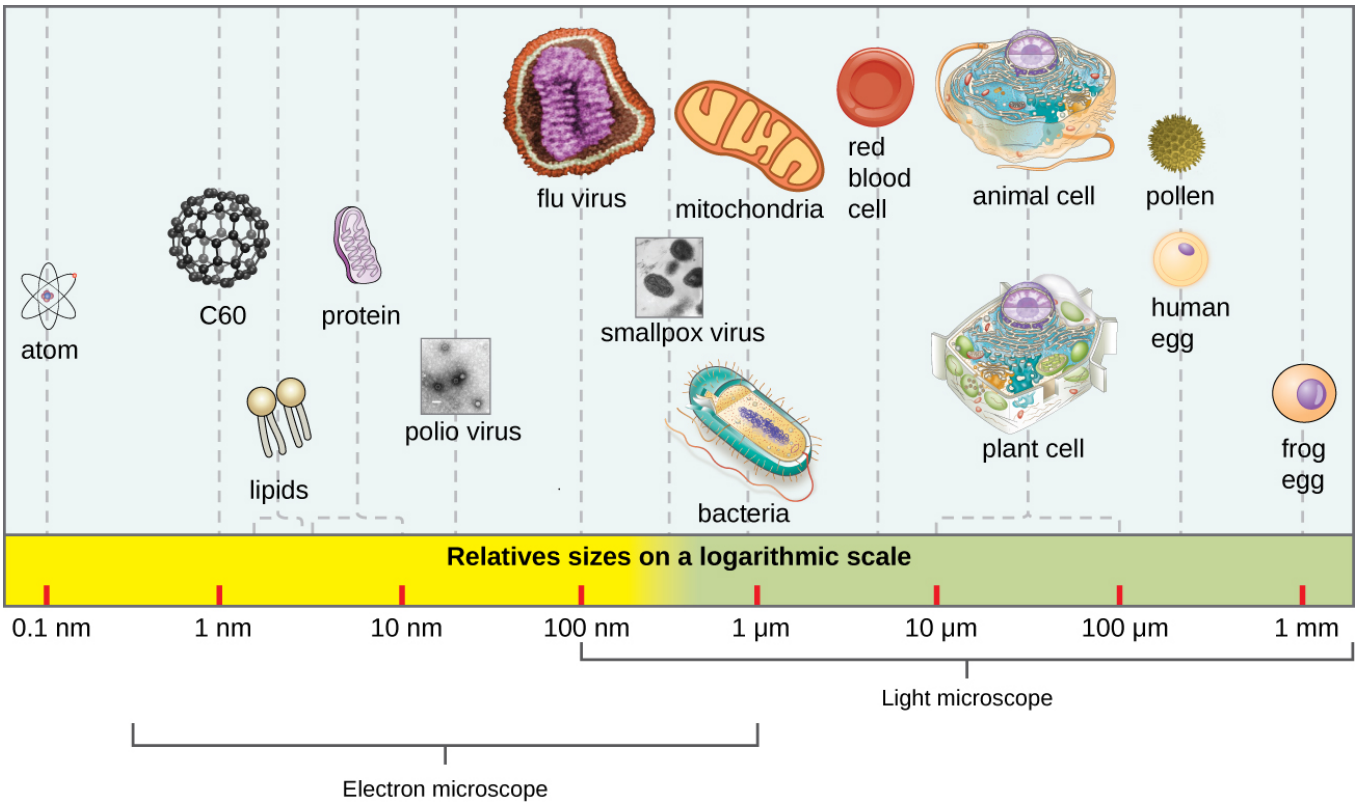


Figure 3.3A.3:The size of a virus is small relative to the size of most bacterial and eukaryotic cells and their organelles.

As a result of continuing research into the nature of viruses, we now know they consist of a nucleic acid (either RNA or DNA, but never both) surrounded by a protein coat called a capsid (see Figure 3.3A.4). The interior of the capsid is not filled with cytosol, as in a cell, but instead it contains the bare necessities in terms of genome and enzymes needed to direct the synthesis of new virions. Each capsid is composed of protein subunits called capsomere**s** made of one or more different types of capsomere proteins that interlock to form the closely packed capsid.

There are two categories of viruses based on general composition. Viruses formed from only a nucleic acid and capsid are called naked virus**es** or nonenveloped virus**es**. Viruses formed with a nucleic-acid packed capsid surrounded by a lipid layer are called enveloped virus**es** (see Figure 3.3A.4). The viral envelope is a small portion of phospholipid membrane obtained as the virion buds from a host cell. The viral envelope may either be intracellular or cytoplasmic in origin.

Extending outward and away from the capsid on some naked viruses and enveloped viruses are protein structures called spike**s**. At the tips of these spikes are structures that allow the virus to attach and enter a cell, like the influenza virus hemagglutinin spikes (H) or enzymes like the neuraminidase (N) influenza virus spikes that allow the virus to detach from the cell surface during release of new virions. Influenza viruses are often identified by their H and N spikes. For example, H1N1 influenza viruses were responsible for the pandemics in 1918 and 2009,[7] H2N2 for the pandemic in 1957, and H3N2 for the pandemic in 1968.

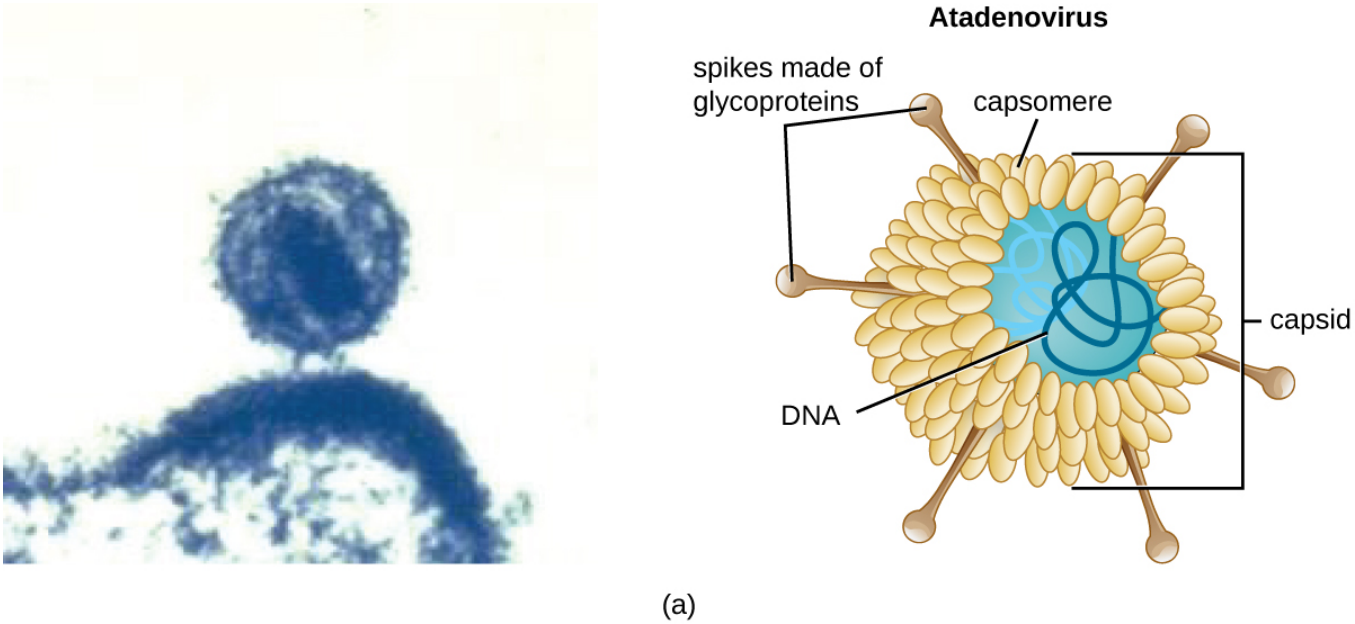


Figure 3.3A.4: *(a) The naked atadenovirus uses spikes made of glycoproteins from its capsid to bind to host cells. (b) The enveloped human immunodeficiency virus uses spikes made of glycoproteins embedded in its envelope to bind to host cells (credit a "micrograph": modification of work by NIAID; credit b "micrograph": modification of work by Centers for Disease Control and Prevention)*

Viruses vary in the shape of their capsids, which can be either helical, polyhedral, or complex. A helical capsid forms the shape of tobacco mosaic virus (TMV), a naked helical virus, and Ebola virus, an enveloped helical virus. The capsid is cylindrical or rod shaped, with the genome fitting just inside the length of the capsid. Polyhedral capsids form the shapes of poliovirus and rhinovirus, and consist of a nucleic acid surrounded by a polyhedral (many-sided) capsid in the form of an icosahedron. An icosahedral capsid is a three-dimensional, 20-sided structure with 12 vertices. These capsids somewhat resemble a soccer ball. Both helical and polyhedral viruses can have envelopes. Viral shapes seen in certain types of bacteriophages, such as T4 phage, and poxviruses, like vaccinia virus, may have features of both polyhedral and helical viruses so they are described as a complex viral shape (see Figure 3.3A.5). In the bacteriophage complex form, the genome is located within the polyhedral head and the sheath

connects the head to the tail fibers and tail pins that help the virus attach to receptors on the host cell's surface. Poxviruses that have complex shapes are often brick shaped, with intricate surface characteristics not seen in the other categories of capsid.

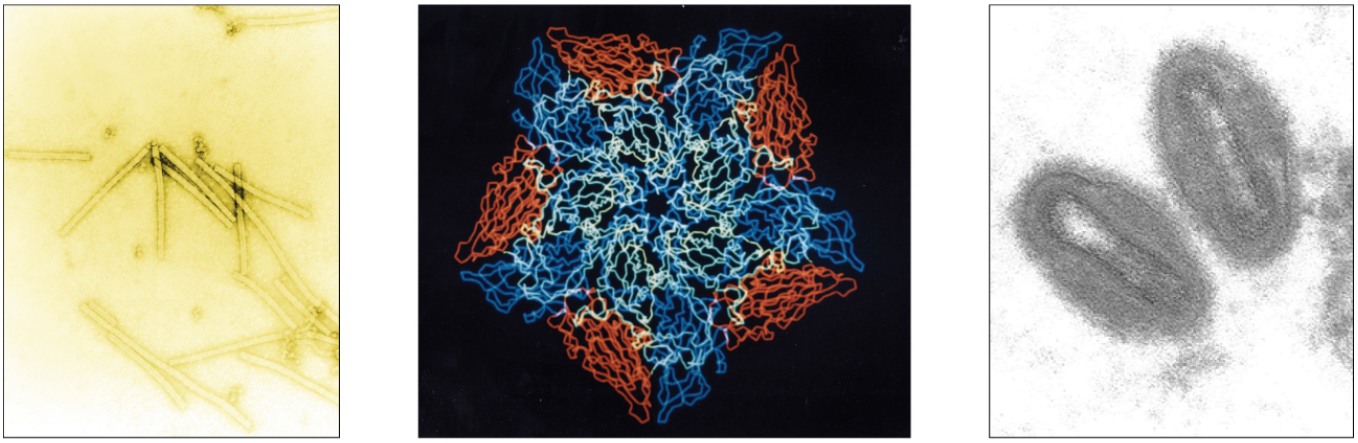


Figure 3.3A.5: Viral capsids can be (a) helical, (b) polyhedral, or (c) have a complex shape. (credit a "micrograph": modification of work by USDA ARS; credit b "micrograph": modification of work by U.S. Department of Energy)

Exercise 3.3A.4

Which types of viruses have spikes?

Classification and Taxonomy of Viruses

Although viruses are not classified in the three domains of life, their numbers are great enough to require classification. Since 1971, the International Union of Microbiological Societies Virology Division has given the task of developing, refining, and maintaining a universal virus taxonomy to the International Committee on Taxonomy of Viruses (ICTV). Since viruses can mutate so quickly, it can be difficult to classify them into a genus and a species epithet using the binomial nomenclature system. Thus, the ICTV's viral nomenclature system classifies viruses into families and genera based on viral genetics, chemistry, morphology, and mechanism of multiplication. To date, the ICTV has classified known viruses in seven orders, 96 families, and 350 genera. Viral family names end in *-viridae* (e.g, *Parvoviridae*) and genus names end in *−virus* (e.g., *Parvovirus*). The names of viral orders, families, and genera are all italicized. When referring to a viral species, we often use a genus and species epithet such as *Pandoravirus dulcis* or *Pandoravirus salinus.*

The Baltimore classification system is an alternative to ICTV nomenclature. The Baltimore system classifies viruses according to their genomes (DNA or RNA, single versus double stranded, and mode of replication). This system thus creates seven groups of

viruses that have common genetics and biology.

Explore the latest virus taxonomy at the ICTV website.

Aside from formal systems of nomenclature, viruses are often informally grouped into categories based on chemistry, morphology, or other characteristics they share in common. Categories may include naked or enveloped structure, single-stranded (ss) or double-stranded (ds) DNA or ss or ds RNA genomes, segmented or nonsegmented genomes, and positive-strand (+) or negative-strand (−) RNA. For example, herpes viruses can be classified as a dsDNA enveloped virus; human immunodeficiency virus (HIV) is a +ssRNA enveloped virus, and tobacco mosaic virus is a +ssRNA virus. Other characteristics such as host specificity, tissue specificity, capsid shape, and special genes or enzymes may also be used to describe groups of similar viruses. Table 3.3A.2 lists some of the most common viruses that are human pathogens by genome type.

Table 3.3A.2: Common Pathogenic Viruses

Genome	Family	Example Virus	Clinical Features
dsDNA, enveloped	*Poxviridae*	*Orthopoxvirus*	Skin papules, pustules, lesions
	Poxviridae	*Parapoxvirus*	Skin lesions
	Herpesviridae	*Simplexvirus*	Cold sores, genital herpes, sexually transmitted disease
dsDNA, naked	*Adenoviridae*	*Atadenovirus*	Respiratory infection (common cold)
	Papillomaviridae	*Papillomavirus*	Genital warts, cervical, vulvar, or vaginal cancer
	Reoviridae	*Reovirus*	Gastroenteritis severe diarrhea (stomach flu)
ssDNA, naked	*Parvoviridae*	*Adeno-associated dependoparvovirus A*	Respiratory tract infection
	Parvoviridae	*Adeno-associated dependoparvovirus B*	Respiratory tract infection
dsRNA, naked	*Reoviridae*	*Rotavirus*	Gastroenteritis
+ssRNA, naked	*Picornaviridae*	*Enterovirus C*	Poliomyelitis
	Picornaviridae	*Rhinovirus*	Upper respiratory tract infection (common cold)
	Picornaviridae	*Hepatovirus*	Hepatitis
+ssRNA, enveloped	*Togaviridae*	*Alphavirus*	Encephalitis, hemorrhagic fever
	Togaviridae	*Rubivirus*	Rubella
	Retroviridae	*Lentivirus*	Acquired immune deficiency syndrome (AIDS)
−ssRNA, enveloped	*Filoviridae*	*Zaire Ebolavirus*	Hemorrhagic fever
	Orthomyxoviridae	*Influenzavirus A, B, C*	Flu
	Rhabdoviridae	*Lyssavirus*	Rabies

Exercise 3.3A.5

What are the types of virus genomes?

https://geo.libretexts.org/@go/page/6195

Classification of Viral Diseases

While the ICTV has been tasked with the biological classification of viruses, it has also played an important role in the classification of diseases caused by viruses. To facilitate the tracking of virus-related human diseases, the ICTV has created classifications that link to the International Classification of Diseases (ICD), the standard taxonomy of disease that is maintained and updated by the World Health Organization (WHO). The ICD assigns an alphanumeric code of up to six characters to every type of viral infection, as well as all other types of diseases, medical conditions, and causes of death. This ICD code is used in conjunction with two other coding systems (the Current Procedural Terminology, and the Healthcare Common Procedure Coding System) to categorize patient conditions for treatment and insurance reimbursement.

For example, when a patient seeks treatment for a viral infection, ICD codes are routinely used by clinicians to order laboratory tests and prescribe treatments specific to the virus suspected of causing the illness. This ICD code is then used by medical laboratories to identify tests that must be performed to confirm the diagnosis. The ICD code is used by the health-care management system to verify that all treatments and laboratory work performed are appropriate for the given virus. Medical coders use ICD codes to assign the proper code for procedures performed, and medical billers, in turn, use this information to process claims for reimbursement by insurance companies. Vital-records keepers use ICD codes to record cause of death on death certificates, and epidemiologists used ICD codes to calculate morbidity and mortality statistics.

Exercise $3.3A.6$

Identify two locations where you would likely find an ICD code.

Clinical Focus - PART 2

David's doctor was concerned that his symptoms included prickling and itching at the site of the dog bite; these sensations could be early symptoms of rabies. Several tests are available to diagnose rabies in live patients, but no single antemortem test is adequate. The doctor decided to take samples of David's blood, saliva, and skin for testing. The skin sample was taken from the nape of the neck (posterior side of the neck near the hairline). It was about 6-mm long and contained at least 10 hair follicles, including the superficial cutaneous nerve. An immunofluorescent staining technique was used on the skin biopsy specimen to detect rabies antibodies in the cutaneous nerves at the base of the hair follicles. A test was also performed on a serum sample from David's blood to determine whether any antibodies for the rabies virus had been produced.

Meanwhile, the saliva sample was used for reverse transcriptase-polymerase chain reaction (RT-PCR) analysis, a test that can detect the presence of viral nucleic acid (RNA). The blood tests came back positive for the presence of rabies virus antigen, prompting David's doctor to prescribe prophylactic treatment. David is given a series of intramuscular injections of human rabies immunoglobulin along with a series of rabies vaccines.

Exercise $3.3A.7$

1. Why does the immunofluorescent technique look for rabies antibodies rather than the rabies virus itself?
2. If David has contracted rabies, what is his prognosis?

Summary

- Viruses are generally ultramicroscopic, typically from 20 nm to 900 nm in length. Some large viruses have been found.
- **Virions** are acellular and consist of a nucleic acid, DNA or RNA, but not both, surrounded by a protein **capsid**. There may also be a phospholipid membrane surrounding the capsid.
- Viruses are obligate intracellular parasites.
- Viruses are known to infect various types of cells found in plants, animals, fungi, protists, bacteria, and archaea. Viruses typically have limited **host ranges** and infect specific cell types.
- Viruses may have **helical**, **polyhedral,** or **complex** shapes.
- Classification of viruses is based on morphology, type of nucleic acid, host range, cell specificity, and enzymes carried within the virion.
- Like other diseases, viral diseases are classified using ICD codes.

Footnotes

1. 1 H. Lecoq. “[Discovery of the First Virus, the Tobacco Mosaic Virus: 1892 or 1898?].” *Comptes Rendus de l’Academie des Sciences – Serie III – Sciences de la Vie* 324, no. 10 (2001): 929–933.
2. 2 US Department of Health and Human Services, Centers for Disease Control and Prevention. “Antibiotic Resistance Threats in the United States, 2013.” http://www.cdc.gov/drugresistance/pd...s-2013-508.pdf (accessed September 22, 2015).
3. 3 M. Clokie et al. “Phages in Nature.” *Bacteriophage* 1, no. 1 (2011): 31–45.
4. 4 A. Sulakvelidze et al. “Bacteriophage Therapy.” *Antimicrobial Agents and Chemotherapy* 45, no. 3 (2001): 649–659.
5. 5 US Food and Drug Administration. “FDA Approval of *Listeria*-specific Bacteriophage Preparation on Ready-to-Eat (RTE) Meat and Poultry Products.” http://www.fda.gov/food/ingredientsp.../ucm083572.htm (accessed September 22, 2015).
6. 6 N. *Philippe et al. “Pandoraviruses: Amoeba Viruses with Genomes up to 2.5 Mb Reaching that of Parasitic Eukaryotes.” Science 341, no. 6143 (2013): 281–286.*
7. 7 J. Cohen. “What’s Old Is New: 1918 Virus Matches 2009 H1N1 Strain. *Science* 327, no. 5973 (2010): 1563–1564.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 3.3A: Viruses is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

3.3B: The Viral Life Cycle

SKILLS TO DEVELOP

- Describe the lytic and lysogenic life cycles
- Describe the replication process of animal viruses
- Describe unique characteristics of retroviruses and latent viruses
- Discuss human viruses and their virus-host cell interactions
- Explain the process of transduction
- Describe the replication process of plant viruses

All viruses depend on cells for reproduction and metabolic processes. By themselves, viruses do not encode for all of the enzymes necessary for viral replication. But within a host cell, a virus can commandeer cellular machinery to produce more viral particles. Bacteriophages replicate only in the cytoplasm, since prokaryotic cells do not have a nucleus or organelles. In eukaryotic cells, most DNA viruses can replicate inside the nucleus, with an exception observed in the large DNA viruses, such as the poxviruses, that can replicate in the cytoplasm. RNA viruses that infect animal cells often replicate in the cytoplasm.

The Life Cycle of Viruses with Prokaryote Hosts

The life cycle of bacteriophages has been a good model for understanding how viruses affect the cells they infect, since similar processes have been observed for eukaryotic viruses, which can cause immediate death of the cell or establish a latent or chronic infection. Virulent phages typically lead to the death of the cell through cell lysis. **Temperate phages**, on the other hand, can become part of a host chromosome and are replicated with the cell genome until such time as they are induced to make newly assembled viruses, or **progeny viruses**.

The Lytic Cycle

During the lytic cycle of virulent phage, the bacteriophage takes over the cell, reproduces new phages, and destroys the cell. T-even phage is a good example of a well-characterized class of virulent phages. There are five stages in the bacteriophage lytic cycle (see Figure 3.3*B*.1). Attachment is the first stage in the infection process in which the phage interacts with specific bacterial surface receptors (e.g., lipopolysaccharides and OmpC protein on host surfaces). Most phages have a narrow host range and may infect one species of bacteria or one strain within a species. This unique recognition can be exploited for targeted treatment of bacterial infection by phage therapy or for phage typing to identify unique bacterial subspecies or strains. The second stage of infection is entry or penetration. This occurs through contraction of the tail sheath, which acts like a hypodermic needle to inject the viral genome through the cell wall and membrane. The phage head and remaining components remain outside the bacteria.

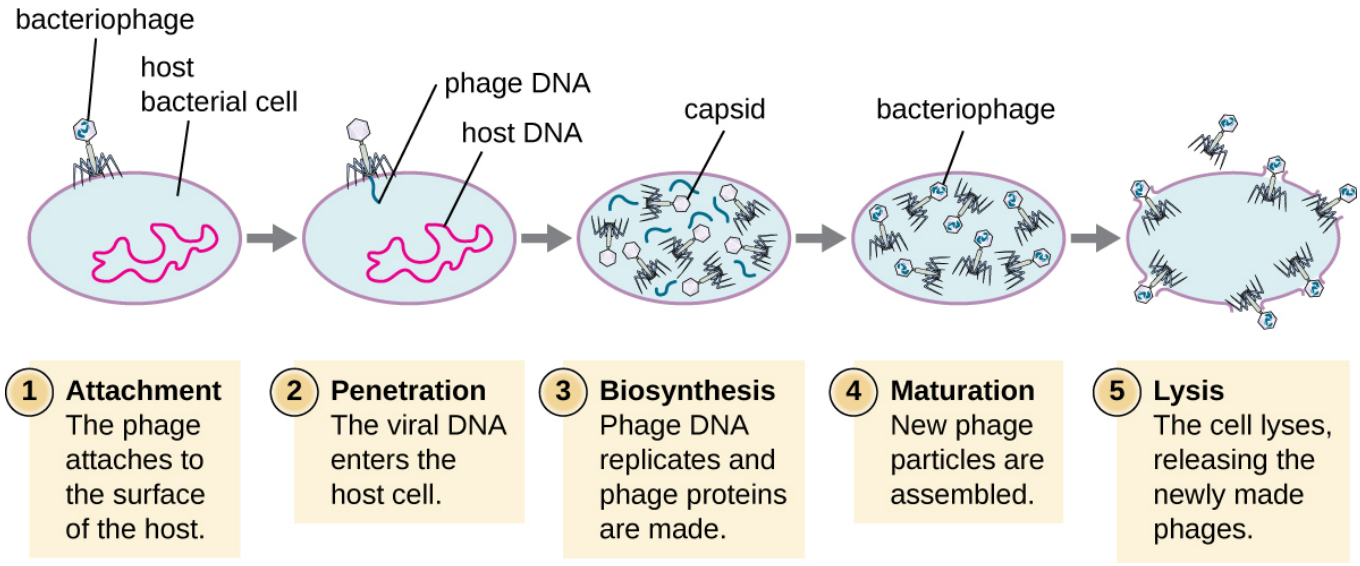


Figure 3.3*B*.1: A virulent phage shows only the lytic cycle pictured here. In the lytic cycle, the phage replicates and lyses the host cell.

The third stage of infection is biosynthesis of new viral components. After entering the host cell, the virus synthesizes virus-encoded endonucleases to degrade the bacterial chromosome. It then hijacks the host cell to replicate, transcribe, and translate the necessary viral components (capsomeres, sheath, base plates, tail fibers, and viral enzymes) for the assembly of new viruses. Polymerase genes are usually expressed early in the cycle, while capsid and tail proteins are expressed later. During the maturation phase, new virions are created. To liberate free phages, the bacterial cell wall is disrupted by phage proteins such as holin or lysozyme. The final stage is release. Mature viruses burst out of the host cell in a process called lysis and the progeny viruses are liberated into the environment to infect new cells.

The Lysogenic Cycle

In a lysogenic cycle, the phage genome also enters the cell through attachment and penetration. A prime example of a phage with this type of life cycle is the lambda phage. During the lysogenic cycle, instead of killing the host, the phage genome integrates into the bacterial chromosome and becomes part of the host. The integrated phage genome is called a prophage. A bacterial host with a prophage is called a lysogen. The process in which a bacterium is infected by a temperate phage is called lysogeny. It is typical of temperate phages to be latent or inactive within the cell. As the bacterium replicates its chromosome, it also replicates the phage's DNA and passes it on to new daughter cells during reproduction. The presence of the phage may alter the phenotype of the bacterium, since it can bring in extra genes (e.g., toxin genes that can increase bacterial virulence). This change in the host phenotype is called lysogenic conversion or phage conversion. Some bacteria, such as *Vibrio cholerae* and *Clostridium botulinum*, are less virulent in the absence of the prophage. The phages infecting these bacteria carry the toxin genes in their genome and enhance the virulence of the host when the toxin genes are expressed. In the case of *V. cholera*, phage encoded toxin can cause severe diarrhea; in *C. botulinum*, the toxin can cause paralysis. During lysogeny, the prophage will persist in the host chromosome until induction, which results in the excision of the viral genome from the host chromosome. After induction has occurred the temperate phage can proceed through a lytic cycle and then undergo lysogeny in a newly infected cell (see Figure 3.3*B*.2).

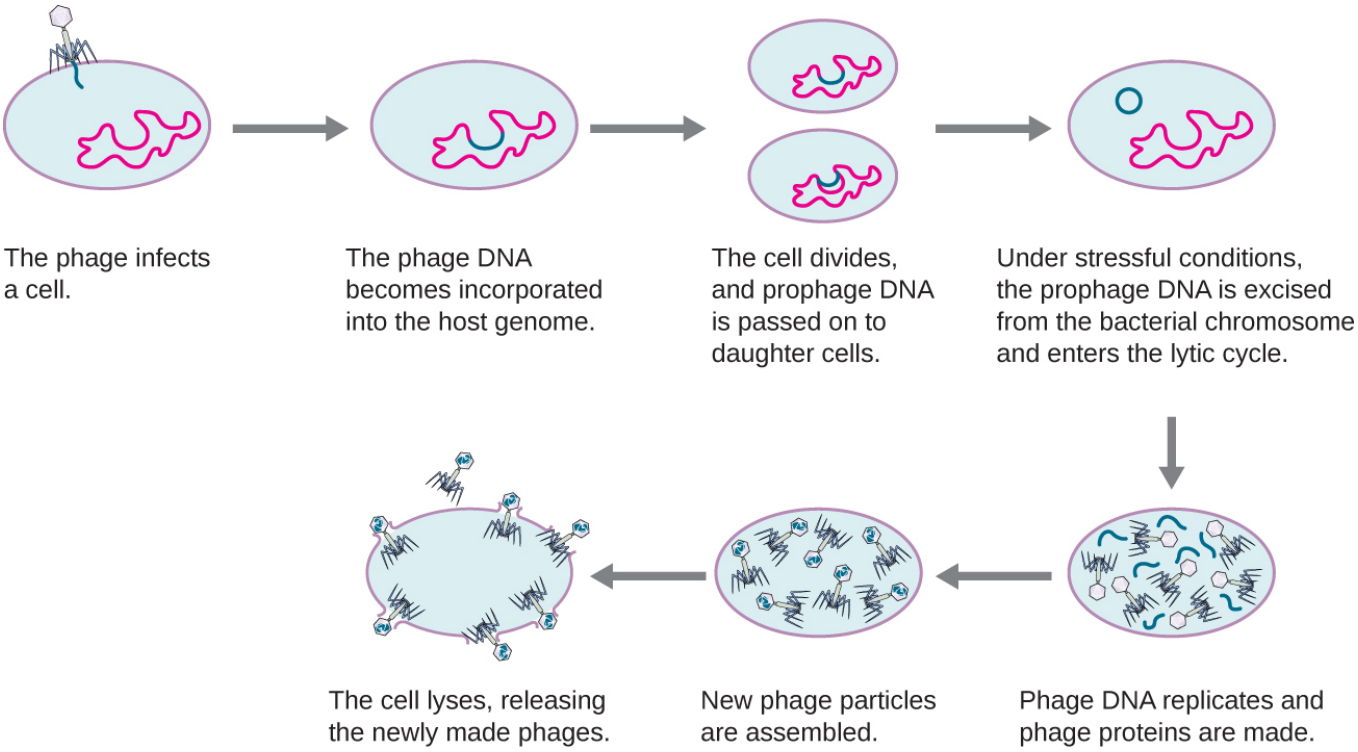


Figure 3.3*B*.2: *A temperate bacteriophage has both lytic and lysogenic cycles. In the lysogenic cycle, phage DNA is incorporated into the host genome, forming a prophage, which is passed on to subsequent generations of cells. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to be excised and enter the lytic cycle.*

This video illustrates the stages of the lysogenic life cycle of a bacteriophage and the transition to a lytic phase.

Exercise 3.3*B*.1

Is a latent phage undetectable in a bacterium?

Transduction

Transduction occurs when a bacteriophage transfers bacterial DNA from one bacterium to another during sequential infections. There are two types of transduction: generalized and specialized transduction. During the lytic cycle of viral replication, the virus hijacks the host cell, degrades the host chromosome, and makes more viral genomes. As it assembles and packages DNA into the phage head, packaging occasionally makes a mistake. Instead of packaging viral DNA, it takes a random piece of host DNA and inserts it into the capsid. Once released, this virion will then inject the former host's DNA into a newly infected host. The asexual transfer of genetic information can allow for DNA recombination to occur, thus providing the new host with new genes (e.g., an antibiotic-resistance gene, or a sugar-metabolizing gene). Generalized transduction occurs when a random piece of bacterial chromosomal DNA is transferred by the phage during the lytic cycle. Specialized transduction occurs at the end of the lysogenic cycle, when the prophage is excised and the bacteriophage enters the lytic cycle. Since the phage is integrated into the host genome, the prophage can replicate as part of the host. However, some conditions (e.g., ultraviolet light exposure or chemical exposure) stimulate the prophage to undergo induction, causing the phage to excise from the genome, enter the lytic cycle, and produce new phages to leave host cells. During the process of excision from the host chromosome, a phage may occasionally remove some bacterial DNA near the site of viral integration. The phage and host DNA from one end or both ends of the integration site are packaged within the capsid and are transferred to the new, infected host. Since the DNA transferred by the phage is not randomly packaged but is instead a specific piece of DNA near the site of integration, this mechanism of gene transfer is referred to as specialized transduction (see Figure 3.3*B*.3). The DNA can then recombine with host chromosome, giving the latter new characteristics. Transduction seems to play an important role in the evolutionary process of bacteria, giving them a mechanism for asexual exchange of genetic information.

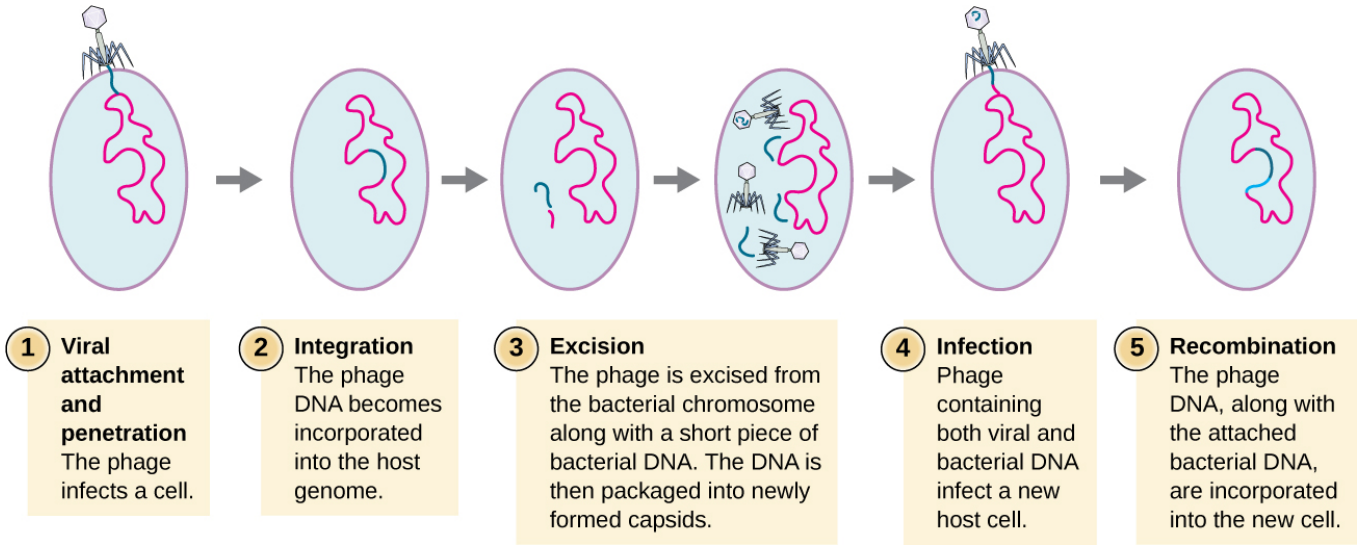


Figure 3.3B.3: This flowchart illustrates the mechanism of specialized transduction. An integrated phage excises, bringing with it a piece of the DNA adjacent to its insertion point. On reinfection of a new bacterium, the phage DNA integrates along with the genetic material acquired from the previous host.

Exercise 3.3B.2

Which phage life cycle is associated with which forms of transduction?

Life Cycle of Viruses with Animal Hosts

Lytic animal viruses follow similar infection stages to bacteriophages: attachment, penetration, biosynthesis, maturation, and release (see Figure 3.3B.4). However, the mechanisms of penetration, nucleic-acid biosynthesis, and release differ between bacterial and animal viruses. After binding to host receptors, animal viruses enter through endocytosis(engulfment by the host cell) or through membrane fusion (viral envelope with the host cell membrane). Many viruses are host specific, meaning they only infect a certain type of host; and most viruses only infect certain types of cells within tissues. This specificity is called a tissue tropism. Examples of this are demonstrated by the poliovirus, which exhibits tropism for the tissues of the brain and spinal cord, or the influenza virus, which has a primary tropism for the respiratory tract.

https://geo.libretexts.org/@go/page/6196

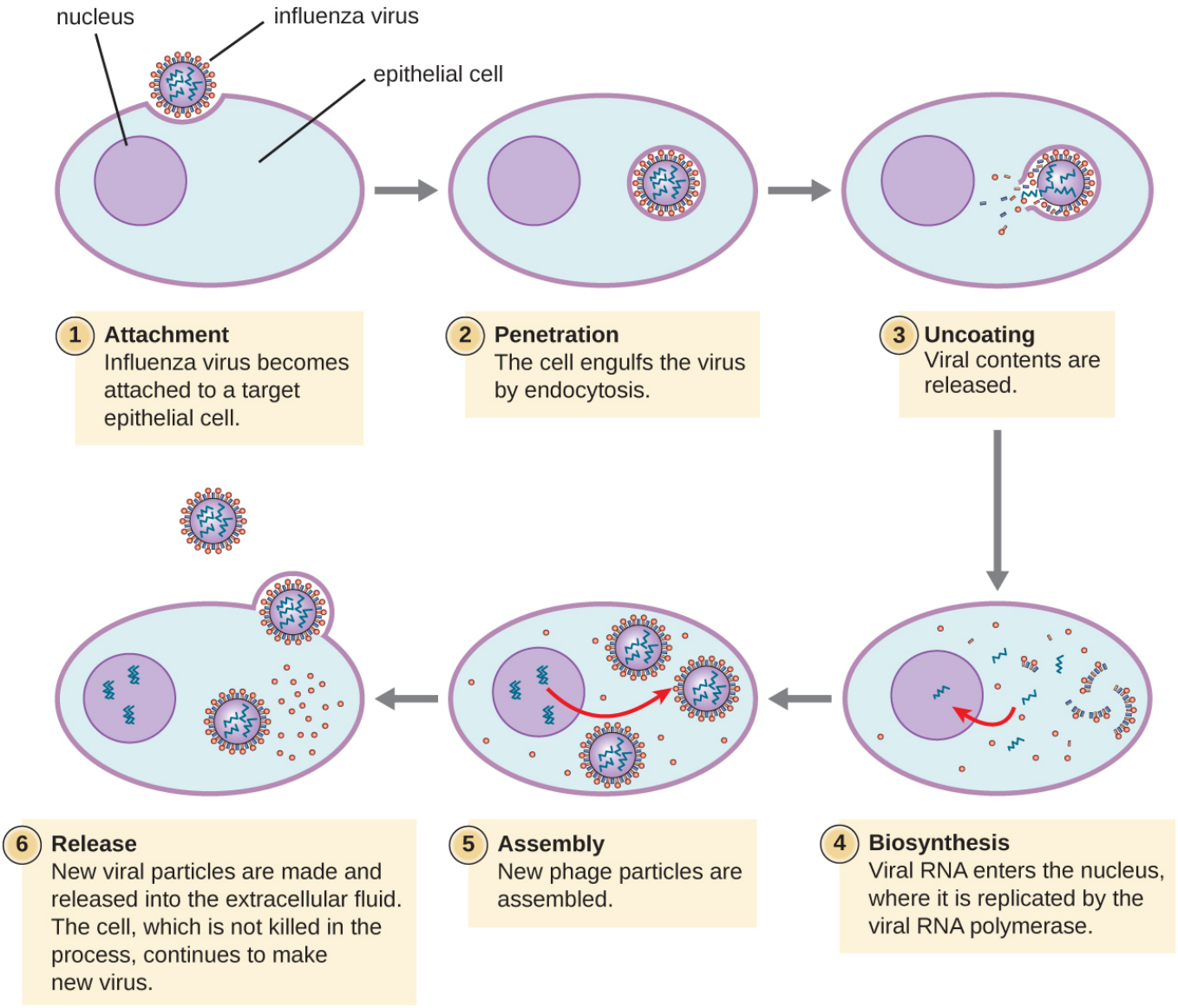


Figure 3.3*B*.4: In influenza virus infection, viral glycoproteins attach the virus to a host epithelial cell. As a result, the virus is engulfed. Viral RNA and viral proteins are made and assembled into new virions that are released by budding.

Animal viruses do not always express their genes using the normal flow of genetic information—from DNA to RNA to protein. Some viruses have a dsDNA genome like cellular organisms and can follow the normal flow. However, others may have ssDNA, dsRNA, or ssRNA genomes. The nature of the genome determines how the genome is replicated and expressed as viral proteins. If a genome is ssDNA, host enzymes will be used to synthesize a second strand that is complementary to the genome strand, thus producing dsDNA. The dsDNA can now be replicated, transcribed, and translated similar to host DNA.

If the viral genome is RNA, a different mechanism must be used. There are three types of RNA genome: dsRNA, positive (+) single-strand (+ssRNA) or negative (−) single-strand RNA (−ssRNA). If a virus has a +ssRNA genome, it can be translated directly to make viral proteins. Viral genomic +ssRNA acts like cellular mRNA. However, if a virus contains a −ssRNA genome, the host ribosomes cannot translate it until the −ssRNA is replicated into +ssRNA by viral RNA-dependent RNA polymerase (RdRP) (see Figure 3.3*B*.5). The RdRP is brought in by the virus and can be used to make +ssRNA from the original −ssRNA genome. The RdRP is also an important enzyme for the replication of dsRNA viruses, because it uses the negative strand of the double-stranded genome as a template to create +ssRNA. The newly synthesized +ssRNA copies can then be translated by cellular ribosomes.

https://geo.libretexts.org/@go/page/6196

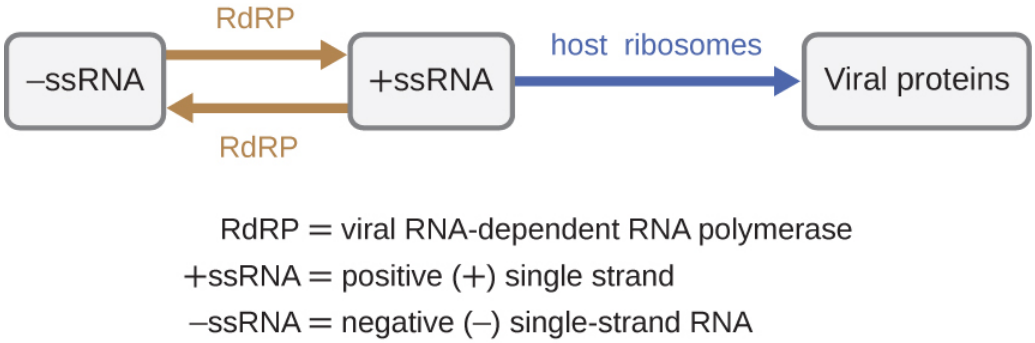


Figure 3.3*B*.5***:*** *RNA viruses can contain +ssRNA that can be directly read by the ribosomes to synthesize viral proteins. Viruses containing −ssRNA must first use the −ssRNA as a template for the synthesis of +ssRNA before viral proteins can be synthesized.*

An alternative mechanism for viral nucleic acid synthesis is observed in the retrovirus**es**, which are +ssRNA viruses (see Figure 3.3*B*.6). Single-stranded RNA viruses such as HIV carry a special enzyme called reverse transcriptase within the capsid that synthesizes a complementary ssDNA (cDNA) copy using the +ssRNA genome as a template. The ssDNA is then made into dsDNA, which can integrate into the host chromosome and become a permanent part of the host. The integrated viral genome is called a provirus. The virus now can remain in the host for a long time to establish a chronic infection. The provirus stage is similar to the prophage stage in a bacterial infection during the lysogenic cycle. However, unlike prophage, the provirus does not undergo excision after splicing into the genome.

https://geo.libretexts.org/@go/page/6196

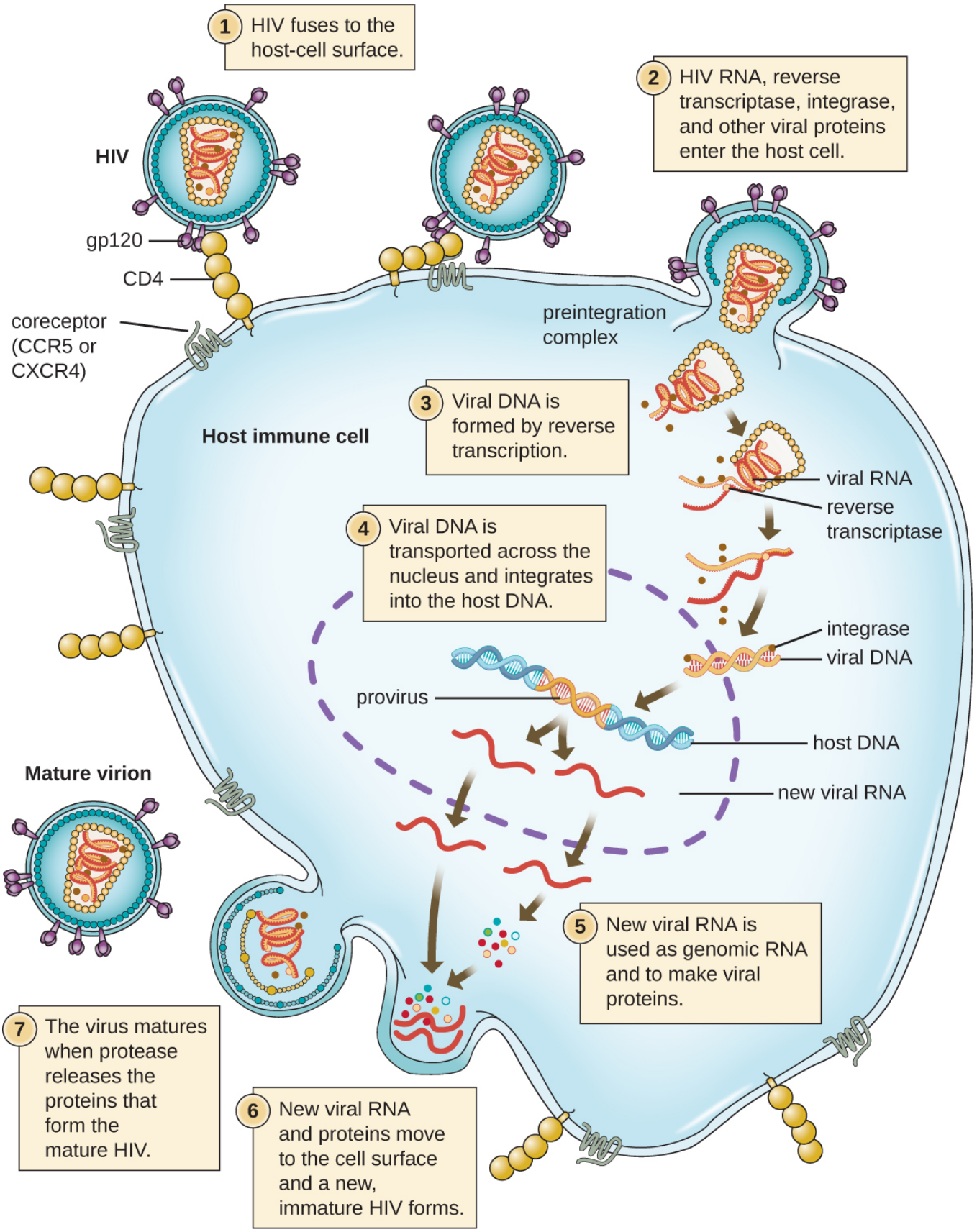


Figure 3.3*B*.6: HIV, an enveloped, icosahedral retrovirus, attaches to a cell surface receptor of an immune cell and fuses with the cell membrane. Viral contents are released into the cell, where viral enzymes convert the single-stranded RNA genome into DNA and incorporate it into the host genome. (credit: modification of work by NIAID, NIH)

https://geo.libretexts.org/@go/page/6196

Exercise 3.3B.3

Is RNA-dependent RNA polymerase made from a viral gene or a host gene?

Persistent Infections

Persistent infection occurs when a virus is not completely cleared from the system of the host but stays in certain tissues or organs of the infected person. The virus may remain silent or undergo productive infection without seriously harming or killing the host. Mechanisms of persistent infection may involve the regulation of the viral or host gene expressions or the alteration of the host immune response. The two primary categories of persistent infections are latent infection and chronic infection. Examples of viruses that cause latent infections include herpes simplex virus (oral and genital herpes), varicella-zoster virus (chickenpox and shingles), and Epstein-Barr virus (mononucleosis). Hepatitis C virus and HIV are two examples of viruses that cause long-term chronic infections.

Latent Infection

Not all animal viruses undergo replication by the lytic cycle. There are viruses that are capable of remaining hidden or dormant inside the cell in a process called latency. These types of viruses are known as latent virus**es** and may cause latent infections. Viruses capable of latency may initially cause an acute infection before becoming dormant.

For example, the varicella-zoster virus infects many cells throughout the body and causes chickenpox, characterized by a rash of blisters covering the skin. About 10 to 12 days postinfection, the disease resolves and the virus goes dormant, living within nerve-cell ganglia for years. During this time, the virus does not kill the nerve cells or continue replicating. It is not clear why the virus stops replicating within the nerve cells and expresses few viral proteins but, in some cases, typically after many years of dormancy, the virus is reactivated and causes a new disease called shingles (Figure 3.3B.7). Whereas chickenpox affects many areas throughout the body, shingles is a nerve cell-specific disease emerging from the ganglia in which the virus was dormant.

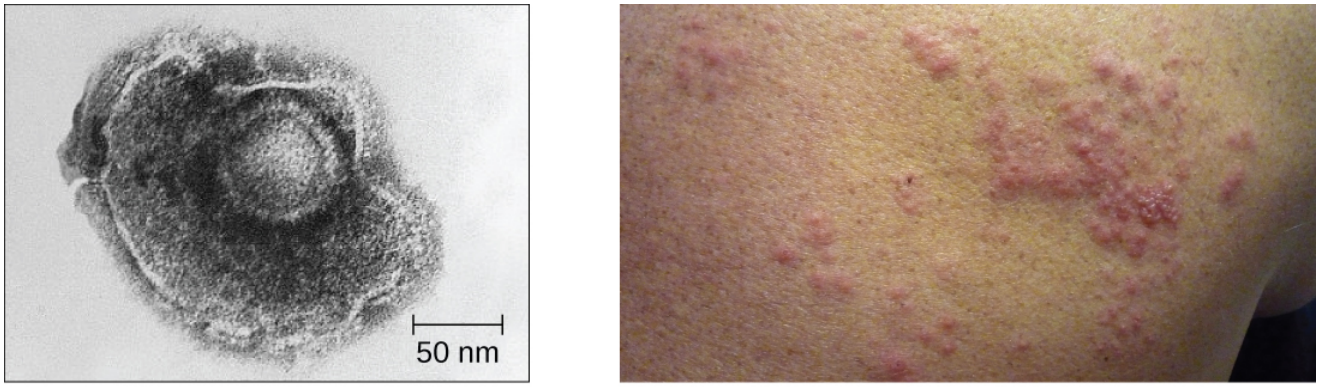


Figure 3.3B.7: (a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome becomes incorporated in the host DNA. (b) After a period of latency, the virus can reactivate in the form of shingles, usually manifesting as a painful, localized rash on one side of the body. (credit a: modification of work by Erskine Palmer and B.G. Partin—scale-bar data from Matt Russell; credit b: modification of work by Rosmarie Voegtli)

Latent viruses may remain dormant by existing as circular viral genome molecules outside of the host chromosome. Others become proviruses by integrating into the host genome. During dormancy, viruses do not cause any symptoms of disease and may be difficult to detect. A patient may be unaware that he or she is carrying the virus unless a viral diagnostic test has been performed.

Chronic Infection

A chronic infection is a disease with symptoms that are recurrent or persistent over a long time. Some viral infections can be chronic if the body is unable to eliminate the virus. HIV is an example of a virus that produces a chronic infection, often after a long period of latency. Once a person becomes infected with HIV, the virus can be detected in tissues continuously thereafter, but untreated patients often experience no symptoms for years. However, the virus maintains chronic persistence through several

mechanisms that interfere with immune function, including preventing expression of viral antigens on the surface of infected cells, altering immune cells themselves, restricting expression of viral genes, and rapidly changing viral antigens through mutation. Eventually, the damage to the immune system results in progression of the disease leading to acquired immunodeficiency syndrome (AIDS). The various mechanisms that HIV uses to avoid being cleared by the immune system are also used by other chronically infecting viruses, including the hepatitis C virus.

Exercise $3.3B.4$

In what two ways can a virus manage to maintain a persistent infection?

Life Cycle of Viruses with Plant Hosts

Plant viruses are more similar to animal viruses than they are to bacteriophages. Plant viruses may be enveloped or non-enveloped. Like many animal viruses, plant viruses can have either a DNA or RNA genome and be single stranded or double stranded. However, most plant viruses do not have a DNA genome; the majority have a +ssRNA genome, which acts like messenger RNA (mRNA). Only a minority of plant viruses have other types of genomes.

Plant viruses may have a narrow or broad host range. For example, the citrus tristeza virus infects only a few plants of the *Citrus* genus, whereas the cucumber mosaic virus infects thousands of plants of various plant families. Most plant viruses are transmitted by contact between plants, or by fungi, nematodes, insects, or other arthropods that act as mechanical vectors. However, some viruses can only be transferred by a specific type of insect vector; for example, a particular virus might be transmitted by aphids but not whiteflies. In some cases, viruses may also enter healthy plants through wounds, as might occur due to pruning or weather damage.

Viruses that infect plants are considered biotrophic parasites, which means that they can establish an infection without killing the host, similar to what is observed in the lysogenic life cycles of bacteriophages. Viral infection can be asymptomatic (latent) or can lead to cell death (lytic infection). The life cycle begins with the penetration of the virus into the host cell. Next, the virus is uncoated within the cytoplasm of the cell when the capsid is removed. Depending on the type of nucleic acid, cellular components are used to replicate the viral genome and synthesize viral proteins for assembly of new virions. To establish a systemic infection, the virus must enter a part of the vascular system of the plant, such as the phloem. The time required for systemic infection may vary from a few days to a few weeks depending on the virus, the plant species, and the environmental conditions. The virus life cycle is complete when it is transmitted from an infected plant to a healthy plant.

Exercise $3.3B.5$

What is the structure and genome of a typical plant virus?

Viral Growth Curve

Unlike the growth curve for a bacterial population, the growth curve for a virus population over its life cycle does not follow a sigmoidal curve. During the initial stage, an inoculum of virus causes infection. In the eclipse phase, viruses bind and penetrate the cells with no virions detected in the medium. The chief difference that next appears in the viral growth curve compared to a bacterial growth curve occurs when virions are released from the lysed host cell at the same time. Such an occurrence is called a burst, and the number of virions per bacterium released is described as the burst size. In a one-step multiplication curve for bacteriophage, the host cells lyse, releasing many viral particles to the medium, which leads to a very steep rise in viral titer (the number of virions per unit volume). If no viable host cells remain, the viral particles begin to degrade during the decline of the culture (see Figure $3.3B.8$).

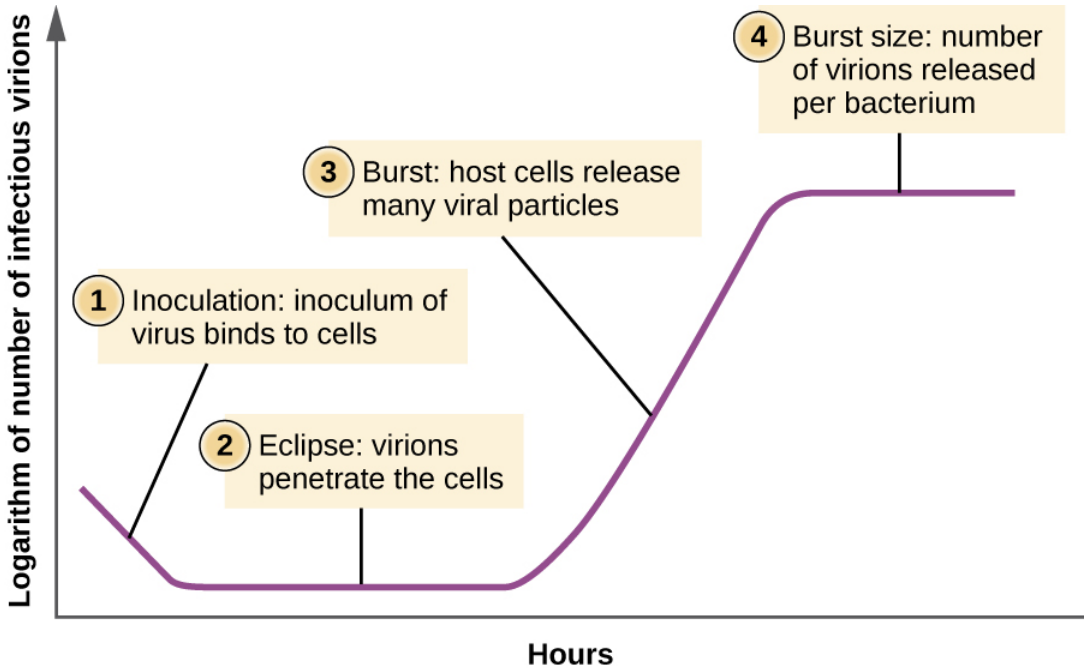


Figure 3.3*B*.8: The one-step multiplication curve for a bacteriophage population follows three steps: 1) inoculation, during which the virions attach to host cells; 2) eclipse, during which entry of the viral genome occurs; and 3) burst, when sufficient numbers of new virions are produced and emerge from the host cell. The burst size is the maximum number of virions produced per bacterium.

Exercise 3.3*B*.6

What aspect of the life cycle of a virus leads to the sudden increase in the growth curve?

unregistered treatments

Ebola is incurable and deadly. The outbreak in West Africa in 2014 was unprecedented, dwarfing other human Ebola epidemics in the level of mortality. Of 24,666 suspected or confirmed cases reported, 10,179 people died.

No approved treatments or vaccines for Ebola are available. While some drugs have shown potential in laboratory studies and animal models, they have not been tested in humans for safety and effectiveness. Not only are these drugs untested or unregistered but they are also in short supply.

Given the great suffering and high mortality rates, it is fair to ask whether unregistered and untested medications are better than none at all. Should such drugs be dispensed and, if so, who should receive them, in light of their extremely limited supplies? Is it ethical to treat untested drugs on patients with Ebola? On the other hand, is it ethical to withhold potentially life-saving drugs from dying patients? Or should the drugs perhaps be reserved for health-care providers working to contain the disease?

In August 2014, two infected US aid workers and a Spanish priest were treated with ZMapp, an unregistered drug that had been tested in monkeys but not in humans. The two American aid workers recovered, but the priest died. Later that month, the WHO released a report on the ethics of treating patients with the drug. Since Ebola is often fatal, the panel reasoned that it is ethical to give the unregistered drugs and unethical to withhold them for safety concerns. This situation is an example of “compassionate use” outside the well-established system of regulation and governance of therapies.

ebola in the us

On September 24, 2014, Thomas Eric Duncan arrived at the Texas Health Presbyterian Hospital in Dallas complaining of a fever, headache, vomiting, and diarrhea—symptoms commonly observed in patients with the cold or the flu. After examination, an emergency department doctor diagnosed him with sinusitis, prescribed some antibiotics, and sent him home. Two days later, Duncan returned to the hospital by ambulance. His condition had deteriorated and additional blood tests confirmed that he has been infected with the Ebola virus.

Further investigations revealed that Duncan had just returned from Liberia, one of the countries in the midst of a severe Ebola epidemic. On September 15, nine days before he showed up at the hospital in Dallas, Duncan had helped transport an Ebola-stricken neighbor to a hospital in Liberia. The hospital continued to treat Duncan, but he died several days after being admitted.

The timeline of the Duncan case is indicative of the life cycle of the Ebola virus. The incubation time for Ebola ranges from 2 days to 21 days. Nine days passed between Duncan's exposure to the virus infection and the appearance of his symptoms. This corresponds, in part, to the eclipse period in the growth of the virus population. During the eclipse phase, Duncan would have been unable to transmit the disease to others. However, once an infected individual begins exhibiting symptoms, the disease becomes very contagious. Ebola virus is transmitted through direct contact with droplets of bodily fluids such as saliva, blood, and vomit. Duncan could conceivably have transmitted the disease to others at any time after he began having symptoms, presumably some time before his arrival at the hospital in Dallas. Once a hospital realizes a patient like Duncan is infected with Ebola virus, the patient is immediately quarantined, and public health officials initiate a back trace to identify everyone with whom a patient like Duncan might have interacted during the period in which he was showing symptoms.

Public health officials were able to track down 10 high-risk individuals (family members of Duncan) and 50 low-risk individuals to monitor them for signs of infection. None contracted the disease. However, one of the nurses charged with Duncan's care did become infected. This, along with Duncan's initial misdiagnosis, made it clear that US hospitals needed to provide additional training to medical personnel to prevent a possible Ebola outbreak in the US.

Exercise $3.3B.7$

1. What types of training can prepare health professionals to contain emerging epidemics like the Ebola outbreak of 2014?
2. What is the difference between a contagious pathogen and an infectious pathogen?

https://geo.libretexts.org/@go/page/6196



Figure 3.3*B*.9: Researchers working with Ebola virus use layers of defenses against accidental infection, including protective clothing, breathing systems, and negative air-pressure cabinets for bench work. (credit: modification of work by Randal J. Schoepp)

For additional information about Ebola, please visit the CDC website.

Summary

- Many viruses target specific hosts or tissues. Some may have more than one host.
- Many viruses follow several stages to infect host cells. These stages include **attachment, penetration, uncoating, biosynthesis, maturation,** and **release**.
- Bacteriophages have a **lytic** or **lysogenic cycle**. The lytic cycle leads to the death of the host, whereas the lysogenic cycle leads to integration of phage into the host genome.
- Bacteriophages inject DNA into the host cell, whereas animal viruses enter by endocytosis or membrane fusion.
- Animal viruses can undergo **latency**, similar to lysogeny for a bacteriophage.
- The majority of plant viruses are positive-strand ssRNA and can undergo latency, chronic, or lytic infection, as observed for animal viruses.
- The growth curve of bacteriophage populations is a **one-step multiplication curve** and not a sigmoidal curve, as compared to the bacterial growth curve.
- Bacteriophages transfer genetic information between hosts using either **generalized** or **specialized transduction**.

Footnotes

1. 1 World Health Organization. “WHO Ebola Data and Statistics.” March 18, 2005. http://apps.who.int/gho/data/view.eb...150318?lang=en

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 3.3B: The Viral Life Cycle is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

CHAPTER OVERVIEW

6: Microbial Metabolism

8.1: Energy, Matter, and Enzymes
8.2: Catabolism of Carbohydrates
8.3: Cellular Respiration
8.4: Fermentation
8.5: Catabolism of Lipids and Proteins
8.6: Photosynthesis and the Importance of Light
8.7: Biogeochemical Cycles

Thumbnail: The Krebs cycle, also known as the citric acid cycle, is summarized here. Note incoming two-carbon acetyl results in the main outputs per turn of two CO_2, three NADH, one $FADH_2$, and one ATP (or GTP) molecules made by substrate-level phosphorylation. Two turns of the Krebs cycle are required to process all of the carbon from one glucose molecule.

This page titled 6: Microbial Metabolism is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.1: Energy, Matter, and Enzymes

Skills to Develop

- Define and describe metabolism
- Compare and contrast autotrophs and heterotrophs
- Describe the importance of oxidation-reduction reactions in metabolism
- Describe why ATP, FAD, NAD^+, and $NADP^+$ are important in a cell
- Identify the structure and structural components of an enzyme
- Describe the differences between competitive and noncompetitive enzyme inhibitors

part 1

Hannah is a 15-month-old girl from Washington state. She is spending the summer in Gambia, where her parents are working for a nongovernmental organization. About 3 weeks after her arrival in Gambia, Hannah's appetite began to diminish and her parents noticed that she seemed unusually sluggish, fatigued, and confused. She also seemed very irritable when she was outdoors, especially during the day. When she began vomiting, her parents figured she had caught a 24-hour virus, but when her symptoms persisted, they took her to a clinic. The local physician noticed that Hannah's reflexes seemed abnormally slow, and when he examined her eyes with a light, she seemed unusually light sensitive. She also seemed to be experiencing a stiff neck.

Exercise 8.1.1

What are some possible causes of Hannah's symptoms?

The term used to describe all of the chemical reactions inside a cell is metabolism (Figure 8.1.1). Cellular processes such as the building or breaking down of complex molecules occur through series of stepwise, interconnected chemical reactions called metabolic pathways. Reactions that are spontaneous and release energy are exergonic reactions, whereas endergonic reactions require energy to proceed. The term anabolism refers to those endergonic metabolic pathways involved in biosynthesis, converting simple molecular building blocks into more complex molecules, and fueled by the use of cellular energy. Conversely, the term catabolism refers to exergonic pathways that break down complex molecules into simpler ones. Molecular energy stored in the bonds of complex molecules is released in catabolic pathways and harvested in such a way that it can be used to produce high-energy molecules, which are used to drive anabolic pathways. Thus, in terms of energy and molecules, cells are continually balancing catabolism with anabolism.

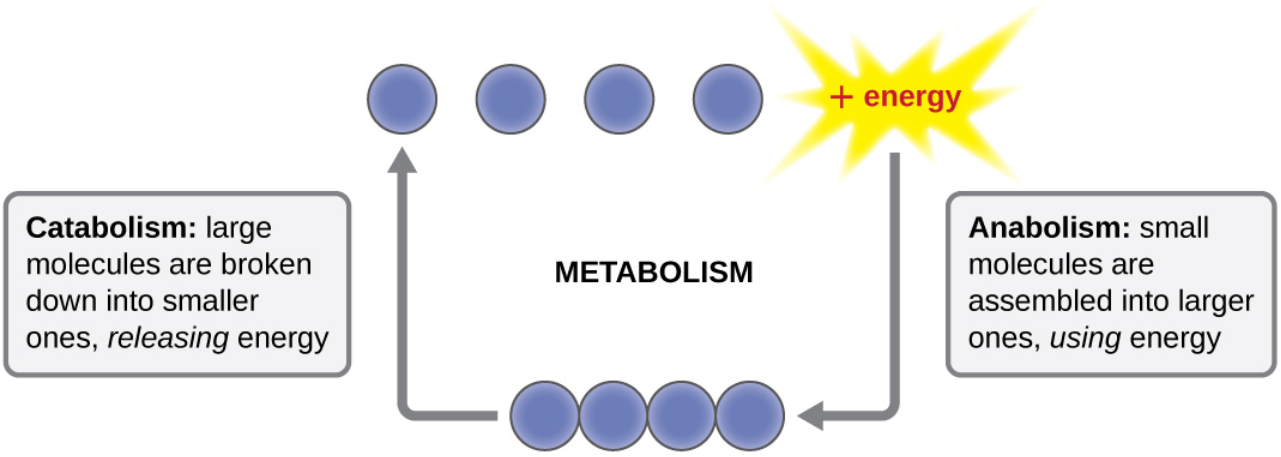


Figure 8.1.1: Metabolism includes catabolism and anabolism. Anabolic pathways require energy to synthesize larger molecules. Catabolic pathways generate energy by breaking down larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Classification by Carbon and Energy Source

Organisms can be identified according to the source of carbon they use for metabolism as well as their energy source. The prefixes auto- ("self") and hetero- ("other") refer to the origins of the carbon sources various organisms can use. Organisms that convert inorganic carbon dioxide (CO_2) into organic carbon compounds are autotroph**s**. Plants and cyanobacteria are well-known examples of autotrophs. Conversely, heterotroph**s** rely on more complex organic carbon compounds as nutrients; these are provided to them initially by autotrophs. Many organisms, ranging from humans to many prokaryotes, including the well-studied *Escherichia coli*, are heterotrophic.

Organisms can also be identified by the energy source they use. All energy is derived from the transfer of electrons, but the source of electrons differs between various types of organisms. The prefixes photo- ("light") and chemo- ("chemical") refer to the energy sources that various organisms use. Those that get their energy for electron transfer from light are phototroph**s**, whereas chemotroph**s** obtain energy for electron transfer by breaking chemical bonds. There are two types of chemotrophs: organotroph**s** and lithotroph**s**. Organotrophs, including humans, fungi, and many prokaryotes, are chemotrophs that obtain energy from organic compounds. Lithotrophs ("litho" means "rock") are chemotrophs that get energy from inorganic compounds, including hydrogen sulfide (H_2S) and reduced iron. Lithotrophy is unique to the microbial world.

The strategies used to obtain both carbon and energy can be combined for the classification of organisms according to nutritional type. Most organisms are chemoheterotrophs because they use organic molecules as both their electron and carbon sources. Table 8.1.1 summarizes this and the other classifications.

Table 8.1.1***:*** *Classifications of Organisms by Energy and Carbon Source*

Classifications		Energy Source	Carbon Source	Examples
Chemotrophs	Chemoautotrophs	Chemical	Inorganic	Hydrogen-, sulfur-, iron-, nitrogen-, and carbon monoxide-oxidizing bacteria
	Chemoheterotrophs	Chemical	Organic compounds	All animals, most fungi, protozoa, and bacteria
Phototrophs	Photoautotrophs	Light	Inorganic	All plants, algae, cyanobacteria, and green and purple sulfur bacteria
	Photoheterotrophs	Light	Organic compounds	Green and purple nonsulfur bacteria, heliobacteria

Exercise 8.1.2

1. Explain the difference between catabolism and anabolism.
2. Explain the difference between autotrophs and heterotrophs.

Oxidation and Reduction in Metabolism

The transfer of electrons between molecules is important because most of the energy stored in atoms and used to fuel cell functions is in the form of high-energy electrons. The transfer of energy in the form of electrons allows the cell to transfer and use energy incrementally; that is, in small packages rather than a single, destructive burst. Reactions that remove electrons from donor molecules, leaving them oxidized, are oxidation reaction**s**; those that add electrons to acceptor molecules, leaving them reduced, are reduction reaction**s**. Because electrons can move from one molecule to another, oxidation and reduction occur in tandem. These pairs of reactions are called oxidation-reduction reactions, or redox reaction**s**.

Energy Carriers: NAD+, NADP+, FAD, and ATP

The energy released from the breakdown of the chemical bonds within nutrients can be stored either through the reduction of electron carriers or in the bonds of adenosine triphosphate (ATP). In living systems, a small class of compounds functions as mobile electron carrier**s**, molecules that bind to and shuttle high-energy electrons between compounds in pathways. The principal electron carriers we will consider originate from the B vitamin group and are derivatives of nucleotides; they are nicotinamide adenine dinucleotide, nicotine adenine dinucleotide phosphate, and flavin adenine dinucleotide. These compounds can be easily reduced or oxidized. Nicotinamide adenine dinucleotide (NAD^+/NADH) is the most common mobile electron carrier used in catabolism. NAD^+ is the oxidized form of the molecule; NADH is the reduced form of the molecule. Nicotine adenine dinucleotide phosphate ($NADP^+$), the oxidized form of an NAD^+ variant that contains an extra phosphate group, is another important electron carrier; it forms NADPH when reduced. The oxidized form of flavin adenine dinucleotide is FAD, and its reduced form is $FADH_2$. Both NAD^+/NADH and FAD/$FADH_2$ are extensively used in energy extraction from sugars during catabolism in chemoheterotrophs, whereas $NADP^+$/NADPH plays an important role in anabolic reactions and photosynthesis. Collectively, $FADH_2$, NADH, and NADPH are often referred to as having reducing power due to their ability to donate electrons to various chemical reactions.

A living cell must be able to handle the energy released during catabolism in a way that enables the cell to store energy safely and release it for use only as needed. Living cells accomplish this by using the compound adenosine triphosphate (ATP). ATP is often called the “energy currency” of the cell, and, like currency, this versatile compound can be used to fill any energy need of the cell. At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to a ribose molecule and a single phosphate group. Ribose is a five-carbon sugar found in RNA, and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in the formation of adenosine diphosphate (ADP); the addition of a third phosphate group forms ATP (Figure 8.1.2). Adding a phosphate group to a molecule, a process called phosphorylation, requires energy. Phosphate groups are negatively charged and thus repel one another when they are arranged in series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. Thus, the bonds between phosphate groups (one in ADP and two in ATP) are called high-energy phosphate bond**s**. When these high-energy bonds are broken to release one phosphate (called inorganic phosphate [P_i]) or two connected phosphate groups (called pyrophosphate [PP_i]) from ATP through a process called dephosphorylation, energy is released to drive endergonic reactions (Figure 8.1.3).

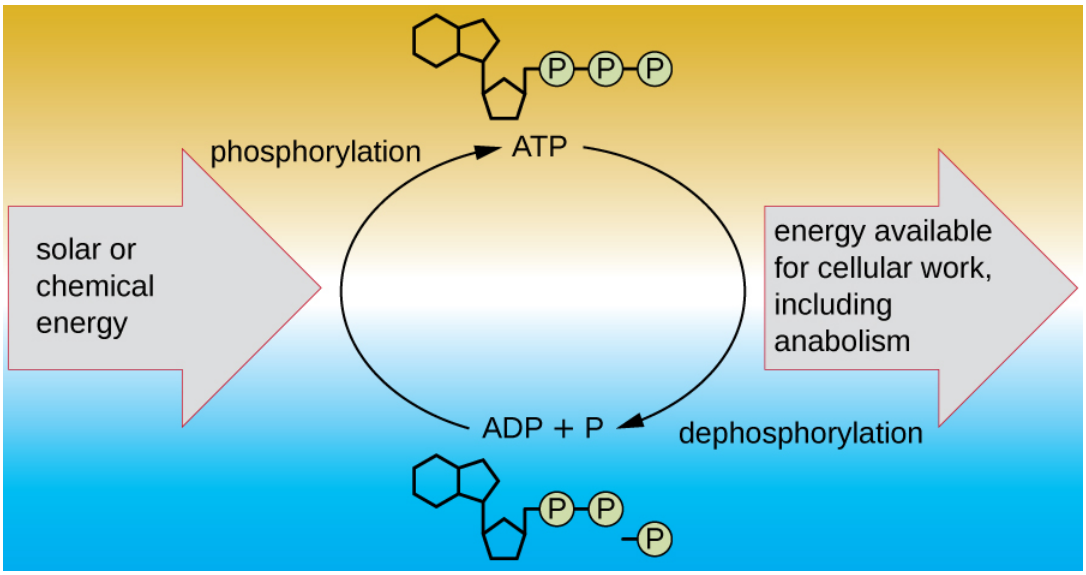


Figure 8.1.2: The energy released from dephosphorylation of ATP is used to drive cellular work, including anabolic pathways. ATP is regenerated through phosphorylation, harnessing the energy found in chemicals or from sunlight. (credit: modification of work by Robert Bear, David Rintoul)

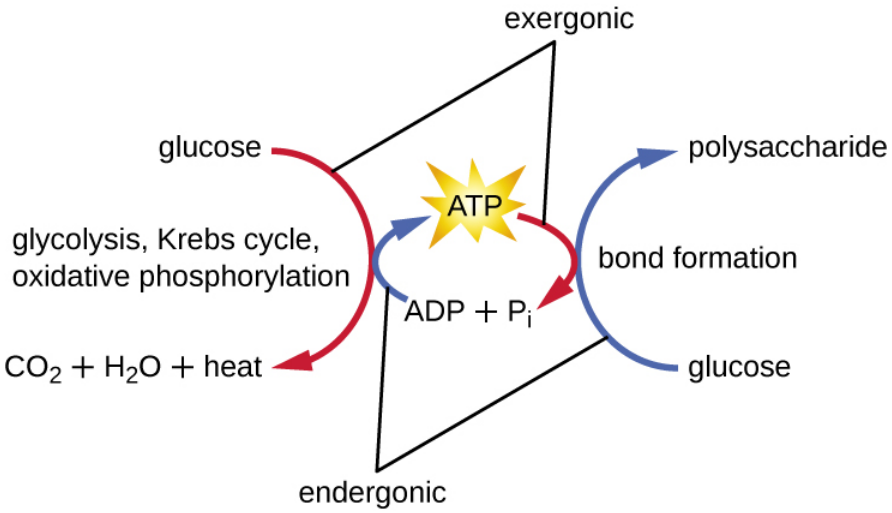


Figure 8.1.3: Exergonic reactions are coupled to endergonic ones, making the combination favorable. Here, the endergonic reaction of ATP phosphorylation is coupled to the exergonic reactions of catabolism. Similarly, the exergonic reaction of ATP dephosphorylation is coupled to the endergonic reaction of polypeptide formation, an example of anabolism.

Exercise 8.1.3

What is the function of an electron carrier?

Enzyme Structure and Function

A substance that helps speed up a chemical reaction is a catalyst. Catalysts are not used or changed during chemical reactions and, therefore, are reusable. Whereas inorganic molecules may serve as catalysts for a wide range of chemical reactions, proteins called enzymes serve as catalysts for biochemical reactions inside cells. Enzymes thus play an important role in controlling cellular metabolism.

An enzyme functions by lowering the activation energy of a chemical reaction inside the cell. Activation energy is the energy needed to form or break chemical bonds and convert reactants to products (Figure 8.1.4). Enzymes lower the activation energy by binding to the reactant molecules and holding them in such a way as to speed up the reaction.

The chemical reactants to which an enzyme binds are called substrates, and the location within the enzyme where the substrate binds is called the enzyme's active site. The characteristics of the amino acids near the active site create a very specific chemical environment within the active site that induces suitability to binding, albeit briefly, to a specific substrate (or substrates). Due to this jigsaw puzzle-like match between an enzyme and its substrates, enzymes are known for their specificity. In fact, as an enzyme binds to its substrate(s), the enzyme structure changes slightly to find the best fit between the transition state (a structural intermediate between the substrate and product) and the active site, just as a rubber glove molds to a hand inserted into it. This active-site modification in the presence of substrate, along with the simultaneous formation of the transition state, is called induced fit (Figure 8.1.5). Overall, there is a specifically matched enzyme for each substrate and, thus, for each chemical reaction; however, there is some flexibility as well. Some enzymes have the ability to act on several different structurally related substrates.

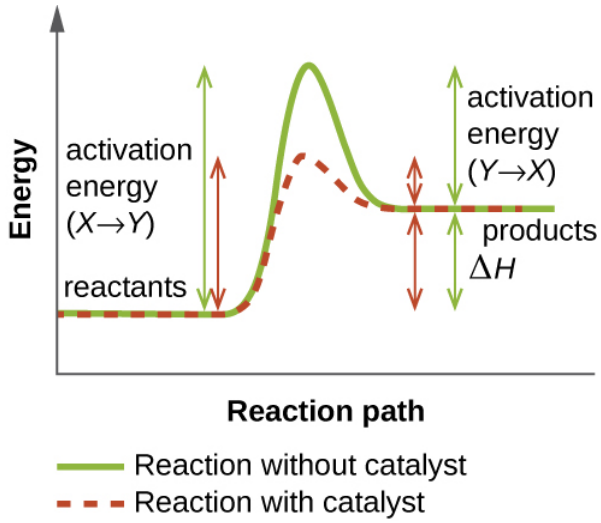


Figure 8.1.4: Enzymes lower the activation energy of a chemical reaction.

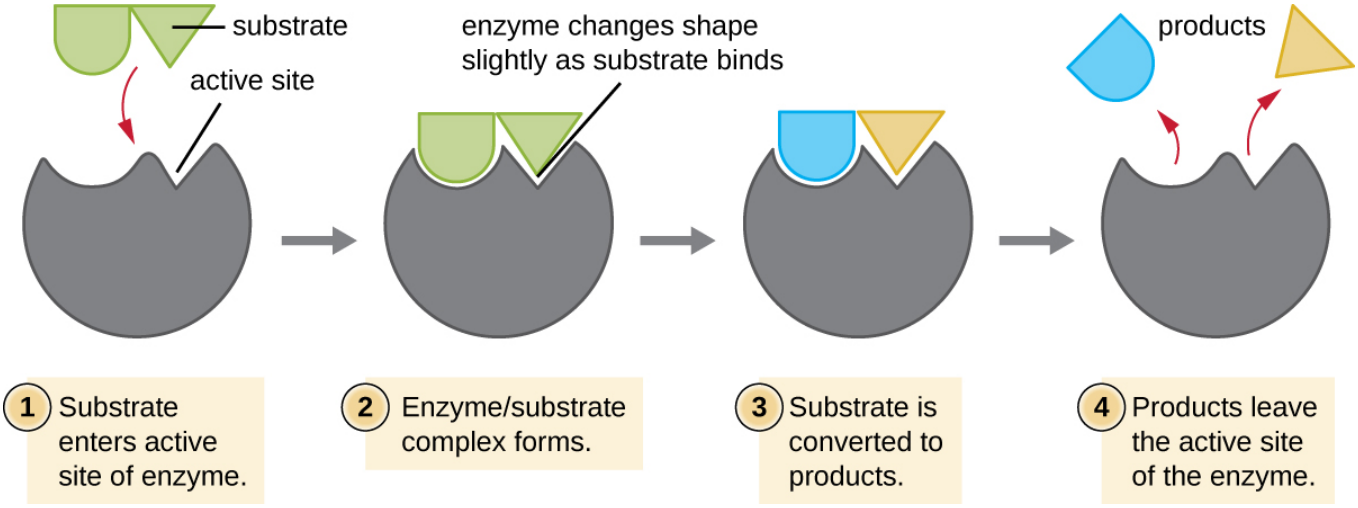


Figure 8.1.5: According to the induced-fit model, the active site of the enzyme undergoes conformational changes upon binding with the substrate.

Enzymes are subject to influences by local environmental conditions such as pH, substrate concentration, and temperature. Although increasing the environmental temperature generally increases reaction rates, enzyme catalyzed or otherwise, increasing or decreasing the temperature outside of an optimal range can affect chemical bonds within the active site, making them less well suited to bind substrates. High temperatures will eventually cause enzymes, like other biological molecules, to denature, losing their three-dimensional structure and function. Enzymes are also suited to function best within a certain pH range, and, as with temperature, extreme environmental pH values (acidic or basic) can cause enzymes to denature. Active-site amino-acid side chains have their own acidic or basic properties that are optimal for catalysis and, therefore, are sensitive to changes in pH.

Another factor that influences enzyme activity is substrate concentration: Enzyme activity is increased at higher concentrations of substrate until it reaches a saturation point at which the enzyme can bind no additional substrate. Overall, enzymes are optimized to work best under the environmental conditions in which the organisms that produce them live. For example, while microbes that inhabit hot springs have enzymes that work best at high temperatures, human pathogens have enzymes that work best at 37°C. Similarly, while enzymes produced by most organisms work best at a neutral pH, microbes growing in acidic environments make enzymes optimized to low pH conditions, allowing for their growth at those conditions.

Many enzymes do not work optimally, or even at all, unless bound to other specific nonprotein helper molecules, either temporarily through ionic or hydrogen bonds or permanently through stronger covalent bonds. Binding to these molecules promotes optimal conformation and function for their respective enzymes. Two types of helper molecules are cofactors and coenzymes. Cofactors are inorganic ions such as iron (Fe^{2+}) and magnesium (Mg^{2+}) that help stabilize enzyme conformation and function. One example of an enzyme that requires a metal ion as a cofactor is the enzyme that builds DNA molecules, DNA polymerase, which requires a bound zinc ion (Zn^{2+}) to function.

Coenzymes are organic helper molecules that are required for enzyme action. Like enzymes, they are not consumed and, hence, are reusable. The most common sources of coenzymes are dietary vitamins. Some vitamins are precursors to coenzymes and others act directly as coenzymes.

Some cofactors and coenzymes, like coenzyme A (CoA), often bind to the enzyme's active site, aiding in the chemistry of the transition of a substrate to a product (Figure 8.1.6). In such cases, an enzyme lacking a necessary cofactor or coenzyme is called an apoenzyme and is inactive. Conversely, an enzyme with the necessary associated cofactor or coenzyme is called a holoenzyme and is active. NADH and ATP are also both examples of commonly used coenzymes that provide high-energy electrons or phosphate groups, respectively, which bind to enzymes, thereby activating them.

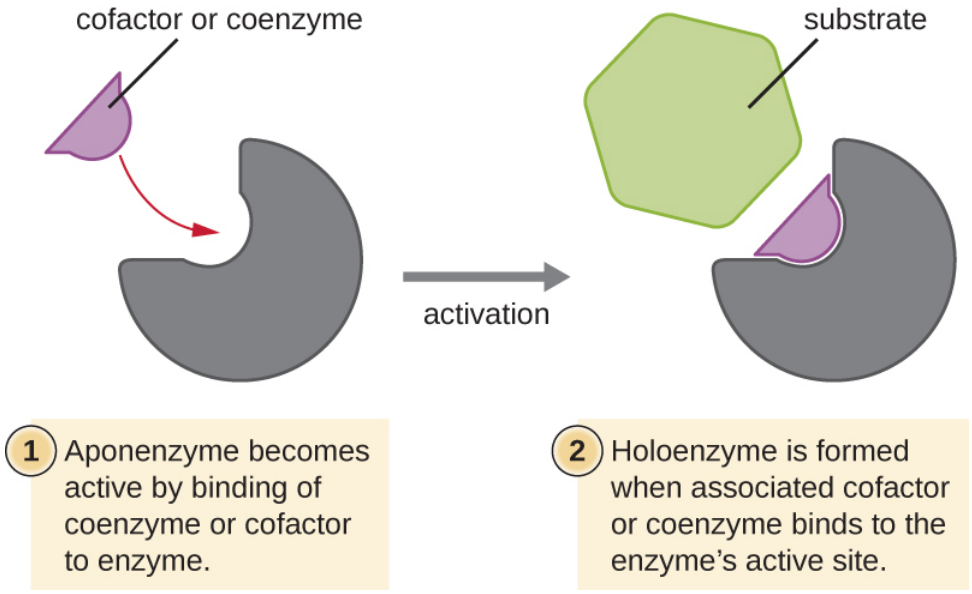


Figure 8.1.6: The binding of a coenzyme or cofactor to an apoenzyme is often required to form an active holoenzyme.

Exercise 8.1.4

What role do enzymes play in a chemical reaction?

Enzyme Inhibitors

Enzymes can be regulated in ways that either promote or reduce their activity. There are many different kinds of molecules that inhibit or promote enzyme function, and various mechanisms exist for doing so (Figure 8.1.7). A competitive inhibitor is a molecule similar enough to a substrate that it can compete with the substrate for binding to the active site by simply blocking the substrate from binding. For a competitive inhibitor to be effective, the inhibitor concentration needs to be approximately equal to the substrate concentration. Sulfa drugs provide a good example of competitive competition. They are used to treat bacterial infections because they bind to the active site of an enzyme within the bacterial folic acid synthesis pathway. When present in a sufficient

dose, a sulfa drug prevents folic acid synthesis, and bacteria are unable to grow because they cannot synthesize DNA, RNA, and proteins. Humans are unaffected because we obtain folic acid from our diets.

On the other hand, a noncompetitive (allosteric) inhibitor binds to the enzyme at an allosteric site, a location other than the active site, and still manages to block substrate binding to the active site by inducing a conformational change that reduces the affinity of the enzyme for its substrate (Figure 8.1.8). Because only one inhibitor molecule is needed per enzyme for effective inhibition, the concentration of inhibitors needed for noncompetitive inhibition is typically much lower than the substrate concentration.

In addition to allosteric inhibitors, there are allosteric activators that bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s).

Allosteric control is an important mechanism of regulation of metabolic pathways involved in both catabolism and anabolism. In a most efficient and elegant way, cells have evolved also to use the products of their own metabolic reactions for feedback inhibition of enzyme activity. Feedback inhibition involves the use of a pathway product to regulate its own further production. The cell responds to the abundance of specific products by slowing production during anabolic or catabolic reactions (Figure 8.1.8).

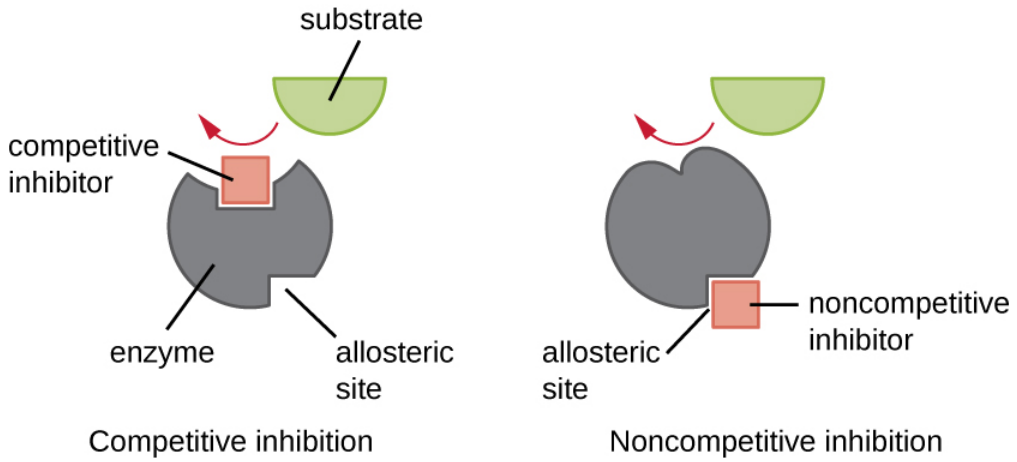


Figure 8.1.7: Enzyme activity can be regulated by either competitive inhibitors, which bind to the active site, or noncompetitive inhibitors, which bind to an allosteric site.

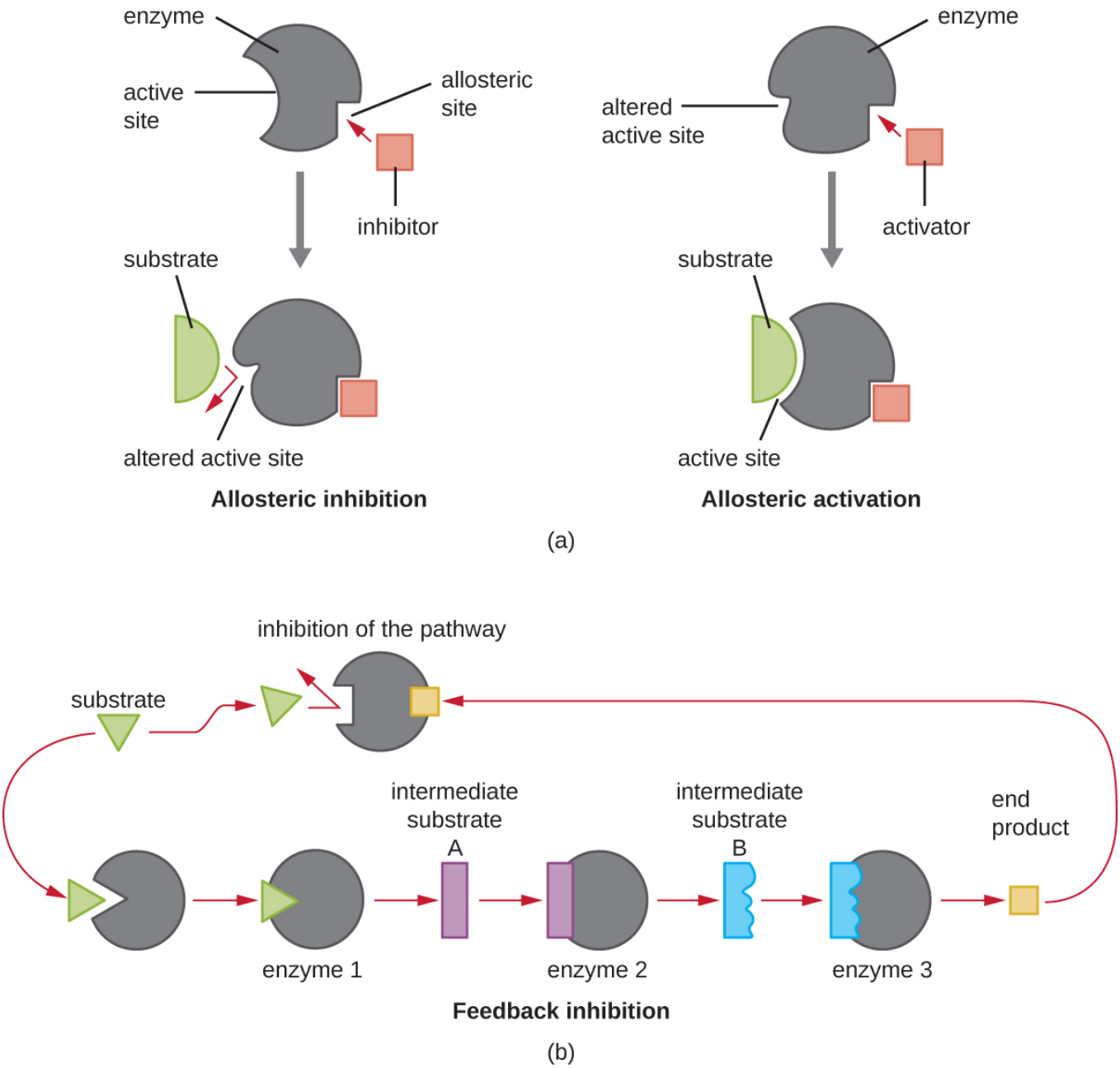


Figure 8.1.8: (a) Binding of an allosteric inhibitor reduces enzyme activity, but binding of an allosteric activator increases enzyme activity. (b) Feedback inhibition, where the end product of the pathway serves as a noncompetitive inhibitor to an enzyme early in the pathway, is an important mechanism of allosteric regulation in cells.

Exercise 8.1.5

Explain the difference between a competitive inhibitor and a noncompetitive inhibitor.

Key Concepts and Summary

- **Metabolism** includes chemical reactions that break down complex molecules (**catabolism**) and those that build complex molecules (**anabolism**).
- Organisms may be classified according to their source of carbon. **Autotrophs** convert inorganic carbon dioxide into organic carbon; **heterotrophs** use fixed organic carbon compounds.
- Organisms may also be classified according to their energy source. **Phototrophs** obtain their energy from light. **Chemotrophs** get their energy from chemical compounds. **Organotrophs** use organic molecules, and **lithotrophs** use inorganic chemicals.

- Cellular **electron carriers** accept high-energy electrons from foods and later serve as electron donors in subsequent **redox reactions**. **FAD/FADH$_2$, NAD$^+$/NADH, and NADP$^+$/NADPH** are important electron carriers.
- **Adenosine triphosphate (ATP)** serves as the energy currency of the cell, safely storing chemical energy in its two **high-energy phosphate bonds** for later use to drive processes requiring energy.
- **Enzymes** are biological **catalysts** that increase the rate of chemical reactions inside cells by lowering the activation energy required for the reaction to proceed.
- In nature, **exergonic reactions** do not require energy beyond activation energy to proceed, and they release energy. They may proceed without enzymes, but at a slow rate. Conversely, **endergonic reactions** require energy beyond activation energy to occur. In cells, endergonic reactions are coupled to exergonic reactions, making the combination energetically favorable.
- **Substrates** bind to the enzyme's **active site**. This process typically alters the structures of both the active site and the substrate, favoring transition-state formation; this is known as **induced fit**.
- **Cofactors** are inorganic ions that stabilize enzyme conformation and function. **Coenzymes** are organic molecules required for proper enzyme function and are often derived from vitamins. An enzyme lacking a cofactor or coenzyme is an **apoenzyme;** an enzyme with a bound cofactor or coenzyme is a **holoenzyme**.
- **Competitive inhibitors** regulate enzymes by binding to an enzyme's active site, preventing substrate binding. **Noncompetitive (allosteric) inhibitors** bind to **allosteric sites**, inducing a conformational change in the enzyme that prevents it from functioning. **Feedback inhibition** occurs when the product of a metabolic pathway noncompetitively binds to an enzyme early on in the pathway, ultimately preventing the synthesis of the product.

Multiple Choice

Which of the following is an organism that obtains its energy from the transfer of electrons originating from chemical compounds and its carbon from an inorganic source?

A. chemoautotroph
B. chemoheterotroph
C. photoheterotroph
D. photoautotroph

A

Which of the following molecules is reduced?

A. NAD^+
B. FAD
C. O_2
D. NADPH

D

Enzymes work by which of the following?

A. increasing the activation energy
B. reducing the activation energy
C.making exergonic reactions endergonic
D. making endergonic reactions exergonic

B

To which of the following does a competitive inhibitor most structurally resemble?

A. the active site
B. the allosteric site

C. the substrate
D. a coenzyme

C

Which of the following are organic molecules that help enzymes work correctly?

A. cofactors
B. coenzymes
C. holoenzymes
D. apoenzymes

B

Fill in the Blank

Processes in which cellular energy is used to make complex molecules from simpler ones are described as _____.

---

anabolic

The loss of an electron from a molecule is called _____.

---

oxidation

The part of an enzyme to which a substrate binds is called the _____.

---

active site

True/False

Competitive inhibitors bind to allosteric sites.

False

Short Answer

In cells, can an oxidation reaction happen in the absence of a reduction reaction? Explain.

What is the function of molecules like NAD^+/NADH and FAD/$FADH_2$ in cells?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.1: Energy, Matter, and Enzymes is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.2: Catabolism of Carbohydrates

Skills to Develop

- Describe why glycolysis is not oxygen dependent
- Define and describe the net yield of three-carbon molecules, ATP, and NADH from glycolysis
- Explain how three-carbon pyruvate molecules are converted into two-carbon acetyl groups that can be funneled into the Krebs cycle.
- Define and describe the net yield of CO_2, GTP/ATP, $FADH_2$, and NADH from the Krebs cycle
- Explain how intermediate carbon molecules of the Krebs cycle can be used in a cell

Extensive enzyme pathways exist for breaking down carbohydrates to capture energy in ATP bonds. In addition, many catabolic pathways produce intermediate molecules that are also used as building blocks for anabolism. Understanding these processes is important for several reasons. First, because the main metabolic processes involved are common to a wide range of chemoheterotrophic organisms, we can learn a great deal about human metabolism by studying metabolism in more easily manipulated bacteria like *E. coli*. Second, because animal and human pathogens are also chemoheterotrophs, learning about the details of metabolism in these bacteria, including possible differences between bacterial and human pathways, is useful for the diagnosis of pathogens as well as for the discovery of antimicrobial therapies targeting specific pathogens. Last, learning specifically about the pathways involved in chemoheterotrophic metabolism also serves as a basis for comparing other more unusual metabolic strategies used by microbes. Although the chemical source of electrons initiating electron transfer is different between chemoheterorophs and chemoautotrophs, many similar processes are used in both types of organisms.

The typical example used to introduce concepts of metabolism to students is carbohydrate catabolism. For chemoheterotrophs, our examples of metabolism start with the catabolism of polysaccharides such as glycogen, starch, or cellulose. Enzymes such as amylase, which breaks down glycogen or starch, and cellulases, which break down cellulose, can cause the hydrolysis of glycosidic bonds between the glucose monomers in these polymers, releasing glucose for further catabolism.

Glycolysis

For bacteria, eukaryotes, and most archaea, glycolysis is the most common pathway for the catabolism of glucose; it produces energy, reduced electron carriers, and precursor molecules for cellular metabolism. Every living organism carries out some form of glycolysis, suggesting this mechanism is an ancient universal metabolic process. The process itself does not use oxygen; however, glycolysis can be coupled with additional metabolic processes that are either aerobic or anaerobic. Glycolysis takes place in the cytoplasm of prokaryotic and eukaryotic cells. It begins with a single six-carbon glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Pyruvate may be broken down further after glycolysis to harness more energy through aerobic or anaerobic respiration, but many organisms, including many microbes, may be unable to respire; for these organisms, glycolysis may be their only source of generating ATP.

The type of glycolysis found in animals and that is most common in microbes is the Embden-Meyerhof-Parnas (EMP) pathway, named after Gustav Embden (1874–1933), Otto Meyerhof (1884–1951), and Jakub Parnas (1884–1949). Glycolysis using the EMP pathway consists of two distinct phases (Figure 8.2.1). The first part of the pathway, called the energy investment phase, uses energy from two ATP molecules to modify a glucose molecule so that the six-carbon sugar molecule can be split evenly into two phosphorylated three-carbon molecules called glyceraldehyde 3-phosphate (G3P). The second part of the pathway, called the energy payoff phase, extracts energy by oxidizing G3P to pyruvate, producing four ATP molecules and reducing two molecules of NAD^+ to two molecules of NADH, using electrons that originated from glucose. (A discussion and illustration of the full EMP pathway with chemical structures and enzyme names appear in Appendix C.)

The ATP molecules produced during the energy payoff phase of glycolysis are formed by substrate-level phosphorylation (Figure 8.2.1), one of two mechanisms for producing ATP. In substrate-level phosphorylation, a phosphate group is removed from an organic molecule and is directly transferred to an available ADP molecule, producing ATP. During glycolysis, high-energy phosphate groups from the intermediate molecules are added to ADP to make ATP.

Overall, in this process of glycolysis, the net gain from the breakdown of a single glucose molecule is:

- two ATP molecules

- two NADH molecule, and
- two pyruvate molecules.

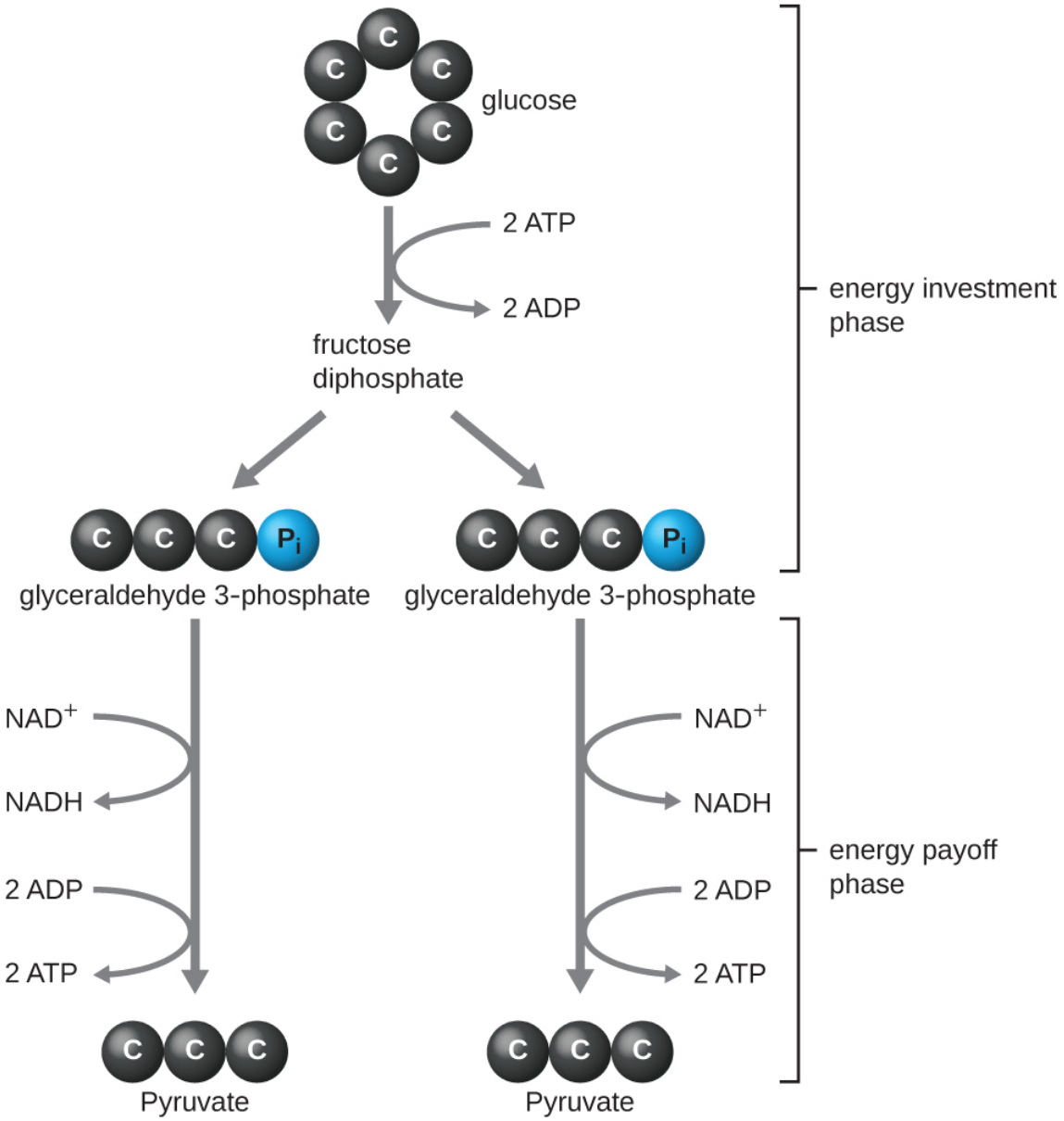


Figure 8.2.1: The energy investment phase of the Embden-Meyerhof-Parnas glycolysis pathway uses two ATP molecules to phosphorylate glucose, forming two glyceraldehyde 3-phosphate (G3P) molecules. The energy payoff phase harnesses the energy in the G3P molecules, producing four ATP molecules, two NADH molecules, and two pyruvates.

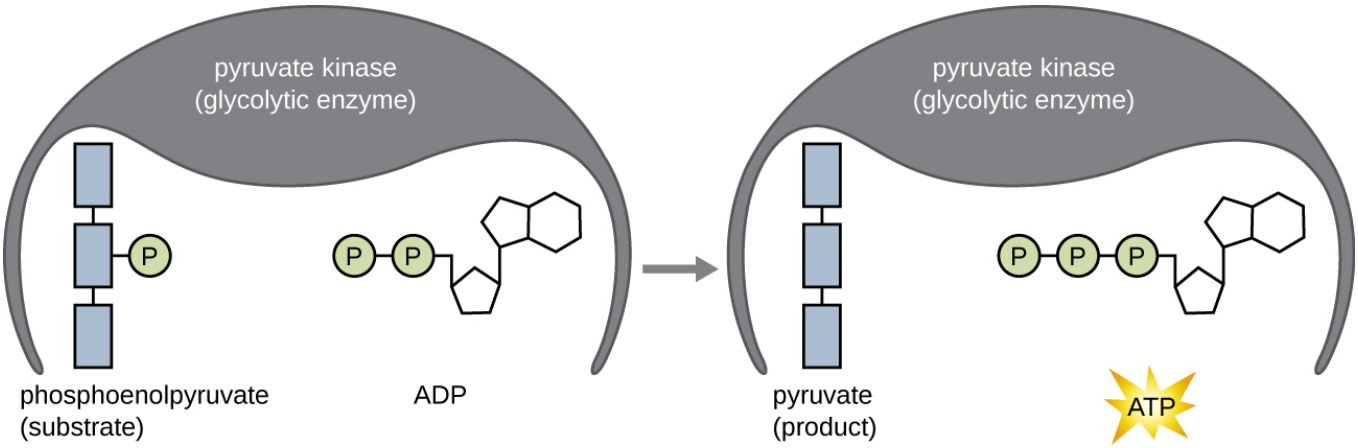


Figure 8.2.2: The ATP made during glycolysis is a result of substrate-level phosphorylation. One of the two enzymatic reactions in the energy payoff phase of Embden Meyerhof-Parnas glycolysis that produce ATP in this way is shown here.

Other Glycolytic Pathways

When we refer to glycolysis, unless otherwise indicated, we are referring to the EMP pathway used by animals and many bacteria. However, some prokaryotes use alternative glycolytic pathways. One important alternative is the Entner-Doudoroff (ED) pathway, named after its discoverers Nathan Entner and Michael Doudoroff (1911–1975). Although some bacteria, including the opportunistic gram-negative pathogen *Pseudomonas aeruginosa*, contain only the ED pathway for glycolysis, other bacteria, like *E. coli*, have the ability to use either the ED pathway or the EMP pathway.

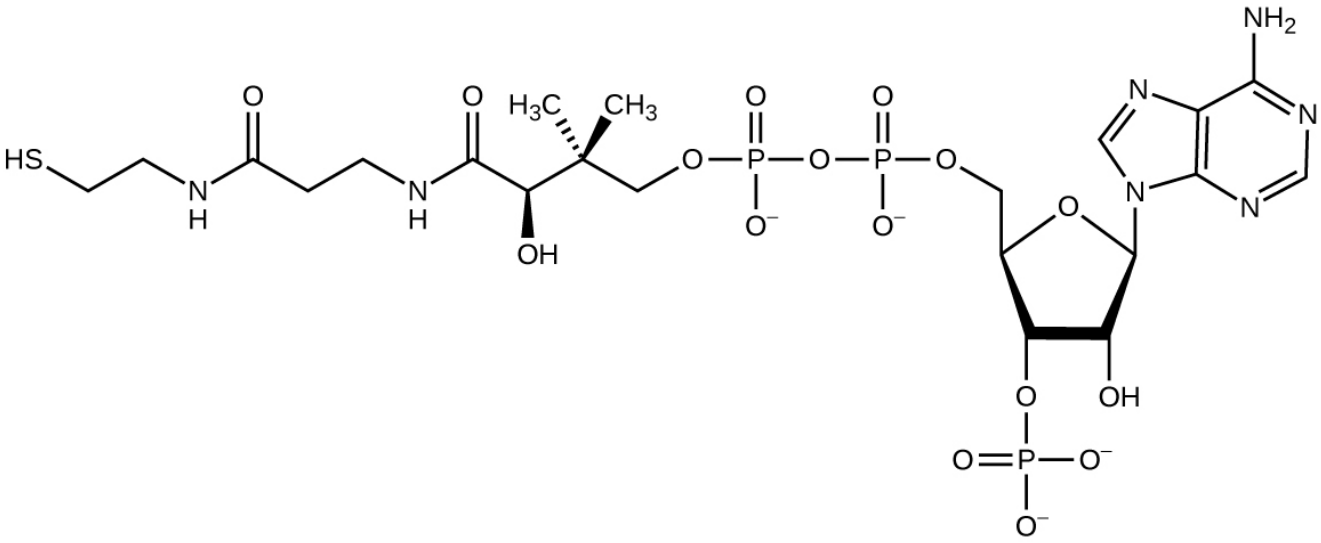
A third type of glycolytic pathway that occurs in all cells, which is quite different from the previous two pathways, is the pentose phosphate pathway (PPP) also called the phosphogluconate pathway or the hexose monophosphate shunt. Evidence suggests that the PPP may be the most ancient universal glycolytic pathway. The intermediates from the PPP are used for the biosynthesis of nucleotides and amino acids. Therefore, this glycolytic pathway may be favored when the cell has need for nucleic acid and/or protein synthesis, respectively. A discussion and illustration of the complete ED pathway and PPP with chemical structures and enzyme names appear in Appendix C.

Exercise 8.2.1

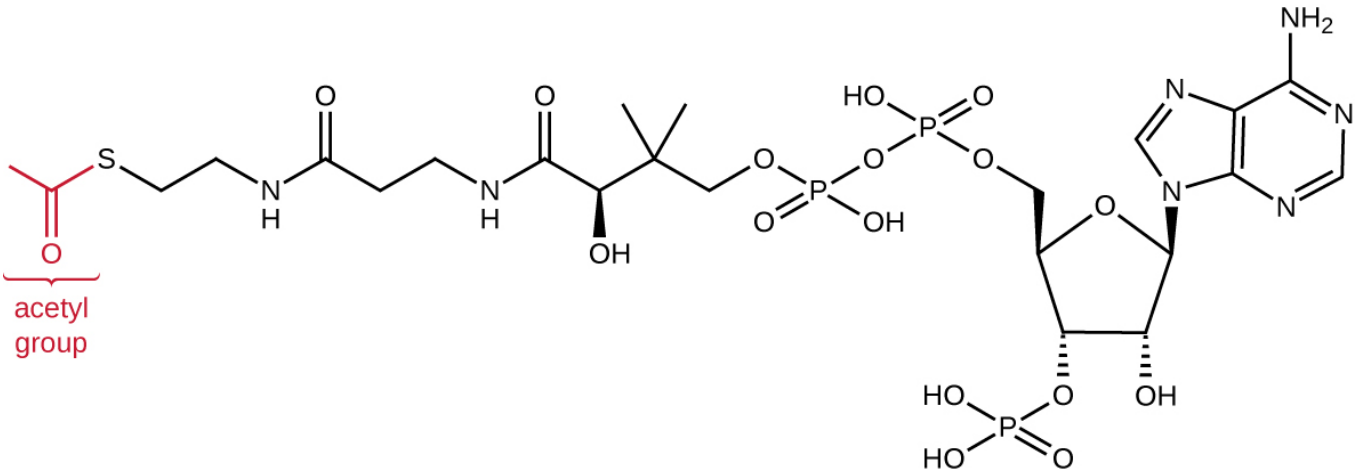
When might an organism use the ED pathway or the PPP for glycolysis?

Transition Reaction, Coenzyme A, and the Krebs Cycle

Glycolysis produces pyruvate, which can be further oxidized to capture more energy. For pyruvate to enter the next oxidative pathway, it must first be decarboxylated by the enzyme complex pyruvate dehydrogenase to a two-carbon acetyl group in the transition reaction, also called the bridge reaction (see Appendix C and Figure 8.2.3). In the transition reaction, electrons are also transferred to NAD^+ to form NADH. To proceed to the next phase of this metabolic process, the comparatively tiny two-carbon acetyl must be attached to a very large carrier compound called coenzyme A (CoA). The transition reaction occurs in the mitochondrial matrix of eukaryotes; in prokaryotes, it occurs in the cytoplasm because prokaryotes lack membrane-enclosed organelles.



(a) coenzyme A without an attached acetyl group



(b) coenzyme A with an attached acetyl group

Figure 8.2.3: *(a) Coenzyme A is shown here without an attached acetyl group. (b) Coenzyme A is shown here with an attached acetyl group.*

The Krebs cycle transfers remaining electrons from the acetyl group produced during the transition reaction to electron carrier molecules, thus reducing them. The Krebs cycle also occurs in the cytoplasm of prokaryotes along with glycolysis and the transition reaction, but it takes place in the mitochondrial matrix of eukaryotic cells where the transition reaction also occurs. The Krebs cycle is named after its discoverer, British scientist Hans Adolf Krebs (1900–1981) and is also called the citric acid cycle, or the tricarboxylic acid cycle (TCA) because citric acid has three carboxyl groups in its structure. Unlike glycolysis, the Krebs cycle is a closed loop: The last part of the pathway regenerates the compound used in the first step (Figure 8.2.4). The eight steps of the cycle are a series of chemical reactions that capture the two-carbon acetyl group (the CoA carrier does not enter the Krebs cycle) from the transition reaction, which is added to a four-carbon intermediate in the Krebs cycle, producing the six-carbon intermediate citric acid (giving the alternate name for this cycle). As one turn of the cycle returns to the starting point of the four-carbon intermediate, the cycle produces two CO_2 molecules, one ATP molecule (or an equivalent, such as guanosine triphosphate [GTP]) produced by substrate-level phosphorylation, and three molecules of NADH and one of $FADH_2$. (A discussion and detailed illustration of the full Krebs cycle appear in Appendix C.)

Although many organisms use the Krebs cycle as described as part of glucose metabolism, several of the intermediate compounds in the Krebs cycle can be used in synthesizing a wide variety of important cellular molecules, including amino acids, chlorophylls,

fatty acids, and nucleotides; therefore, the cycle is both anabolic and catabolic (Figure 8.2.5).

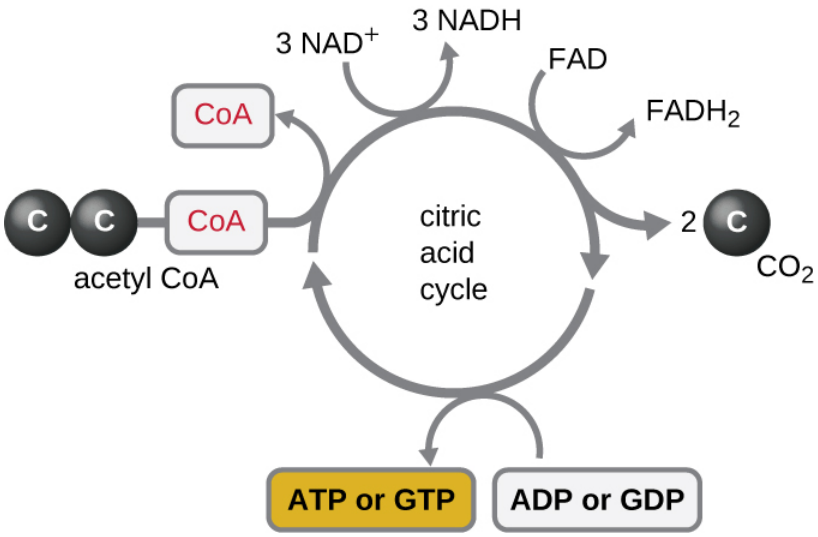


Figure 8.2.4: The Krebs cycle, also known as the citric acid cycle, is summarized here. Note incoming two-carbon acetyl results in the main outputs per turn of two CO_2, three NADH, one $FADH_2$, and one ATP (or GTP) molecules made by substrate-level phosphorylation. Two turns of the Krebs cycle are required to process all of the carbon from one glucose molecule.

https://geo.libretexts.org/@go/page/6219

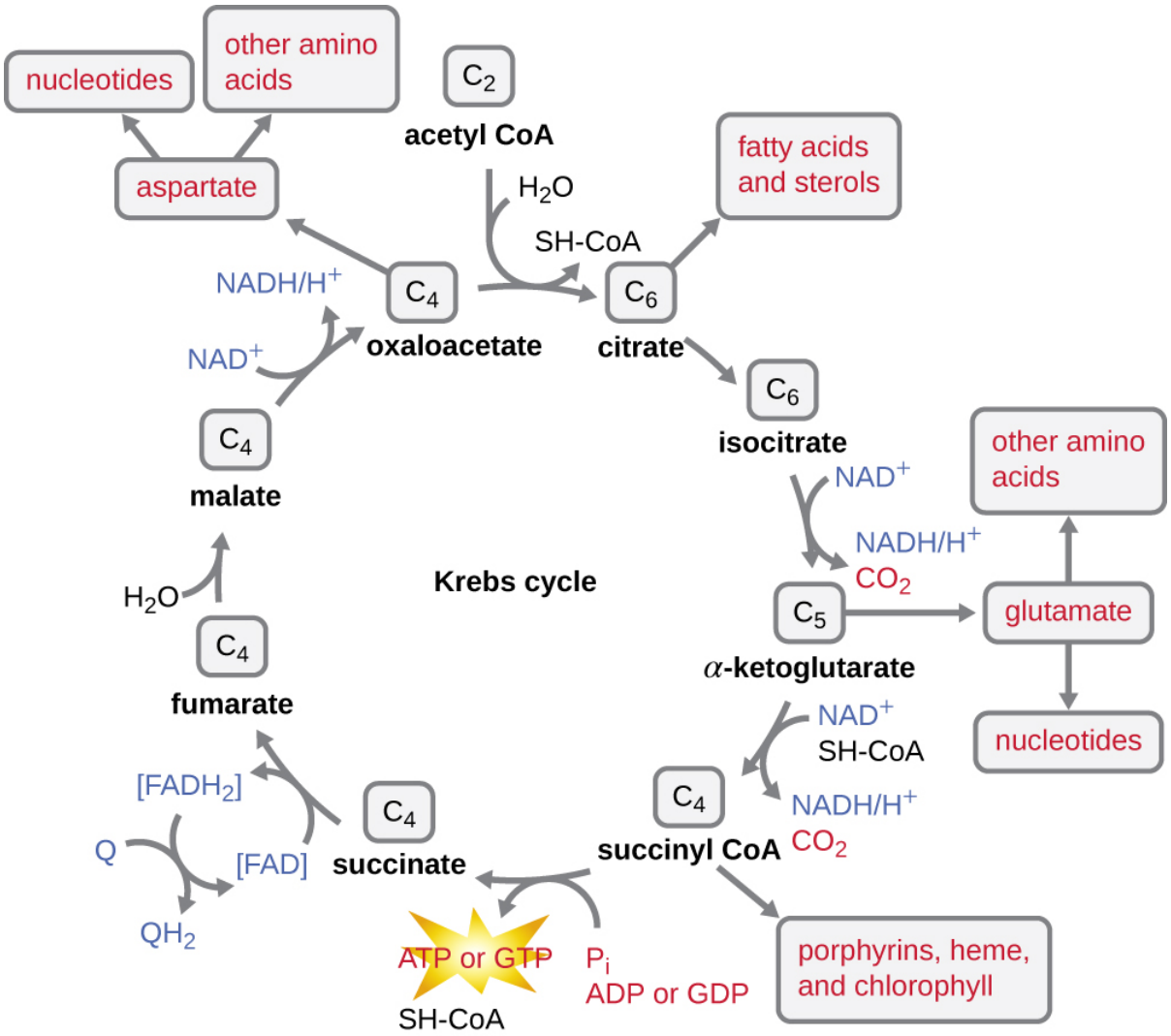


Figure 8.2.5: *Many organisms use intermediates from the Krebs cycle, such as amino acids, fatty acids, and nucleotides, as building blocks for biosynthesis.*

Key Concepts and Summary

- **Glycolysis** is the first step in the breakdown of glucose, resulting in the formation of ATP, which is produced by **substrate-level phosphorylation**; NADH; and two pyruvate molecules. Glycolysis does not use oxygen and is not oxygen dependent.
- After glycolysis, a three-carbon pyruvate is decarboxylated to form a two-carbon acetyl group, coupled with the formation of NADH. The acetyl group is attached to a large carrier compound called coenzyme A.
- After the transition step, coenzyme A transports the two-carbon acetyl to the **Krebs cycle**, where the two carbons enter the cycle. Per turn of the cycle, one acetyl group derived from glycolysis is further oxidized, producing three NADH molecules, one $FADH_2$, and one ATP by **substrate-level phosphorylation**, and releasing two CO_2molecules.
- The Krebs cycle may be used for other purposes. Many of the intermediates are used to synthesize important cellular molecules, including amino acids, chlorophylls, fatty acids, and nucleotides.

Multiple Choice

During which of the following is ATP not made by substrate-level phosphorylation?

A. Embden-Meyerhof pathway
B. Transition reaction
C. Krebs cycle
D. Entner-Doudoroff pathway

B

Which of the following products is made during Embden-Meyerhof glycolysis?

A. NAD+
B. pyruvate
C. CO_2
D. two-carbon acetyl

B

During the catabolism of glucose, which of the following is produced only in the Krebs cycle?

A. ATP
B. NADH
C. NADPH
D. $FADH_2$

D

Which of the following is not a name for the cycle resulting in the conversion of a two-carbon acetyl to one ATP, two CO_2, one $FADH_2$, and three NADH molecules?

A. Krebs cycle
B. tricarboxylic acid cycle
C. Calvin cycle
D. citric acid cycle

C

True/False

Glycolysis requires oxygen or another inorganic final electron acceptor to proceed.

False

Fill in the Blank

Per turn of the Krebs cycle, one acetyl is oxidized, forming ____ CO_2, ____ ATP, ____ NADH, and ____ $FADH_2$molecules.

2; 1; 3; 1

Most commonly, glycolysis occurs by the _____ pathway.

Embden-Meyerhof

Short Answer

What is substrate-level phosphorylation? When does it occur during the breakdown of glucose to CO_2?

Why is the Krebs cycle important in both catabolism and anabolism?

Critical Thinking

What would be the consequences to a cell of having a mutation that knocks out coenzyme A synthesis?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.2: Catabolism of Carbohydrates is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.3: Cellular Respiration

skills to develop

- Compare and contrast the electron transport system location and function in a prokaryotic cell and a eukaryotic cell
- Compare and contrast the differences between substrate-level and oxidative phosphorylation
- Explain the relationship between chemiosmosis and proton motive force
- Describe the function and location of ATP synthase in a prokaryotic versus eukaryotic cell
- Compare and contrast aerobic and anaerobic respiration

We have just discussed two pathways in glucose catabolism—glycolysis and the Krebs cycle—that generate ATP by substrate-level phosphorylation. Most ATP, however, is generated during a separate process called oxidative phosphorylation, which occurs during cellular respiration. Cellular respiration begins when electrons are transferred from NADH and $FADH_2$—made in glycolysis, the transition reaction, and the Krebs cycle—through a series of chemical reactions to a final inorganic electron acceptor (either oxygen in aerobic respiration or non-oxygen inorganic molecules in anaerobic respiration). These electron transfers take place on the inner part of the cell membrane of prokaryotic cells or in specialized protein complexes in the inner membrane of the mitochondria of eukaryotic cells. The energy of the electrons is harvested to generate an electrochemical gradient across the membrane, which is used to make ATP by oxidative phosphorylation.

Electron Transport System

The electron transport system (ETS) is the last component involved in the process of cellular respiration; it comprises a series of membrane-associated protein complexes and associated mobile accessory electron carriers. Electron transport is a series of chemical reactions that resembles a bucket brigade in that electrons from NADH and $FADH_2$ are passed rapidly from one ETS electron carrier to the next. These carriers can pass electrons along in the ETS because of their redox potential. For a protein or chemical to accept electrons, it must have a more positive redox potential than the electron donor. Therefore, electrons move from electron carriers with more negative redox potential to those with more positive redox potential. The four major classes of electron carriers involved in both eukaryotic and prokaryotic electron transport systems are the cytochromes, flavoproteins, iron-sulfur proteins, and the quinones.

In aerobic respiration, the final electron acceptor (i.e., the one having the most positive redox potential) at the end of the ETS is an oxygen molecule (O_2) that becomes reduced to water (H_2O) by the final ETS carrier. This electron carrier, cytochrome oxidase, differs between bacterial types and can be used to differentiate closely related bacteria for diagnoses. For example, the gram-negative opportunist *Pseudomonas aeruginosa* and the gram-negative cholera-causing *Vibrio cholerae* use cytochrome c oxidase, which can be detected by the oxidase test, whereas other gram-negative Enterobacteriaceae, like *E. coli*, are negative for this test because they produce different cytochrome oxidase types.

There are many circumstances under which aerobic respiration is not possible, including any one or more of the following:

- The cell lacks genes encoding an appropriate cytochrome oxidase for transferring electrons to oxygen at the end of the electron transport system.
- The cell lacks genes encoding enzymes to minimize the severely damaging effects of dangerous oxygen radicals produced during aerobic respiration, such as hydrogen peroxide (H_2O_2) or superoxide (O2–).(O2–).
- The cell lacks a sufficient amount of oxygen to carry out aerobic respiration.

One possible alternative to aerobic respiration is anaerobic respiration, using an inorganic molecule other than oxygen as a final electron acceptor. There are many types of anaerobic respiration found in bacteria and archaea. Denitrifiers are important soil bacteria that use nitrate (NO3–)(NO3–) and nitrite (NO2–)(NO2–) as final electron acceptors, producing nitrogen gas (N_2). Many aerobically respiring bacteria, including *E. coli*, switch to using nitrate as a final electron acceptor and producing nitrite when oxygen levels have been depleted.

Microbes using anaerobic respiration commonly have an intact Krebs cycle, so these organisms can access the energy of the NADH and $FADH_2$ molecules formed. However, anaerobic respirers use altered ETS carriers encoded by their genomes, including distinct complexes for electron transfer to their final electron acceptors. Smaller electrochemical gradients are generated from these electron transfer systems, so less ATP is formed through anaerobic respiration.

Exercise 8.3.1

Do both aerobic respiration and anaerobic respiration use an electron transport chain?

Chemiosmosis, Proton Motive Force, and Oxidative Phosphorylation

In each transfer of an electron through the ETS, the electron loses energy, but with some transfers, the energy is stored as potential energy by using it to pump hydrogen ions (H^+) across a membrane. In prokaryotic cells, H^+ is pumped to the outside of the cytoplasmic membrane (called the periplasmic space in gram-negative and gram-positive bacteria), and in eukaryotic cells, they are pumped from the mitochondrial matrix across the inner mitochondrial membrane into the intermembrane space. There is an uneven distribution of H^+ across the membrane that establishes an electrochemical gradient because H^+ ions are positively charged (electrical) and there is a higher concentration (chemical) on one side of the membrane. This electrochemical gradient formed by the accumulation of H^+ (also known as a proton) on one side of the membrane compared with the other is referred to as the proton motive force (PMF). Because the ions involved are H^+, a pH gradient is also established, with the side of the membrane having the higher concentration of H^+ being more acidic. Beyond the use of the PMF to make ATP, as discussed in this chapter, the PMF can also be used to drive other energetically unfavorable processes, including nutrient transport and flagella rotation for motility.

The potential energy of this electrochemical gradient generated by the ETS causes the H^+ to diffuse across a membrane (the plasma membrane in prokaryotic cells and the inner membrane in mitochondria in eukaryotic cells). This flow of hydrogen ions across the membrane, called chemiosmosis, must occur through a channel in the membrane via a membrane-bound enzyme complex called ATP synthase (Figure 8.3.1). The tendency for movement in this way is much like water accumulated on one side of a dam, moving through the dam when opened. ATP synthase (like a combination of the intake and generator of a hydroelectric dam) is a complex protein that acts as a tiny generator, turning by the force of the H^+ diffusing through the enzyme, down their electrochemical gradient from where there are many mutually repelling H^+ to where there are fewer H^+. In prokaryotic cells, H^+ flows from the outside of the cytoplasmic membrane into the cytoplasm, whereas in eukaryotic mitochondria, H^+ flows from the intermembrane space to the mitochondrial matrix. The turning of the parts of this molecular machine regenerates ATP from ADP and inorganic phosphate (P_i) by oxidative phosphorylation, a second mechanism for making ATP that harvests the potential energy stored within an electrochemical gradient.

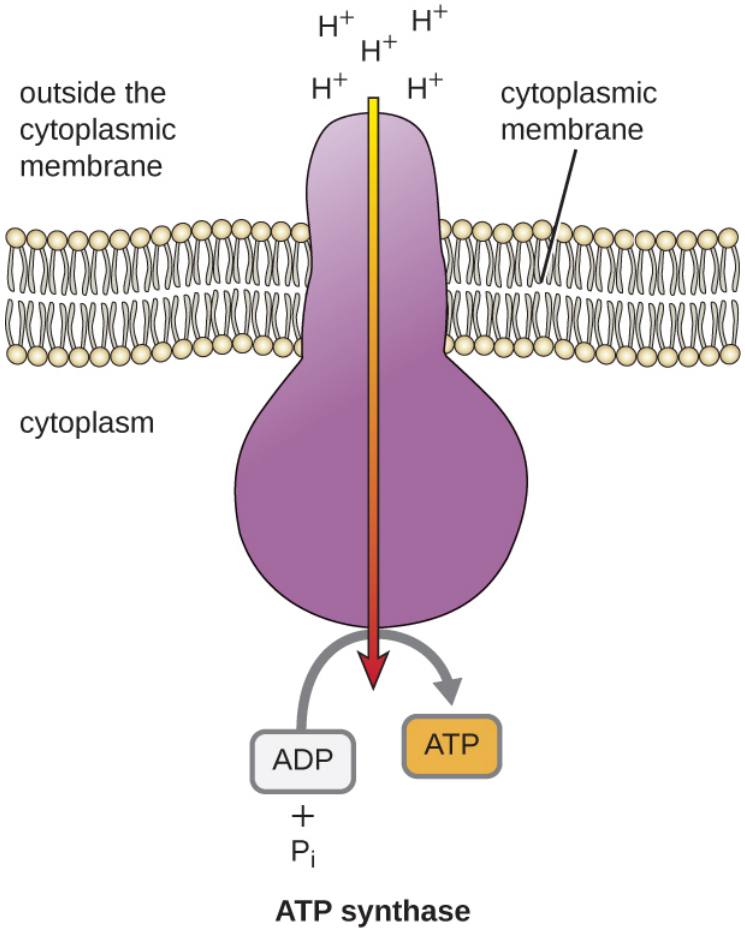


Figure 8.3.1: ATP synthase is a complex integral membrane protein through which H^+ flows down an electrochemical gradient, providing the energy for ATP production by oxidative phosphorylation. (credit: modification of work by Klaus Hoffmeier)

The number of ATP molecules generated from the catabolism of glucose varies. For example, the number of hydrogen ions that the electron transport system complexes can pump through the membrane varies between different species of organisms. In aerobic respiration in mitochondria, the passage of electrons from one molecule of NADH generates enough proton motive force to make three ATP molecules by oxidative phosphorylation, whereas the passage of electrons from one molecule of $FADH_2$ generates enough proton motive force to make only two ATP molecules. Thus, the 10 NADH molecules made per glucose during glycolysis, the transition reaction, and the Krebs cycle carry enough energy to make 30 ATP molecules, whereas the two $FADH_2$ molecules made per glucose during these processes provide enough energy to make four ATP molecules. Overall, the theoretical maximum yield of ATP made during the complete aerobic respiration of glucose is 38 molecules, with four being made by substrate-level phosphorylation and 34 being made by oxidative phosphorylation (Figure 8.3.2). In reality, the total ATP yield is usually less, ranging from one to 34 ATP molecules, depending on whether the cell is using aerobic respiration or anaerobic respiration; in eukaryotic cells, some energy is expended to transport intermediates from the cytoplasm into the mitochondria, affecting ATP yield.

Figure 8.3.2 summarizes the theoretical maximum yields of ATP from various processes during the complete aerobic respiration of one glucose molecule.

Source	Carbon Flow	Molecules of Reduced Coenzymes Produced	Net ATP Molecules Made by Substrate-Level Phosphory-lation	Net ATP Molecules Made by Oxidative Phosphory-lation	Theoretical Maximum Yield of ATP Molecules
Glycolysis (EMP)	Glucose (6C) ⟶ 2 pyruvates (2C)	2 NADH	2 ATP	6 ATP from 2 NADH	8
Transition reaction	2 pyruvates (3C) ⟶ 2 acetyl (2C) + 2 CO_2	2 NADH		6 ATP from 2 NADH	6
Krebs cycle	2 acetyl (2C) ⟶ 4 CO_2	6 NADH 2 $FADH_2$	2 ATP	18 ATP from 6 NADH 4 ATP from 2 $FADH_2$	24
Total:	glucose (6C) ⟶ 6 CO_2	10 NADH 2 $FADH_2$	4 ATP	34 ATP	38 ATP

Figure 8.3.2: Theoretical maximum yields of ATP from various processes during the complete aerobic respiration of one glucose molecule.

Exercise 8.3.1

What are the functions of the proton motive force?

Summary

- Most ATP generated during the cellular respiration of glucose is made by **oxidative phosphorylation**.
- An **electron transport system (ETS)** is composed of a series of membrane-associated protein complexes and associated mobile accessory electron carriers. The ETS is embedded in the cytoplasmic membrane of prokaryotes and the inner mitochondrial membrane of eukaryotes.
- Each ETS complex has a different redox potential, and electrons move from electron carriers with more negative redox potential to those with more positive redox potential.
- To carry out **aerobic respiration**, a cell requires oxygen as the final electron acceptor. A cell also needs a complete Krebs cycle, an appropriate cytochrome oxidase, and oxygen detoxification enzymes to prevent the harmful effects of oxygen radicals produced during aerobic respiration.
- Organisms performing **anaerobic respiration** use alternative electron transport system carriers for the ultimate transfer of electrons to the final non-oxygen electron acceptors.
- Microbes show great variation in the composition of their electron transport systems, which can be used for diagnostic purposes to help identify certain pathogens.
- As electrons are passed from NADH and $FADH_2$ through an ETS, the electron loses energy. This energy is stored through the pumping of H^+ across the membrane, generating a **proton motive force**.
- The energy of this proton motive force can be harnessed by allowing hydrogen ions to diffuse back through the membrane by **chemiosmosis** using **ATP synthase**. As hydrogen ions diffuse through down their electrochemical gradient, components of ATP synthase spin, making ATP from ADP and P_i by oxidative phosphorylation.

- Aerobic respiration forms more ATP (a maximum of 34 ATP molecules) during oxidative phosphorylation than does anaerobic respiration (between one and 32 ATP molecules).

Multiple Choice

Which is the location of electron transports systems in prokaryotes?

A. the outer mitochondrial membrane
B. the cytoplasm
C. the inner mitochondrial membrane
D. the cytoplasmic membrane

D

Which is the source of the energy used to make ATP by oxidative phosphorylation?

A. oxygen
B. high-energy phosphate bonds
C. the proton motive force
D. P_i

C

A cell might perform anaerobic respiration for which of the following reasons?

A. It lacks glucose for degradation.
B. It lacks the transition reaction to convert pyruvate to acetyl-CoA.
C. It lacks Krebs cycle enzymes for processing acetyl-CoA to CO_2.
D. It lacks a cytochrome oxidase for passing electrons to oxygen.

D

In prokaryotes, which of the following is true?

A. As electrons are transferred through an ETS, H^+ is pumped out of the cell.
B. As electrons are transferred through an ETS, H^+ is pumped into the cell.
C. As protons are transferred through an ETS, electrons are pumped out of the cell.
D. As protons are transferred through an ETS, electrons are pumped into the cell.

A

Which of the following is not an electron carrier within an electron transport system?

A. flavoprotein
B. ATP synthase
C. ubiquinone
D. cytochrome oxidase

B

Fill in the Blank

The final ETS complex used in aerobic respiration that transfers energy-depleted electrons to oxygen to form H_2O is called _____.

cytochrome oxidase

The passage of hydrogen ions through _____ down their electrochemical gradient harnesses the energy needed for ATP synthesis by oxidative phosphorylation.

ATP synthase

True/False

All organisms that use aerobic cellular respiration have cytochrome oxidase.

True

Short Answer

What is the relationship between chemiosmosis and the proton motive force?

How does oxidative phosphorylation differ from substrate-level phosphorylation?

How does the location of ATP synthase differ between prokaryotes and eukaryotes? Where do protons accumulate as a result of the ETS in each cell type?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.3: Cellular Respiration is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.4: Fermentation

Skills to Develop

- Define fermentation and explain why it does not require oxygen
- Describe the fermentation pathways and their end products and give examples of microorganisms that use these pathways
- Compare and contrast fermentation and anaerobic respiration

Many cells are unable to carry out respiration because of one or more of the following circumstances:

1. The cell lacks a sufficient amount of any appropriate, inorganic, final electron acceptor to carry out cellular respiration.
2. The cell lacks genes to make appropriate complexes and electron carriers in the electron transport system.
3. The cell lacks genes to make one or more enzymes in the Krebs cycle.

Whereas lack of an appropriate inorganic final electron acceptor is environmentally dependent, the other two conditions are genetically determined. Thus, many prokaryotes, including members of the clinically important genus *Streptococcus*, are permanently incapable of respiration, even in the presence of oxygen. Conversely, many prokaryotes are facultative, meaning that, should the environmental conditions change to provide an appropriate inorganic final electron acceptor for respiration, organisms containing all the genes required to do so will switch to cellular respiration for glucose metabolism because respiration allows for much greater ATP production per glucose molecule.

If respiration does not occur, NADH must be reoxidized to NAD^+ for reuse as an electron carrier for glycolysis, the cell's only mechanism for producing any ATP, to continue. Some living systems use an organic molecule (commonly pyruvate) as a final electron acceptor through a process called fermentation. Fermentation does not involve an electron transport system and does not directly produce any additional ATP beyond that produced during glycolysis by substrate-level phosphorylation. Organisms carrying out fermentation, called fermenters, produce a maximum of two ATP molecules per glucose during glycolysis. Table 8.4.1 compares the final electron acceptors and methods of ATP synthesis in aerobic respiration, anaerobic respiration, and fermentation. Note that the number of ATP molecules shown for glycolysis assumes the Embden-Meyerhof-Parnas pathway. The number of ATP molecules made by substrate-level phosphorylation (SLP) versus oxidative phosphorylation (OP) are indicated.

Table 8.4.1**:** *Comparison of Respiration Versus Fermentation*

Type of Metabolism	Example	Final Electron Acceptor	Pathways Involved in ATP Synthesis (Type of Phosphorylation)	Maximum Yield of ATP Molecules
Aerobic respiration	*Pseudomonas aeruginosa*	O2O2	EMP glycolysis (SLP)	2
			Krebs cycle (SLP)	2
			Electron transport and chemiosmosis (OP):	34
			Total	**38**
Anaerobic respiration	*Paracoccus denitrificans*	NO3−,SO−24,Fe+3,CO2 ,NO3−,SO4−2,Fe+3,CO 2, other inorganics	EMP glycolysis (SLP)	2
			Krebs cycle (SLP)	2
			Electron transport and chemiosmosis (OP):	1–32
			Total	**5–36**
Fermentation	*Candida albicans*	Organics (usually pyruvate)	EMP glycolysis (SLP) Fermentation	2 0
			Total	**2**

Microbial fermentation processes have been manipulated by humans and are used extensively in the production of various foods and other commercial products, including pharmaceuticals. Microbial fermentation can also be useful for identifying microbes for diagnostic purposes.

Fermentation by some bacteria, like those in yogurt and other soured food products, and by animals in muscles during oxygen depletion, is lactic acid fermentation. The chemical reaction of lactic acid fermentation is as follows:

$$\text{Pyruvate} + \text{NADH} \leftrightarrow \text{lactic acid} + \text{NAD+}\text{Pyruvate} + \text{NADH} \quad \leftrightarrow \quad \text{lactic acid} + \text{NAD+}$$

Bacteria of several gram-positive genera, including *Lactobacillus*, *Leuconostoc*, and *Streptococcus*, are collectively known as the lactic acid bacteria (LAB), and various strains are important in food production. During yogurt and cheese production, the highly acidic environment generated by lactic acid fermentation denatures proteins contained in milk, causing it to solidify. When lactic acid is the only fermentation product, the process is said to be homolactic fermentation; such is the case for *Lactobacillus delbrueckii* and *S. thermophiles* used in yogurt production. However, many bacteria perform heterolactic fermentation, producing a mixture of lactic acid, ethanol and/or acetic acid, and CO_2 as a result, because of their use of the branched pentose phosphate pathway instead of the EMP pathway for glycolysis. One important heterolactic fermenter is *Leuconostoc mesenteroides*, which is used for souring vegetables like cucumbers and cabbage, producing pickles and sauerkraut, respectively.

Lactic acid bacteria are also important medically. The production of low pH environments within the body inhibits the establishment and growth of pathogens in these areas. For example, the vaginal microbiota is composed largely of lactic acid bacteria, but when these bacteria are reduced, yeast can proliferate, causing a yeast infection. Additionally, lactic acid bacteria are important in maintaining the health of the gastrointestinal tract and, as such, are the primary component of probiotics.

Another familiar fermentation process is alcohol fermentation, which produces ethanol. The ethanol fermentation reaction is shown in Figure 8.4.1. In the first reaction, the enzyme pyruvate decarboxylase removes a carboxyl group from pyruvate, releasing CO_2 gas while producing the two-carbon molecule acetaldehyde. The second reaction, catalyzed by the enzyme alcohol dehydrogenase, transfers an electron from NADH to acetaldehyde, producing ethanol and NAD^+. The ethanol fermentation of pyruvate by the yeast *Saccharomyces cerevisiae* is used in the production of alcoholic beverages and also makes bread products rise due to CO_2 production. Outside of the food industry, ethanol fermentation of plant products is important in biofuel production.

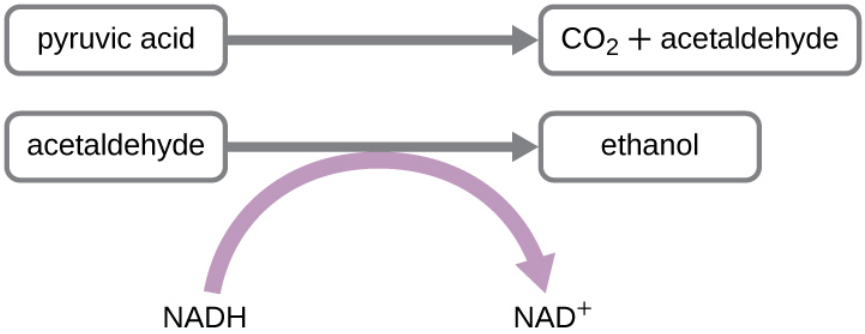


Figure 8.4.1: The chemical reactions of alcohol fermentation are shown here. Ethanol fermentation is important in the production of alcoholic beverages and bread.

Beyond lactic acid fermentation and alcohol fermentation, many other fermentation methods occur in prokaryotes, all for the purpose of ensuring an adequate supply of NAD^+ for glycolysis (Table 8.4.2). Without these pathways, glycolysis would not occur and no ATP would be harvested from the breakdown of glucose. It should be noted that most forms of fermentation besides homolactic fermentation produce gas, commonly CO_2 and/or hydrogen gas. Many of these different types of fermentation pathways are also used in food production and each results in the production of different organic acids, contributing to the unique flavor of a particular fermented food product. The propionic acid produced during propionic acid fermentation contributes to the distinctive flavor of Swiss cheese, for example.

Several fermentation products are important commercially outside of the food industry. For example, chemical solvents such as acetone and butanol are produced during acetone-butanol-ethanol fermentation. Complex organic pharmaceutical compounds used in antibiotics (e.g., penicillin), vaccines, and vitamins are produced through mixed acid fermentation. Fermentation products are used in the laboratory to differentiate various bacteria for diagnostic purposes. For example, enteric bacteria are known for their ability to perform mixed acid fermentation, reducing the pH, which can be detected using a pH indicator. Similarly, the bacterial

production of acetoin during butanediol fermentation can also be detected. Gas production from fermentation can also be seen in an inverted Durham tube that traps produced gas in a broth culture.

Microbes can also be differentiated according to the substrates they can ferment. For example, *E. coli* can ferment lactose, forming gas, whereas some of its close gram-negative relatives cannot. The ability to ferment the sugar alcohol sorbitol is used to identify the pathogenic enterohemorrhagic O157:H7 strain of *E. coli* because, unlike other *E. coli* strains, it is unable to ferment sorbitol. Last, mannitol fermentation differentiates the mannitol-fermenting *Staphylococcus aureus* from other non–mannitol-fermenting staphylococci.

Table 8.4.2***:*** *Common Fermentation Pathways*

Pathway	End Products	Example Microbes	Commercial Products
Acetone-butanol-ethanol	Acetone, butanol, ethanol, CO_2	*Clostridium acetobutylicum*	Commercial solvents, gasoline alternative
Alcohol	Ethanol, CO_2	*Candida*, *Saccharomyces*	Beer, bread
Butanediol	Formic and lactic acid; ethanol; acetoin; 2,3 butanediol; CO_2; hydrogen gas	*Klebsiella*, *Enterobacter*	Chardonnay wine
Butyric acid	Butyric acid, CO_2, hydrogen gas	*Clostridium butyricum*	Butter
Lactic acid	Lactic acid	*Streptococcus*, *Lactobacillus*	Sauerkraut, yogurt, cheese
Mixed acid	Acetic, formic, lactic, and succinic acids; ethanol, CO_2, hydrogen gas	*Escherichia*, *Shigella*	Vinegar, cosmetics, pharmaceuticals
Propionic acid	Acetic acid, propionic acid, CO_2	*Propionibacterium*, *Bifidobacterium*	Swiss cheese

Exercise 8.4.1

When would a metabolically versatile microbe perform fermentation rather than cellular respiration?

IDENTIFYING BACTERIA BY USING API TEST PANELS

Identification of a microbial isolate is essential for the proper diagnosis and appropriate treatment of patients. Scientists have developed techniques that identify bacteria according to their biochemical characteristics. Typically, they either examine the use of specific carbon sources as substrates for fermentation or other metabolic reactions, or they identify fermentation products or specific enzymes present in reactions. In the past, microbiologists have used individual test tubes and plates to conduct biochemical testing. However, scientists, especially those in clinical laboratories, now more frequently use plastic, disposable, multitest panels that contain a number of miniature reaction tubes, each typically including a specific substrate and pH indicator. After inoculation of the test panel with a small sample of the microbe in question and incubation, scientists can compare the results to a database that includes the expected results for specific biochemical reactions for known microbes, thus enabling rapid identification of a sample microbe. These test panels have allowed scientists to reduce costs while improving efficiency and reproducibility by performing a larger number of tests simultaneously.

Many commercial, miniaturized biochemical test panels cover a number of clinically important groups of bacteria and yeasts. One of the earliest and most popular test panels is the Analytical Profile Index (API) panel invented in the 1970s. Once some basic laboratory characterization of a given strain has been performed, such as determining the strain's Gram morphology, an appropriate test strip that contains 10 to 20 different biochemical tests for differentiating strains within that microbial group can be used. Currently, the various API strips can be used to quickly and easily identify more than 600 species of bacteria, both aerobic and anaerobic, and approximately 100 different types of yeasts. Based on the colors of the reactions when metabolic end products are present, due to the presence of pH indicators, a metabolic profile is created from the results (Figure 8.4.2). Microbiologists can then compare the sample's profile to the database to identify the specific microbe.



Figure 8.4.2: The API 20NE test strip is used to identify specific strains of gram-negative bacteria outside the Enterobacteriaceae. Here is an API 20NE test strip result for *Photobacterium damselae* ssp. *piscicida*.

part 2

Many of Hannah's symptoms are consistent with several different infections, including influenza and pneumonia. However, her sluggish reflexes along with her light sensitivity and stiff neck suggest some possible involvement of the central nervous system, perhaps indicating meningitis. Meningitis is an infection of the cerebrospinal fluid (CSF) around the brain and spinal cord that causes inflammation of the meninges, the protective layers covering the brain. Meningitis can be caused by viruses, bacteria, or fungi. Although all forms of meningitis are serious, bacterial meningitis is particularly serious. Bacterial meningitis may be caused by several different bacteria, but the bacterium *Neisseria meningitidis*, a gram-negative, bean-shaped diplococcus, is a common cause and leads to death within 1 to 2 days in 5% to 10% of patients.

Given the potential seriousness of Hannah's conditions, her physician advised her parents to take her to the hospital in the Gambian capital of Banjul and there have her tested and treated for possible meningitis. After a 3-hour drive to the hospital, Hannah was immediately admitted. Physicians took a blood sample and performed a lumbar puncture to test her CSF. They also immediately started her on a course of the antibiotic ceftriaxone, the drug of choice for treatment of meningitis caused by *N. meningitidis*, without waiting for laboratory test results.

Exercise 8.4.2

1. How might biochemical testing be used to confirm the identity of *N. meningitidis*?
2. Why did Hannah's doctors decide to administer antibiotics without waiting for the test results?

Key Concepts and Summary

- Fermentation uses an organic molecule as a final electron acceptor to regenerate NAD^+ from NADH so that glycolysis can continue.

- Fermentation does not involve an electron transport system, and no ATP is made by the fermentation process directly. Fermenters make very little ATP—only two ATP molecules per glucose molecule during glycolysis.
- Microbial fermentation processes have been used for the production of foods and pharmaceuticals, and for the identification of microbes.
- During lactic acid fermentation, pyruvate accepts electrons from NADH and is reduced to lactic acid. Microbes performing **homolactic fermentation** produce only lactic acid as the fermentation product; microbes performing **heterolactic fermentation** produce a mixture of lactic acid, ethanol and/or acetic acid, and CO_2.
- Lactic acid production by the normal microbiota prevents growth of pathogens in certain body regions and is important for the health of the gastrointestinal tract.
- During ethanol fermentation, pyruvate is first decarboxylated (releasing CO_2) to acetaldehyde, which then accepts electrons from NADH, reducing acetaldehyde to ethanol. Ethanol fermentation is used for the production of alcoholic beverages, for making bread products rise, and for biofuel production.
- Fermentation products of pathways (e.g., propionic acid fermentation) provide distinctive flavors to food products. Fermentation is used to produce chemical solvents (acetone-butanol-ethanol fermentation) and pharmaceuticals (mixed acid fermentation).
- Specific types of microbes may be distinguished by their fermentation pathways and products. Microbes may also be differentiated according to the substrates they are able to ferment.

Multiple Choice

Which of the following is the purpose of fermentation?

A. to make ATP
B. to make carbon molecule intermediates for anabolism
C. to make NADH
D. to make NAD^+

D

Which molecule typically serves as the final electron acceptor during fermentation?

A. oxygen
B. NAD^+
C. pyruvate
D. CO_2

C

Which fermentation product is important for making bread rise?

A. ethanol
B. CO_2
C. lactic acid
D. hydrogen gas

B

Which of the following is not a commercially important fermentation product?

A. ethanol
B. pyruvate
C. butanol
D. penicillin

B

Fill in the Blank

The microbe responsible for ethanol fermentation for the purpose of producing alcoholic beverages is _____.

yeast (*Saccharomyces cerevisiae*)

_____ results in the production of a mixture of fermentation products, including lactic acid, ethanol and/or acetic acid, and CO_2.

Heterolactic fermentation

Fermenting organisms make ATP through the process of _____.

glycolysis

Matching

Match the fermentation pathway with the correct commercial product it is used to produce:

___acetone-butanol-ethanol fermentation	a. bread
___alcohol fermentation	b. pharmaceuticals
___lactic acid fermentation	c. Swiss cheese
___mixed acid fermentation	d. yogurt
___propionic acid fermentation	e. industrial solvents

e; 2. a; 3. d; 4. b; 5. c

Short Answer

Why are some microbes, including *Streptococcus* spp., unable to perform aerobic respiration, even in the presence of oxygen?

How can fermentation be used to differentiate various types of microbes?

Critical Thinking

The bacterium *E. coli* is capable of performing aerobic respiration, anaerobic respiration, and fermentation. When would it perform each process and why? How is ATP made in each case?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.4: Fermentation is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.5: Catabolism of Lipids and Proteins

skills to develop

- Describe how lipids are catabolized
- Describe how lipid catabolism can be used to identify microbes
- Describe how proteins are catabolized
- Describe how protein catabolism can be used to identify bacteria

Previous sections have discussed the catabolism of glucose, which provides energy to living cells, as well as how polysaccharides like glycogen, starch, and cellulose are degraded to glucose monomers. But microbes consume more than just carbohydrates for food. In fact, the microbial world is known for its ability to degrade a wide range of molecules, both naturally occurring and those made by human processes, for use as carbon sources. In this section, we will see that the pathways for both lipid and protein catabolism connect to those used for carbohydrate catabolism, eventually leading into glycolysis, the transition reaction, and the Krebs cycle pathways. Metabolic pathways should be considered to be porous—that is, substances enter from other pathways, and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways.

Lipid Catabolism

Triglycerides are a form of long-term energy storage in animals. They are made of glycerol and three fatty acids (see [link]). Phospholipids compose the cell and organelle membranes of all organisms except the archaea. Phospholipid structure is similar to triglycerides except that one of the fatty acids is replaced by a phosphorylated head group (see [link]). Triglycerides and phospholipids are broken down first by releasing fatty acid chains (and/or the phosphorylated head group, in the case of phospholipids) from the three-carbon glycerol backbone. The reactions breaking down triglycerides are catalyzed by lipases and those involving phospholipids are catalyzed by phospholipases. These enzymes contribute to the virulence of certain microbes, such as the bacterium *Staphylococcus aureus* and the fungus *Cryptococcus neoformans*. These microbes use phospholipases to destroy lipids and phospholipids in host cells and then use the catabolic products for energy (see Virulence Factors of Bacterial and Viral Pathogens).

The resulting products of lipid catabolism, glycerol and fatty acids, can be further degraded. Glycerol can be phosphorylated to glycerol-3-phosphate and easily converted to glyceraldehyde 3-phosphate, which continues through glycolysis. The released fatty acids are catabolized in a process called β-oxidation, which sequentially removes two-carbon acetyl groups from the ends of fatty acid chains, reducing NAD^+ and FAD to produce NADH and $FADH_2$, respectively, whose electrons can be used to make ATP by oxidative phosphorylation. The acetyl groups produced during β-oxidation are carried by coenzyme A to the Krebs cycle, and their movement through this cycle results in their degradation to CO_2, producing ATP by substrate-level phosphorylation and additional NADH and $FADH_2$ molecules (see Appendix C for a detailed illustration of β-oxidation).

Other types of lipids can also be degraded by certain microbes. For example, the ability of certain pathogens, like *Mycobacterium tuberculosis*, to degrade cholesterol contributes to their virulence. The side chains of cholesterol can be easily removed enzymatically, but degradation of the remaining fused rings is more problematic. The four fused rings are sequentially broken in a multistep process facilitated by specific enzymes, and the resulting products, including pyruvate, can be further catabolized in the Krebs cycle.

Exercise 8.5.1

How can lipases and phospholipases contribute to virulence in microbes?

Protein Catabolism

Proteins are degraded through the concerted action of a variety of microbial protease enzymes. Extracellular proteases cut proteins internally at specific amino acid sequences, breaking them down into smaller peptides that can then be taken up by cells. Some clinically important pathogens can be identified by their ability to produce a specific type of extracellular protease. For example, the production of the extracellular protease gelatinase by members of the genera *Proteus* and *Serratia* can be used to distinguish them from other gram-negative enteric bacteria. Following inoculation and growth of microbes in gelatin broth, degradation of the

gelatin protein due to gelatinase production prevents solidification of gelatin when refrigerated. Other pathogens can be distinguished by their ability to degrade casein, the main protein found in milk. When grown on skim milk agar, production of the extracellular protease caseinase causes degradation of casein, which appears as a zone of clearing around the microbial growth. Caseinase production by the opportunist pathogen *Pseudomonas aeruginosa* can be used to distinguish it from other related gram-negative bacteria.

After extracellular protease degradation and uptake of peptides in the cell, the peptides can then be broken down further into individual amino acids by additional intracellular proteases, and each amino acid can be enzymatically deaminated to remove the amino group. The remaining molecules can then enter the transition reaction or the Krebs cycle.

Exercise 8.5.2

How can protein catabolism help identify microbes?

part 3

Because bacterial meningitis progresses so rapidly, Hannah's doctors had decided to treat her aggressively with antibiotics, based on empirical observation of her symptoms. However, laboratory testing to confirm the cause of Hannah's meningitis was still important for several reasons. *N. meningitidis* is an infectious pathogen that can be spread from person to person through close contact; therefore, if tests confirm *N. meningitidis* as the cause of Hannah's symptoms, Hannah's parents and others who came into close contact with her might need to be vaccinated or receive prophylactic antibiotics to lower their risk of contracting the disease. On the other hand, if it turns out that *N. meningitidis* is not the cause, Hannah's doctors might need to change her treatment.

The clinical laboratory performed a Gram stain on Hannah's blood and CSF samples. The Gram stain showed the presence of a bean-shaped gram-negative diplococcus. The technician in the hospital lab cultured Hannah's blood sample on both blood agar and chocolate agar, and the bacterium that grew on both media formed gray, nonhemolytic colonies. Next, he performed an oxidase test on this bacterium and determined that it was oxidase positive. Last, he examined the repertoire of sugars that the bacterium could use as a carbon source and found that the bacterium was positive for glucose and maltose use but negative for lactose and sucrose use. All of these test results are consistent with characteristics of *N. meningitidis*.

Exercise 8.5.3

1. What do these test results tell us about the metabolic pathways of *N. meningitidis*?
2. Why do you think that the hospital used these biochemical tests for identification in lieu of molecular analysis by DNA testing?

Key Concepts and Summary

- Collectively, microbes have the ability to degrade a wide variety of carbon sources besides carbohydrates, including lipids and proteins. The catabolic pathways for all of these molecules eventually connect into glycolysis and the Krebs cycle.
- Several types of lipids can be microbially degraded. Triglycerides are degraded by extracellular **lipases**, releasing fatty acids from the glycerol backbone. Phospholipids are degraded by **phospholipases**, releasing fatty acids and the phosphorylated head group from the glycerol backbone. Lipases and phospholipases act as virulence factors for certain pathogenic microbes.
- Fatty acids can be further degraded inside the cell through **β-oxidation**, which sequentially removes two-carbon acetyl groups from the ends of fatty acid chains.
- Protein degradation involves extracellular **proteases** that degrade large proteins into smaller peptides. Detection of the extracellular proteases gelatinase and caseinase can be used to differentiate clinically relevant bacteria.

Multiple Choice

Which of the following molecules is not produced during the breakdown of phospholipids?

A. glucose
B. glycerol
C. acetyl groups
D. fatty acids

A

Caseinase is which type of enzyme?

A. phospholipase
B. lipase
C. extracellular protease
D. intracellular protease

C

Which of the following is the first step in triglyceride degradation?

A. removal of fatty acids
B. β-oxidation
C. breakage of fused rings
D. formation of smaller peptides

A

Fill in the Blank

The process by which two-carbon units are sequentially removed from fatty acids, producing acetyl-CoA, $FADH_2$, and NADH is called _____.

β-oxidation

The NADH and $FADH_2$ produced during β-oxidation are used to make _____.

ATP by oxidative phosphorylation

_____ is a type of medium used to detect the production of an extracellular protease called caseinase.

Skim milk agar

Short Answer

How are the products of lipid and protein degradation connected to glucose metabolism pathways?

What is the general strategy used by microbes for the degradation of macromolecules?

Critical Thinking

Do you think that β-oxidation can occur in an organism incapable of cellular respiration? Why or why not?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.5: Catabolism of Lipids and Proteins is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.6: Photosynthesis and the Importance of Light

skills to develop

- Describe the function and locations of photosynthetic pigments in eukaryotes and prokaryotes
- Describe the major products of the light-dependent and light-independent reactions
- Describe the reactions that produce glucose in a photosynthetic cell
- Compare and contrast cyclic and noncyclic photophosphorylation

Heterotrophic organisms ranging from *E. coli* to humans rely on the chemical energy found mainly in carbohydrate molecules. Many of these carbohydrates are produced by photosynthesis, the biochemical process by which phototrophic organisms convert solar energy (sunlight) into chemical energy. Although photosynthesis is most commonly associated with plants, microbial photosynthesis is also a significant supplier of chemical energy, fueling many diverse ecosystems. In this section, we will focus on microbial photosynthesis.

Photosynthesis takes place in two sequential stages: the light-dependent reactions and the light-independent reactions (Figure 8.6.1). In the light-dependent reactions, energy from sunlight is absorbed by pigment molecules in photosynthetic membranes and converted into stored chemical energy. In the light-independent reactions, the chemical ener gy produced by the light-dependent reactions is used to drive the assembly of sugar molecules using CO_2; however, these reactions are still light dependent because the products of the light-dependent reactions necessary for driving them are short-lived. The light-dependent reactions produce ATP and either NADPH or NADH to temporarily store energy. These energy carriers are used in the light-independent reactions to drive the energetically unfavorable process of "fixing" inorganic CO_2 in an organic form, sugar.

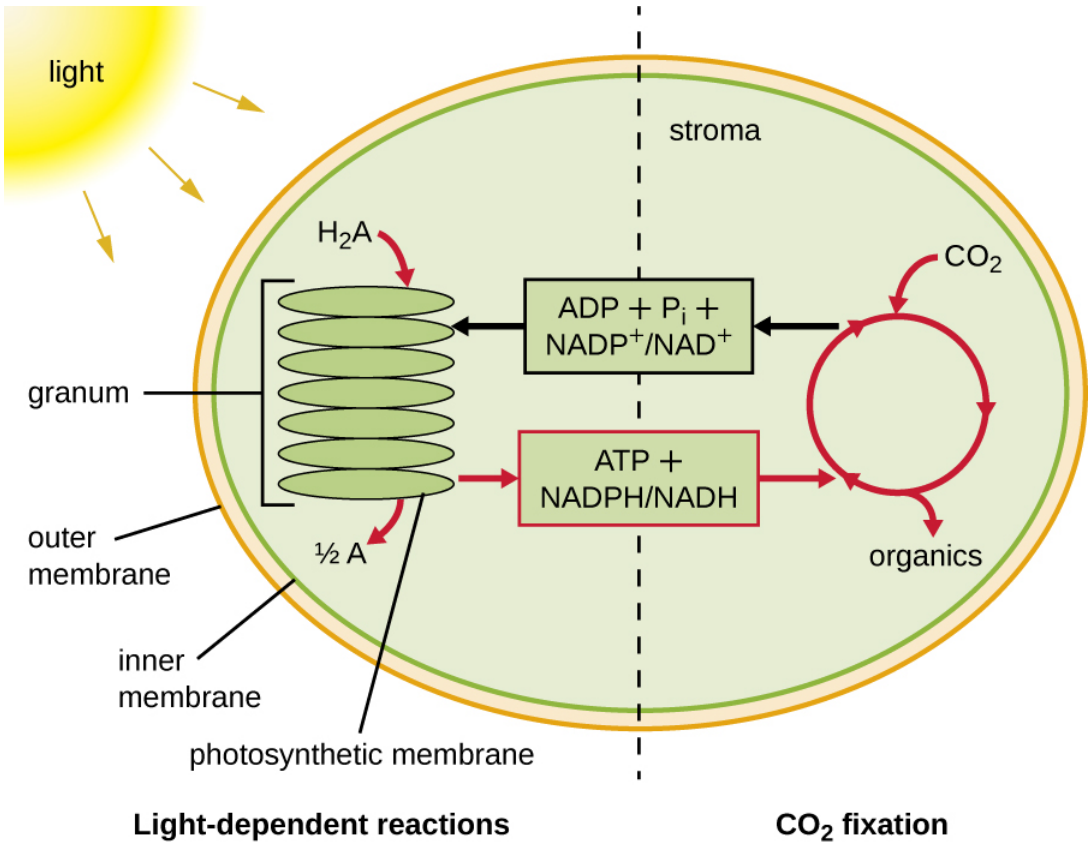


Figure 8.6.1: *The light-dependent reactions of photosynthesis (left) convert light energy into chemical energy, forming ATP and NADPH. These products are used by the light-independent reactions to fix CO_2, producing organic carbon molecules.*

Photosynthetic Structures in Eukaryotes and Prokaryotes

In all phototrophic eukaryotes, photosynthesis takes place inside a chloroplast, an organelle that arose in eukaryotes by endosymbiosis of a photosynthetic bacterium (see Unique Characteristics of Eukaryotic Cells). These chloroplasts are enclosed by a double membrane with inner and outer layers. Within the chloroplast is a third membrane that forms stacked, disc-shaped photosynthetic structures called thylakoids (Figure 8.6.2). A stack of thylakoids is called a granum, and the space surrounding the granum within the chloroplast is called stroma.

Photosynthetic membranes in prokaryotes, by contrast, are not organized into distinct membrane-enclosed organelles; rather, they are infolded regions of the plasma membrane. In cyanobacteria, for example, these infolded regions are also referred to as thylakoids. In either case, embedded within the thylakoid membranes or other photosynthetic bacterial membranes are photosynthetic pigment molecules organized into one or more photosystems, where light energy is actually converted into chemical energy.

Photosynthetic pigments within the photosynthetic membranes are organized into photosystems, each of which is composed of a light-harvesting (antennae) complex and a reaction center. The light-harvesting complex consists of multiple proteins and associated pigments that each may absorb light energy and, thus, become excited. This energy is transferred from one pigment molecule to another until eventually (after about a millionth of a second) it is delivered to the reaction center. Up to this point, only energy—not electrons—has been transferred between molecules. The reaction center contains a pigment molecule that can undergo oxidation upon excitation, actually giving up an electron. It is at this step in photosynthesis that light energy is converted into an excited electron.

Different kinds of light-harvesting pigments absorb unique patterns of wavelengths (colors) of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear the corresponding color. Examples of photosynthetic pigments (molecules used to absorb solar energy) are bacteriochlorophylls (green, purple, or red), carotenoids (orange, red, or yellow), chlorophylls (green), phycocyanins (blue), and phycoerythrins (red). By having mixtures of pigments, an organism can absorb energy from more wavelengths. Because photosynthetic bacteria commonly grow in competition for sunlight, each type of photosynthetic bacteria is optimized for harvesting the wavelengths of light to which it is commonly exposed, leading to stratification of microbial communities in aquatic and soil ecosystems by light quality and penetration.

Once the light harvesting complex transfers the energy to the reaction center, the reaction center delivers its high-energy electrons, one by one, to an electron carrier in an electron transport system, and electron transfer through the ETS is initiated. The ETS is similar to that used in cellular respiration and is embedded within the photosynthetic membrane. Ultimately, the electron is used to produce NADH or NADPH. The electrochemical gradient that forms across the photosynthetic membrane is used to generate ATP by chemiosmosis through the process of photophosphorylation, another example of oxidative phosphorylation (Figure 8.6.3).

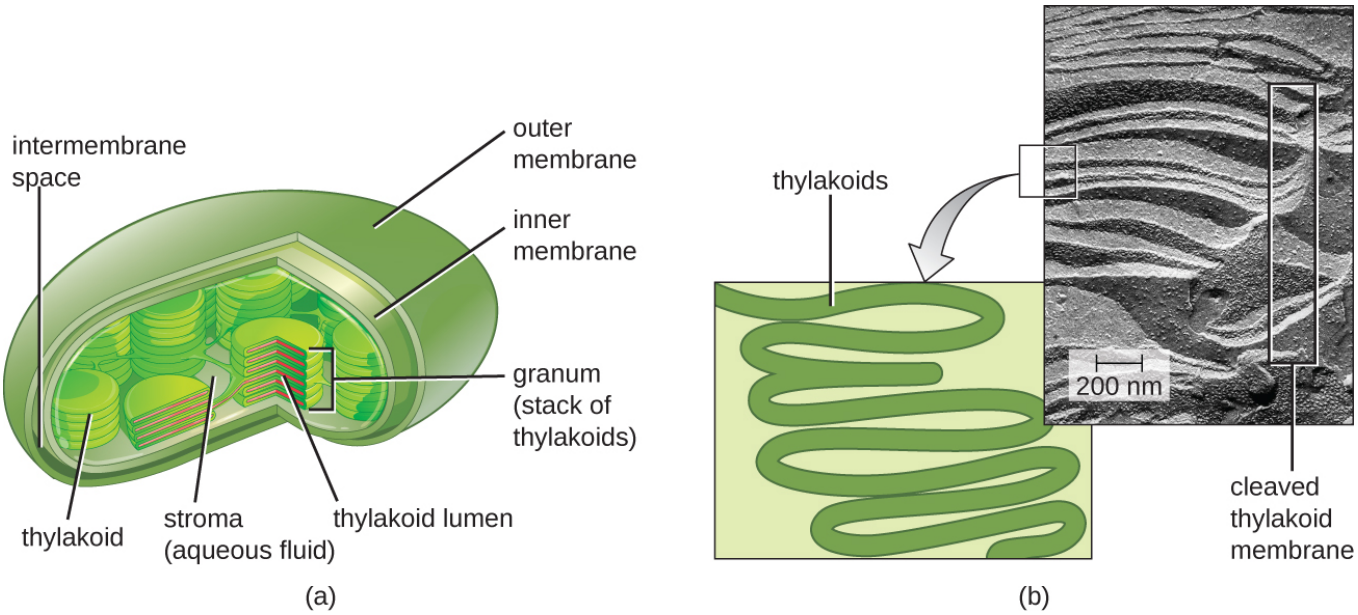


Figure 8.6.2: (a) Photosynthesis in eukaryotes takes place in chloroplasts, which contain thylakoids stacked into grana. (b) A photosynthetic prokaryote has infolded regions of the plasma membrane that function like thylakoids. (credit: scale bar data from Matt Russell.)

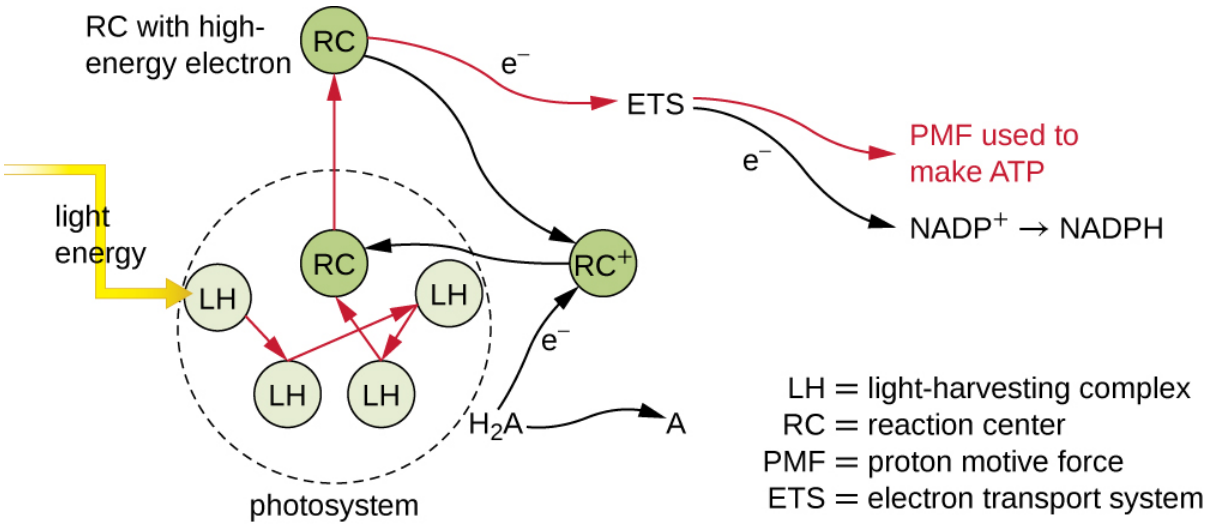


Figure 8.6.3: This figure summarizes how a photosystem works. Light harvesting (LH) pigments absorb light energy, converting it to chemical energy. The energy is passed from one LH pigment to another until it reaches a reaction center (RC) pigment, exciting an electron. This high-energy electron is lost from the RC pigment and passed through an electron transport system (ETS), ultimately producing NADH or NADPH and ATP. A reduced molecule (H_2A) donates an electron, replacing electrons to the electron-deficient RC pigment.

Exercise 8.6.1

In a phototrophic eukaryote, where does photosynthesis take place?

Oxygenic and Anoxygenic Photosynthesis

For photosynthesis to continue, the electron lost from the reaction center pigment must be replaced. The source of this electron (H_2A) differentiates the oxygenic photosynthesis of plants and cyanobacteria from anoxygenic photosynthesis carried out by other types of bacterial phototrophs (Figure 8.6.4). In oxygenic photosynthesis, H_2O is split and supplies the electron to the reaction center. Because oxygen is generated as a byproduct and is released, this type of photosynthesis is referred to as oxygenic photosynthesis. However, when other reduced compounds serve as the electron donor, oxygen is not generated; these types of

photosynthesis are called anoxygenic photosynthesis. Hydrogen sulfide (H_2S) or thiosulfate ($S2O2-3$)($S2O32-$) can serve as the electron donor, generating elemental sulfur and sulfate ($SO2-4$)($SO42-$)ions, respectively, as a result.

Photosystems have been classified into two types: photosystem I (PSI) and photosystem II (PSII) (Figure 8.6.5). Cyanobacteria and plant chloroplasts have both photosystems, whereas anoxygenic photosynthetic bacteria use only one of the photosystems. Both photosystems are excited by light energy simultaneously. If the cell requires both ATP and NADPH for biosynthesis, then it will carry out noncyclic photophosphorylation. Upon passing of the PSII reaction center electron to the ETS that connects PSII and PSI, the lost electron from the PSII reaction center is replaced by the splitting of water. The excited PSI reaction center electron is used to reduce $NADP^+$ to NADPH and is replaced by the electron exiting the ETS. The flow of electrons in this way is called the Z-scheme.

If a cell's need for ATP is significantly greater than its need for NADPH, it may bypass the production of reducing power through cyclic photophosphorylation. Only PSI is used during cyclic photophosphorylation; the high-energy electron of the PSI reaction center is passed to an ETS carrier and then ultimately returns to the oxidized PSI reaction center pigment, thereby reducing it.

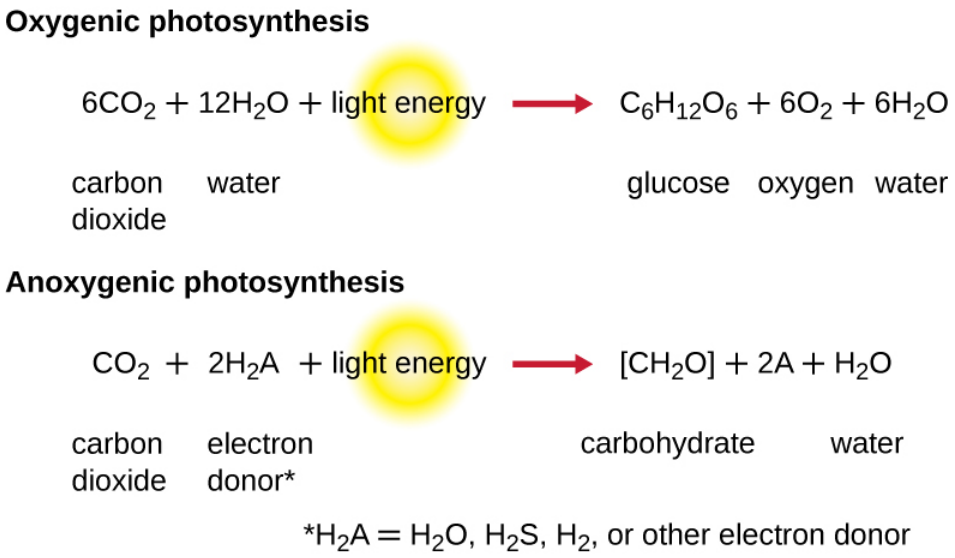
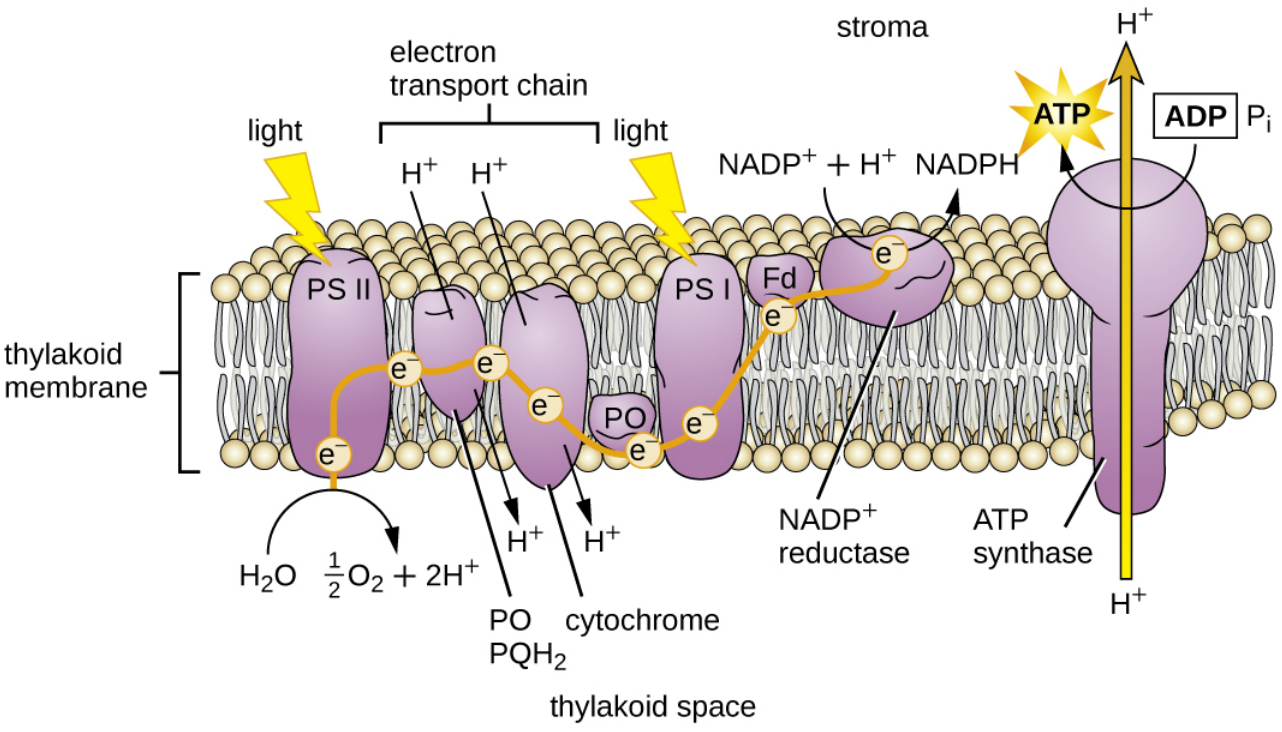
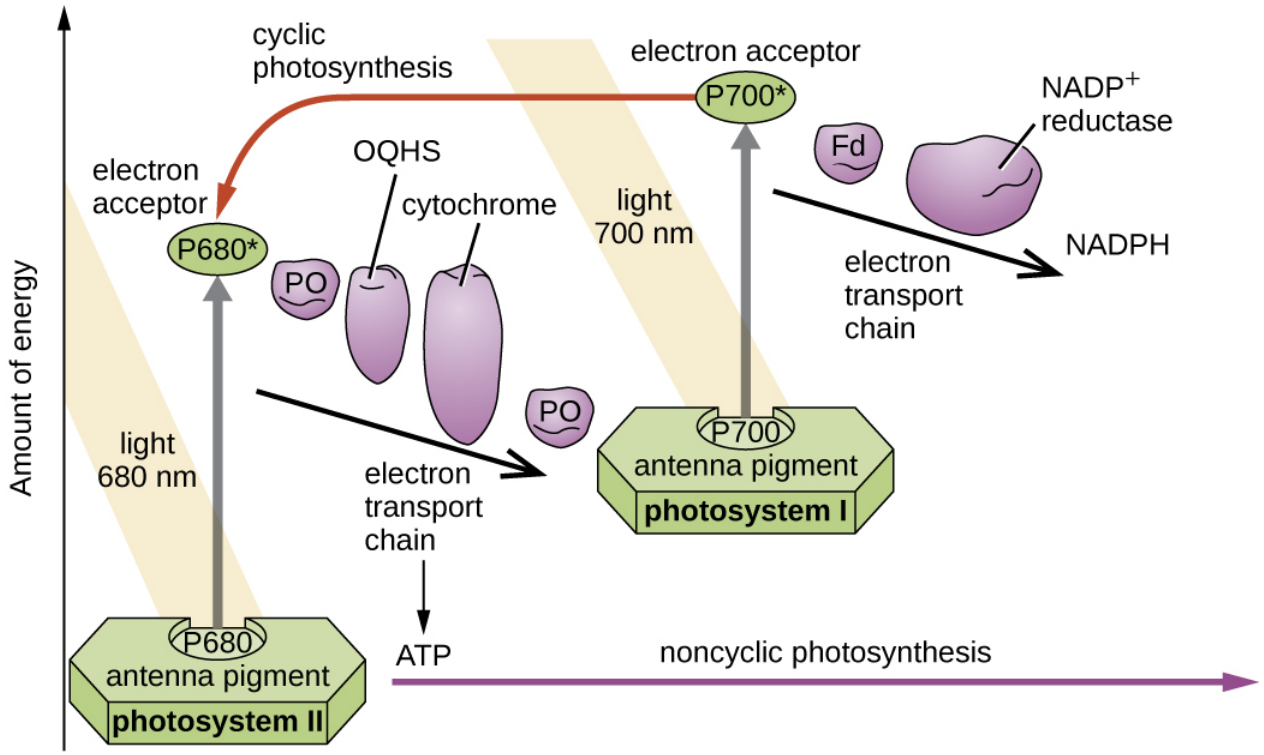


Figure 8.6.4: Eukaryotes and cyanobacteria carry out oxygenic photosynthesis, producing oxygen, whereas other bacteria carry out anoxygenic photosynthesis, which does not produce oxygen.


stroma
H+
electron
transport chain
light
light
ATP
ADP
Pi
H+ H+
NADP+ + H+
NADPH
PS II
PS I
Fd
e−
thylakoid
membrane
PO
H2O
½O2 + 2H+
H+
H+
NADP+
reductase
ATP
synthase
H+
PO
PQH2
cytochrome
thylakoid space

(a)


cyclic
photosynthesis
electron acceptor
P700*
NADP+
reductase
Fd
OQHS
electron
acceptor
cytochrome
light
700 nm
P680*
PO
NADPH
electron
transport
chain
Amount of energy
PO
light
680 nm
P700
antenna pigment
photosystem I
electron
transport
chain
P680
antenna pigment
photosystem II
ATP
noncyclic photosynthesis

(b)

Figure 8.6.5: (a) PSI and PSII are found on the thylakoid membrane. The high-energy electron from PSII is passed to an ETS, which generates a proton motive force for ATP synthesis by chemiosmosis, and ultimately replaces the electron lost by the PSI reaction center. The PSI reaction center electron is used to make NADPH. (b) When both ATP and NADPH are required, noncyclic photophosphorylation (in cyanobacteria and plants) provides both. The electron flow described here is referred to as the Z-scheme (shown in yellow in [a]). When the cell's ATP needs outweigh those for NADPH, cyanobacteria and plants will use only PSI, and its reaction center electron is passed to the ETS to generate a proton motive force used for ATP synthesis.

Exercise 8.6.2

Why would a photosynthetic bacterium have different pigments?

Light-Independent Reactions

After the energy from the sun is converted into chemical energy and temporarily stored in ATP and NADPH molecules (having lifespans of millionths of a second), photoautotrophs have the fuel needed to build multicarbon carbohydrate molecules, which can survive for hundreds of millions of years, for long-term energy storage. The carbon comes from CO_2, the gas that is a waste product of cellular respiration.

The Calvin-Benson cycle (named for Melvin Calvin [1911–1997] and Andrew Benson [1917–2015]), the biochemical pathway used for fixation of CO_2, is located within the cytoplasm of photosynthetic bacteria and in the stroma of eukaryotic chloroplasts. The light-independent reactions of the Calvin cycle can be organized into three basic stages: fixation, reduction, and regeneration (see Appendix C for a detailed illustration of the Calvin cycle).

- **Fixation**: The enzyme ribulose bisphosphate carboxylase (RuBisCO) catalyzes the addition of a CO_2 to ribulose bisphosphate (RuBP). This results in the production of 3-phosphoglycerate (3-PGA).
- **Reduction**: Six molecules of both ATP and NADPH (from the light-dependent reactions) are used to convert 3-PGA into glyceraldehyde 3-phosphate (G3P). Some G3P is then used to build glucose.
- **Regeneration**: The remaining G3P not used to synthesize glucose is used to regenerate RuBP, enabling the system to continue CO_2 fixation. Three more molecules of ATP are used in these regeneration reactions.

The Calvin cycle is used extensively by plants and photoautotrophic bacteria, and the enzyme RuBisCO is said to be the most plentiful enzyme on earth, composing 30%–50% of the total soluble protein in plant chloroplasts.[1] However, besides its prevalent use in photoautotrophs, the Calvin cycle is also used by many nonphotosynthetic chemoautotrophs to fix CO_2. Additionally, other bacteria and archaea use alternative systems for CO_2 fixation. Although most bacteria using Calvin cycle alternatives are chemoautotrophic, certain green sulfur photoautotrophic bacteria have been also shown to use an alternative CO_2 fixation pathway.

Exercise 8.6.3

Describe the three stages of the Calvin cycle.

Key Concepts and Summary

- Heterotrophs depend on the carbohydrates produced by autotrophs, many of which are photosynthetic, converting solar energy into chemical energy.
- Different photosynthetic organisms use different mixtures of **photosynthetic pigments**, which increase the range of the wavelengths of light an organism can absorb.
- **Photosystems** (PSI and PSII) each contain a **light-harvesting complex**, composed of multiple proteins and associated pigments that absorb light energy. The **light-dependent reactions** of photosynthesis convert solar energy into chemical energy, producing ATP and NADPH or NADH to temporarily store this energy.
- In **oxygenic photosynthesis**, H_2O serves as the electron donor to replace the reaction center electron, and oxygen is formed as a byproduct. In **anoxygenic photosynthesis**, other reduced molecules like H_2S or thiosulfate may be used as the electron donor; as such, oxygen is not formed as a byproduct.
- **Noncyclic photophosphorylation** is used in oxygenic photosynthesis when there is a need for both ATP and NADPH production. If a cell's needs for ATP outweigh its needs for NADPH, then it may carry out **cyclic photophosphorylation** instead, producing only ATP.
- The **light-independent reactions** of photosynthesis use the ATP and NADPH from the light-dependent reactions to fix CO_2 into organic sugar molecules.

Multiple Choice

During the light-dependent reactions, which molecule loses an electron?

A. a light-harvesting pigment molecule
B. a reaction center pigment molecule
C. NADPH
D. 3-phosphoglycerate

B

In prokaryotes, in which direction are hydrogen ions pumped by the electron transport system of photosynthetic membranes?

A. to the outside of the plasma membrane
B. to the inside (cytoplasm) of the cell
C. to the stroma
D. to the intermembrane space of the chloroplast

A

Which of the following does not occur during cyclic photophosphorylation in cyanobacteria?

A. electron transport through an ETS
B. photosystem I use
C. ATP synthesis
D. NADPH formation

D

Which are two products of the light-dependent reactions are _____.

A. glucose and NADPH
B. NADPH and ATP
C. glyceraldehyde 3-phosphate and CO_2
D. glucose and oxygen

B

True/False

Photosynthesis always results in the formation of oxygen.

False

Fill in the Blank

The enzyme responsible for CO_2 fixation during the Calvin cycle is called _____.

---

ribulose bisphosphate carboxylase (RuBisCO)

The types of pigment molecules found in plants, algae, and cyanobacteria are _____ and _____.

---

chlorophylls and carotenoids

Short Answer

Why would an organism perform cyclic phosphorylation instead of noncyclic phosphorylation?

What is the function of photosynthetic pigments in the light-harvesting complex?

Critical Thinking

Is life dependent on the carbon fixation that occurs during the light-independent reactions of photosynthesis? Explain.

Footnotes

1. 1 A. Dhingra et al. “Enhanced Translation of a Chloroplast-Expressed *Rbc*S Gene Restores Small Subunit Levels and Photosynthesis in Nuclear *Rbc*S Antisense Plants.” *Proceedings of the National Academy of Sciences of the United States of America* 101 no. 16 (2004):6315–6320.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.6: Photosynthesis and the Importance of Light is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

8.7: Biogeochemical Cycles

skills to develop

- Define and describe the importance of microorganisms in the biogeochemical cycles of carbon, nitrogen, and sulfur
- Define and give an example of bioremediation

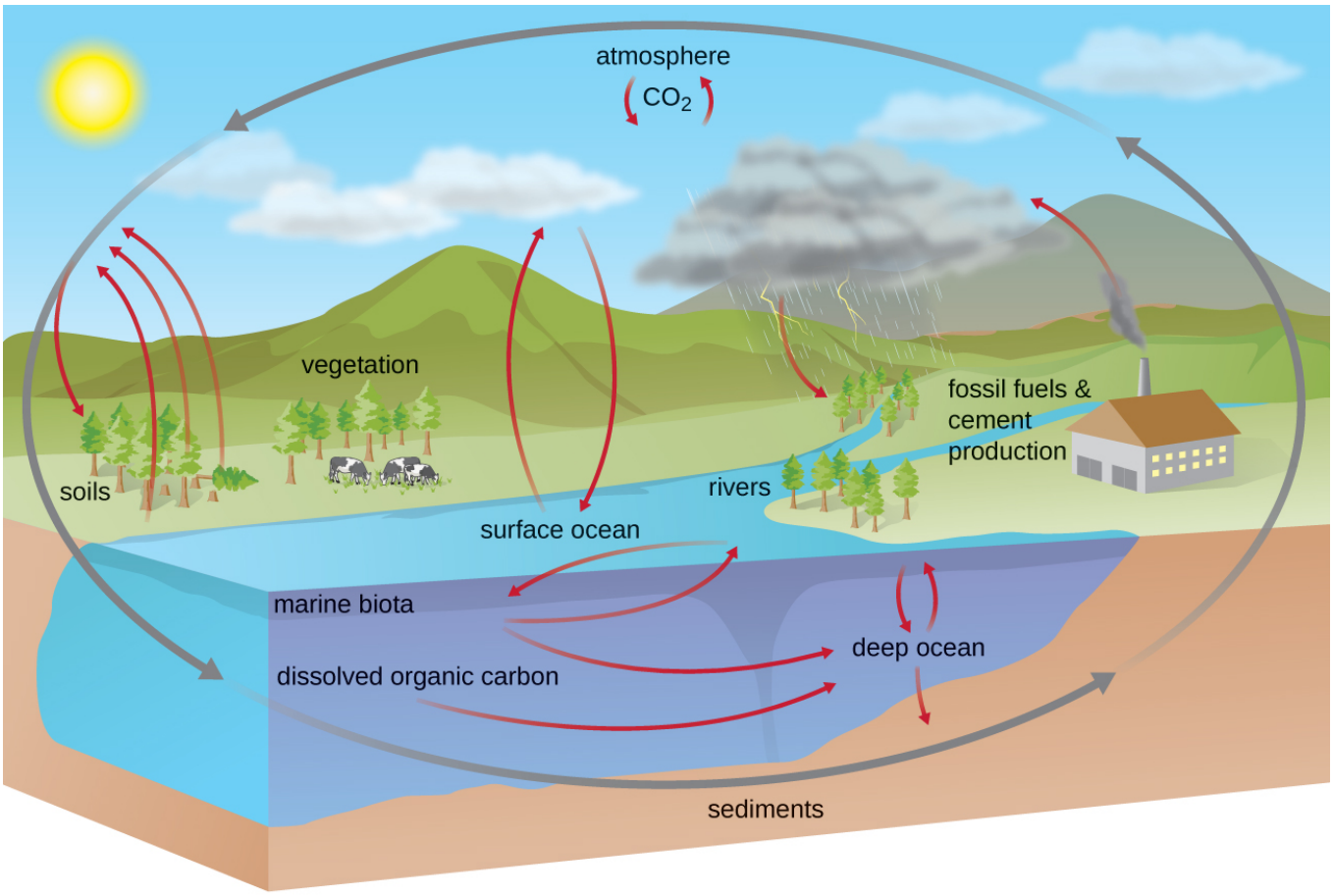
Energy flows directionally through ecosystems, entering as sunlight for phototrophs or as inorganic molecules for chemoautotrophs. The six most common elements associated with organic molecules—carbon, hydrogen, nitrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath earth's surface. Geologic processes, such as erosion, water drainage, the movement of the continental plates, and weathering, all are involved in the cycling of elements on earth. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their nonliving environment is called a biogeochemical cycle. Here, we will focus on the function of microorganisms in these cycles, which play roles at each step, most frequently interconverting oxidized versions of molecules with reduced ones.

Carbon Cycle

Carbon is one of the most important elements to living organisms, as shown by its abundance and presence in all organic molecules. The carbon cycle exemplifies the connection between organisms in various ecosystems. Carbon is exchanged between heterotrophs and autotrophs within and between ecosystems primarily by way of atmospheric CO_2, a fully oxidized version of carbon that serves as the basic building block that autotrophs use to build multicarbon, high-energy organic molecules such as glucose. Photoautotrophs and chemoautotrophs harness energy from the sun and from inorganic chemical compounds, respectively, to covalently bond carbon atoms together into reduced organic compounds whose energy can be later accessed through the processes of respiration and fermentation (Figure 8.7.1).

Overall, there is a constant exchange of CO_2 between the heterotrophs (which produce CO_2 as a result of respiration or fermentation) and the autotrophs (which use the CO_2 for fixation). Autotrophs also respire or ferment, consuming the organic molecules they form; they do not fix carbon for heterotrophs, but rather use it for their own metabolic needs.

Bacteria and archaea that use methane as their carbon source are called methanotrophs. Reduced one-carbon compounds like methane accumulate in certain anaerobic environments when CO_2 is used as a terminal electron acceptor in anaerobic respiration by archaea called methanogens. Some methanogens also ferment acetate (carbons) to produce methane and CO_2. Methane accumulation due to methanogenesis occurs in both natural anaerobic soil and aquatic environments; methane accumulation also occurs as a result of animal husbandry because methanogens are members of the normal microbiota of ruminants. Environmental methane accumulation due to methanogenesis is of consequence because it is a strong greenhouse gas, and methanotrophs help to reduce atmospheric methane levels.



Carbon cycle

Figure 8.7.1: *This figure summarizes the carbon cycle. Eukaryotes participate in aerobic respiration, fermentation, and oxygenic photosynthesis. Prokaryotes participate in all the steps shown. (credit: modification of work by NOAA)*

Exercise 8.7.1

Describe the interaction between heterotrophs and autotrophs in the carbon cycle.

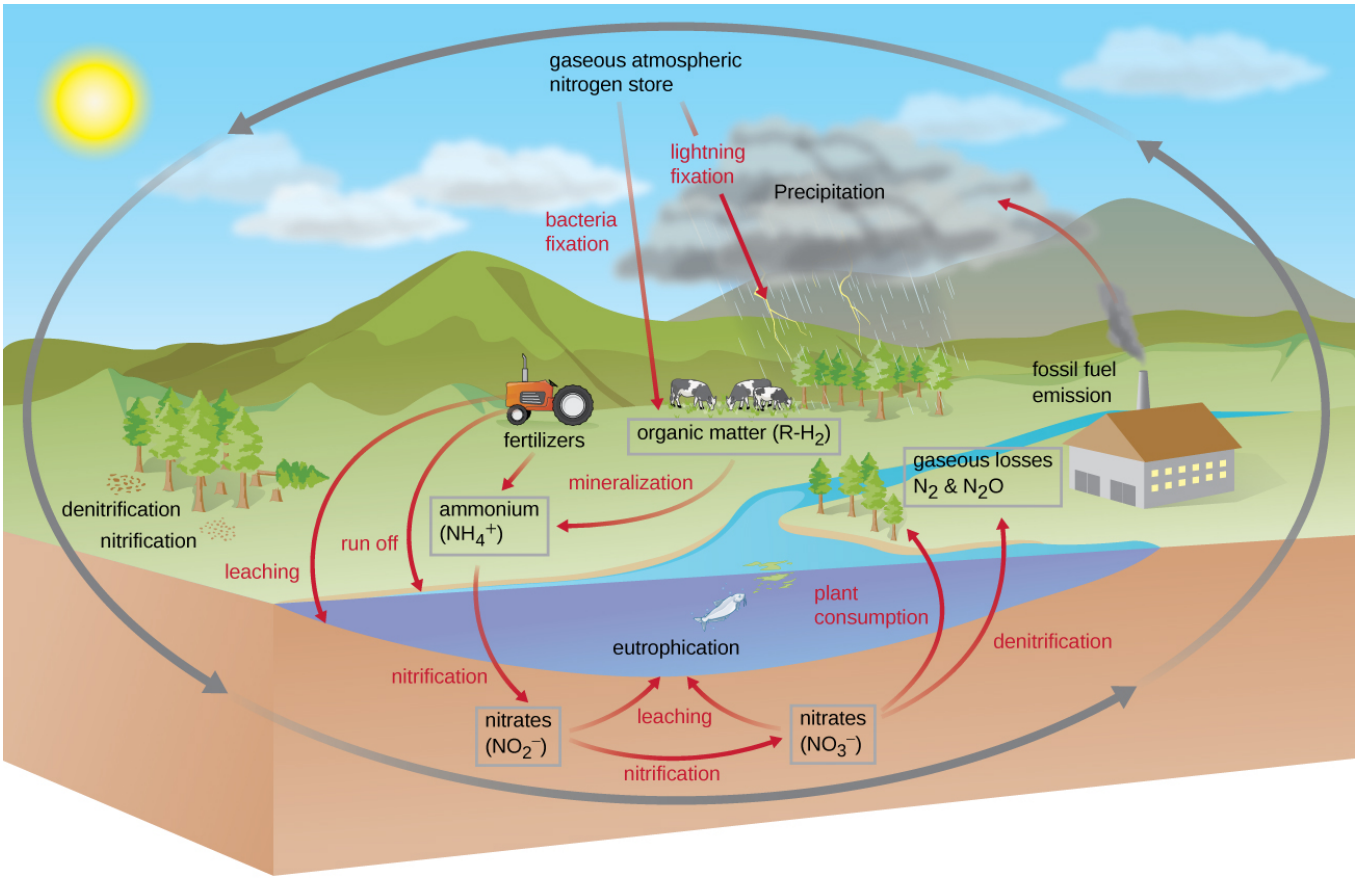
Nitrogen Cycle

Many biological macromolecules, including proteins and nucleic acids, contain nitrogen; however, getting nitrogen into living organisms is difficult. Prokaryotes play essential roles in the nitrogen cycle (Figure 8.7.2), transforming nitrogen between various forms for their own needs, benefiting other organisms indirectly. Plants and phytoplankton cannot incorporate nitrogen from the atmosphere (where it exists as tightly bonded, triple covalent N_2), even though this molecule composes approximately 78% of the atmosphere. Nitrogen enters the living world through free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through specialized biochemical pathways called nitrogen fixation. Cyanobacteria in aquatic ecosystems fix inorganic nitrogen (from nitrogen gas) into ammonia (NH_3) that can be easily incorporated into biological macromolecules. *Rhizobium* bacteria ([link]) also fix nitrogen and live symbiotically in the root nodules of legumes (such as beans, peanuts, and peas), providing them with needed organic nitrogen while receiving fixed carbon as sugar in exchange. Free-living bacteria, such as members of the genus *Azotobacter*, are also able to fix nitrogen.

The nitrogen that enters living systems by nitrogen fixation is eventually converted from organic nitrogen back into nitrogen gas by microbes through three steps: ammonification, nitrification, and denitrification. In terrestrial systems, the first step is the ammonification process, in which certain bacteria and fungi convert nitrogenous waste from living animals or from the remains of dead organisms into ammonia (NH_3). This ammonia is then oxidized to nitrite (NO−2),(NO2−),then to nitrate (NO−3),(NO3−), by nitrifying soil bacteria such as members of the genus *Nitrosomonas*, through the process of nitrification. Last, the process of denitrification occurs, whereby soil bacteria, such as members of the genera *Pseudomonas* and *Clostridium*, use nitrate as a

terminal electron acceptor in anaerobic respiration, converting it into nitrogen gas that reenters the atmosphere. A similar process occurs in the marine nitrogen cycle, where these three processes are performed by marine bacteria and archaea.

Human activity releases nitrogen into the environment by the use of artificial fertilizers that contain nitrogen and phosphorus compounds, which are then washed into lakes, rivers, and streams by surface runoff. A major effect from fertilizer runoff is saltwater and freshwater eutrophication, in which nutrient runoff causes the overgrowth and subsequent death of aquatic algae, making water sources anaerobic and inhospitable for the survival of aquatic organisms.



Nitrogen cycle

Figure 8.7.2: *This figure summarizes the nitrogen cycle. Note that specific groups of prokaryotes each participate in every step in the cycle. (credit: modification of work by NOAA)*

Exercise 8.7.2

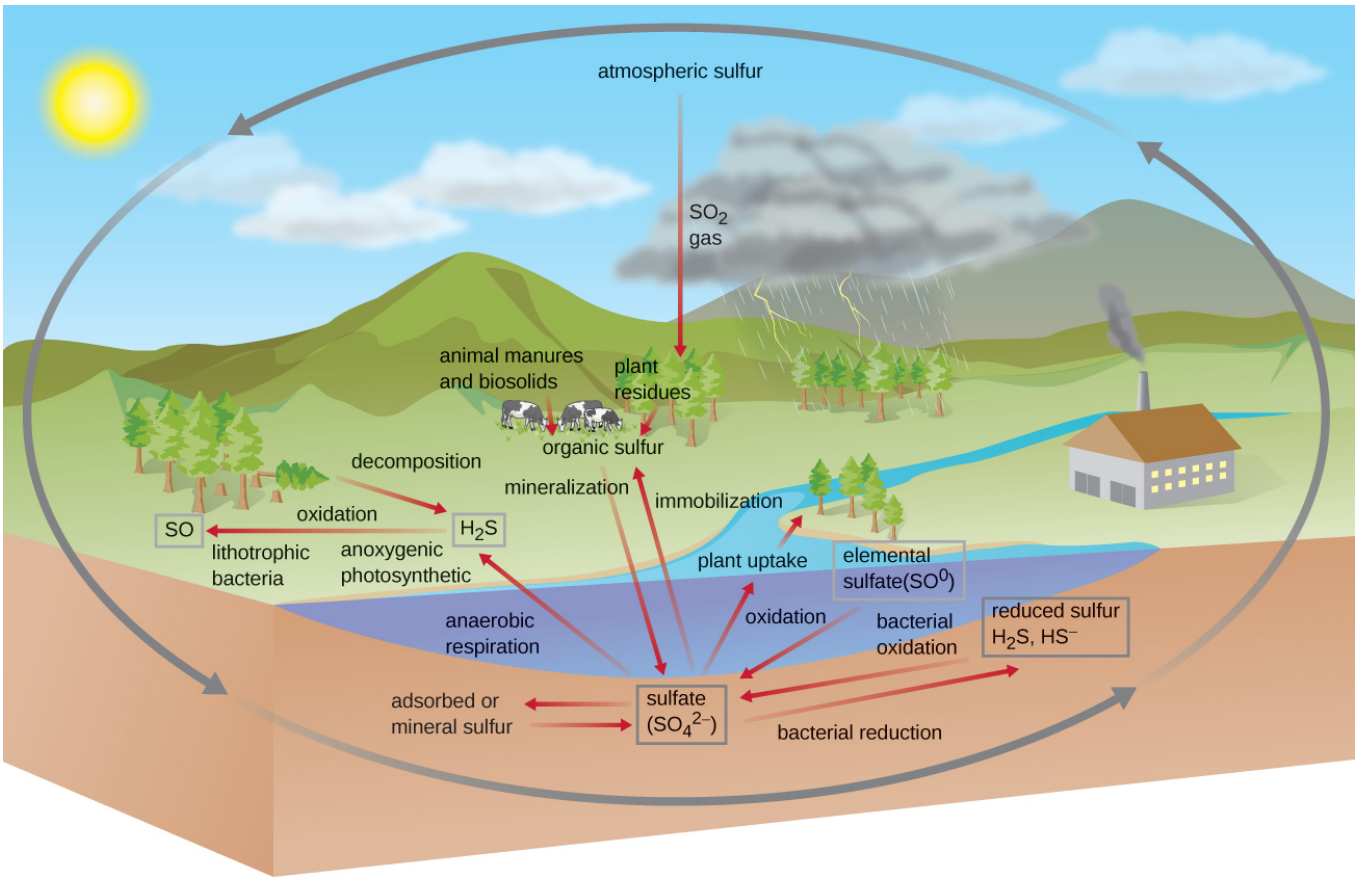
What are the three steps of the nitrogen cycle?

To learn more about the nitrogen cycle, visit the PBS website.

Sulfur Cycle

Sulfur is an essential element for the macromolecules of living organisms. As part of the amino acids cysteine and methionine, it is involved in the formation of proteins. It is also found in several vitamins necessary for the synthesis of important biological molecules like coenzyme A. Several groups of microbes are responsible for carrying out processes involved in the sulfur cycle (Figure 8.7.3). Anoxygenic photosynthetic bacteria as well as chemoautotrophic archaea and bacteria use hydrogen sulfide as an electron donor, oxidizing it first to elemental sulfur (S^0), then to sulfate (SO42−).(SO42−).This leads to stratification of hydrogen sulfide in soil, with levels increasing at deeper, more anaerobic depths.

Many bacteria and plants can use sulfate as a sulfur source. Decomposition dead organisms by fungi and bacteria remove sulfur groups from amino acids, producing hydrogen sulfide, returning inorganic sulfur to the environment.



Sulfur cycle

Figure 8.7.3: This figure summarizes the sulfur cycle. Note that specific groups of prokaryotes each may participate in every step in the cycle. (credit: modification of work by NOAA)

Exercise 8.7.3

Which groups of microbes carry out the sulfur cycle?

Other Biogeochemical Cycles

Beyond their involvement in the carbon, nitrogen, and sulfur cycles, prokaryotes are involved in other biogeochemical cycles as well. Like the carbon, nitrogen, and sulfur cycles, several of these additional biogeochemical cycles, such as the iron (Fe), manganese (Mn), and chromium (Cr) cycles, also involve redox chemistry, with prokaryotes playing roles in both oxidation and reduction. Several other elements undergo chemical cycles that do not involve redox chemistry. Examples of these are phosphorus (P), calcium (Ca), and silica (Si) cycles. The cycling of these elements is particularly important in oceans because large quantities of these elements are incorporated into the exoskeletons of marine organisms. These biogeochemical cycles do not involve redox chemistry but instead involve fluctuations in the solubility of compounds containing calcium, phosphorous, and silica. The overgrowth of naturally occurring microbial communities is typically limited by the availability of nitrogen (as previously mentioned), phosphorus, and iron. Human activities introducing excessive amounts of iron, nitrogen, or phosphorus (typically from detergents) may lead to eutrophication.

Bioremediation

Microbial bioremediation leverages microbial metabolism to remove xenobiotics or other pollutants. Xenobiotics are compounds synthesized by humans and introduced into the environment in much higher concentrations than would naturally occur. Such environmental contamination may involve adhesives, dyes, flame retardants, lubricants, oil and petroleum products, organic solvents, pesticides, and products of the combustion of gasoline and oil. Many xenobiotics resist breakdown, and some accumulate in the food chain after being consumed or absorbed by fish and wildlife, which, in turn, may be eaten by humans. Of particular

concern are contaminants like polycyclic aromatic hydrocarbon (PAH), a carcinogenic xenobiotic found in crude oil, and trichloroethylene (TCE), a common groundwater contaminant.

Bioremediation processes can be categorized as in situ or ex situ. Bioremediation conducted at the site of contamination is called in situ bioremediation and does not involve movement of contaminated material. In contrast, ex situ bioremediation involves the removal of contaminated material from the original site so that it can be treated elsewhere, typically in a large, lined pit where conditions are optimized for degradation of the contaminant.

Some bioremediation processes rely on microorganisms that are indigenous to the contaminated site or material. Enhanced bioremediation techniques, which may be applied to either in situ or ex situ processing, involve the addition of nutrients and/or air to encourage the growth of pollution-degrading microbes; they may also involve the addition of non-native microbes known for their ability to degrade contaminants. For example, certain bacteria of the genera *Rhodococcus* and *Pseudomonas* are known for their ability to degrade many environmental contaminants, including aromatic compounds like those found in oil, down to CO_2. The genes encoding their degradatory enzymes are commonly found on plasmids. Others, like *Alcanivorax borkumensis*, produce surfactants that are useful in the solubilization of the hydrophobic molecules found in oil, making them more accessible to other microbes for degradation.

Exercise 8.7.4

Compare and contrast the benefits of in situ and ex situ bioremediation.

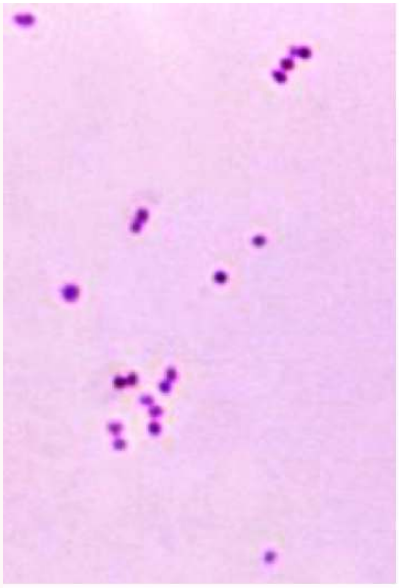
resolution

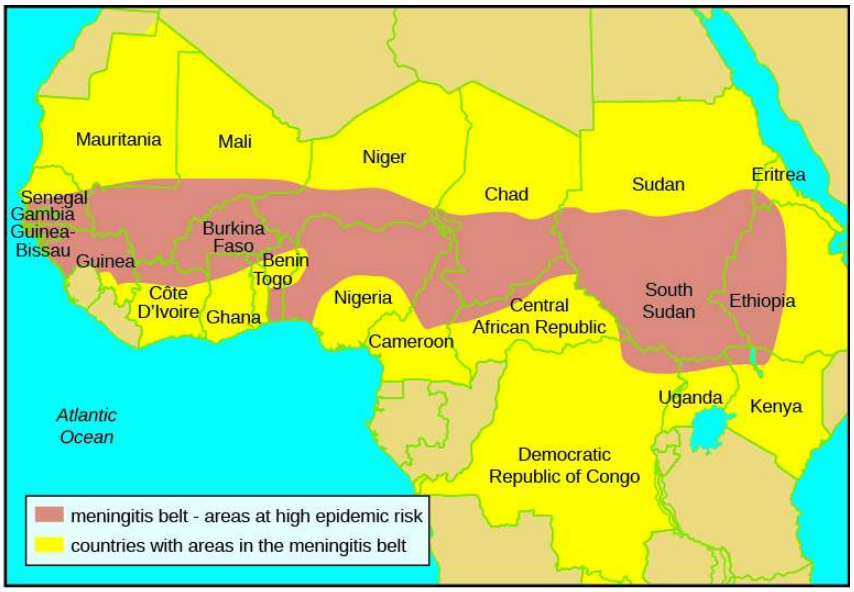
Although there is a DNA test specific for *Neisseria meningitidis*, it is not practical for use in some developing countries because it requires expensive equipment and a high level of expertise to perform. The hospital in Banjul was not equipped to perform DNA testing. Biochemical testing, however, is much less expensive and is still effective for microbial identification.

Fortunately for Hannah, her symptoms began to resolve with antibiotic therapy. Patients who survive bacterial meningitis often suffer from long-term complications such as brain damage, hearing loss, and seizures, but after several weeks of recovery, Hannah did not seem to be exhibiting any long-term effects and her behavior returned to normal. Because of her age, her parents were advised to monitor her closely for any signs of developmental issues and have her regularly evaluated by her pediatrician.

N. meningitidis is found in the normal respiratory microbiota in 10%–20% of the human population.[1] In most cases, it does not cause disease, but for reasons not fully understood, the bacterium can sometimes invade the bloodstream and cause infections in other areas of the body, including the brain. The disease is more common in infants and children, like Hannah.

The prevalence of meningitis caused by *N. meningitidis* is particularly high in the so-called meningitis belt, a region of sub-Saharan African that includes 26 countries stretching from Senegal to Ethiopia (Figure 8.7.4). The reasons for this high prevalence are not clear, but several factors may contribute to higher rates of transmission, such as the dry, dusty climate; overcrowding and low standards of living; and the relatively low immunocompetence and nutritional status of the population.[2] A vaccine against four bacterial strains of *N. meningitidis* is available. Vaccination is recommended for 11- and 12-year-old children, with a booster at age 16 years. Vaccination is also recommended for young people who live in close quarters with others (e.g., college dormitories, military barracks), where the disease is more easily transmitted. Travelers visiting the “meningitis belt” should also be vaccinated, especially during the dry season (December through June) when the prevalence is highest.[3,4]





(a) (b)

Figure 8.7.4: (a) Neisseria meningitidis is a gram-negative diplococcus, as shown in this gram-stained sample. (b) The "meningitis belt" is the area of sub-Saharan Africa with high prevalence of meningitis caused by N. meningitidis. (credit a, b: modification of work by Centers for Disease Control and Prevention)

Key Concepts and Summary

- The recycling of inorganic matter between living organisms and their nonliving environment is called a **biogeochemical cycle**. Microbes play significant roles in these cycles.
- In the **carbon cycle**, heterotrophs degrade reduced organic molecule to produce carbon dioxide, whereas autotrophs fix carbon dioxide to produce organics. **Methanogens** typically form methane by using CO_2 as a final electron acceptor during anaerobic respiration; methanotrophs oxidize the methane, using it as their carbon source.
- In the **nitrogen cycle**, nitrogen-fixing bacteria convert atmospheric nitrogen into ammonia (ammonification). The ammonia can then be oxidized to nitrite and nitrate (nitrification). Nitrates can then be assimilated by plants. Soil bacteria convert nitrate back to nitrogen gas (denitrification).
- In **sulfur cycling**, many anoxygenic photosynthesizers and chemoautotrophs use hydrogen sulfide as an electron donor, producing elemental sulfur and then sulfate; sulfate-reducing bacteria and archaea then use sulfate as a final electron acceptor in anaerobic respiration, converting it back to hydrogen sulfide.
- Human activities that introduce excessive amounts of naturally limited nutrients (like iron, nitrogen, or phosphorus) to aquatic systems may lead to eutrophication.
- Microbial **bioremediation** is the use of microbial metabolism to remove or degrade **xenobiotics** and other environmental contaminants and pollutants. Enhanced bioremediation techniques may involve the introduction of non-native microbes specifically chosen or engineered for their ability to degrade contaminants.

Multiple Choice

Which of the following is the group of archaea that can use CO_2 as their final electron acceptor during anaerobic respiration, producing CH_4?

A. methylotrophs
B. methanotrophs
C. methanogens
D. anoxygenic photosynthesizers

C

Which of the following processes is not involved in the conversion of organic nitrogen to nitrogen gas?

A. nitrogen fixation
B. ammonification
C. nitrification
D. denitrification

A

Which of the following processes produces hydrogen sulfide?

A. anoxygenic photosynthesis
B. oxygenic photosynthesis
C. anaerobic respiration
D. chemoautrophy

C

The biogeochemical cycle of which of the following elements is based on changes in solubility rather than redox chemistry?

A. carbon
B. sulfur
C. nitrogen
D. phosphorus

D

Fill in the Blank

The molecule central to the carbon cycle that is exchanged within and between ecosystems, being produced by heterotrophs and used by autotrophs, is _____.

carbon dioxide

The use of microbes to remove pollutants from a contaminated system is called _____.

bioremediation

True/False

There are many naturally occurring microbes that have the ability to degrade several of the compounds found in oil.

True

Short Answer

Why must autotrophic organisms also respire or ferment in addition to fixing CO_2?

How can human activity lead to eutrophication?

Critical Thinking

In considering the symbiotic relationship between *Rhizobium* species and their plant hosts, what metabolic activity does each organism perform that benefits the other member of the pair?

Footnotes

1. 1 Centers for Disease Control and Prevention. “Meningococcal Disease: Causes and Transmission.” http://www.cdc.gov/meningococcal/abo...nsmission.html. Accessed September 12, 2016.
2. 2 Centers for Disease Control and Prevention. “Meningococcal Disease in Other Countries.” http://www.cdc.gov/meningococcal/global.html. Accessed September 12, 2016.
3. 3 Centers for Disease Control and Prevention. “Health Information for Travelers to the Gambia: Traveler View.” http://wwwnc.cdc.gov/travel/destinat...one/the-gambia. Accessed September 12, 2016.
4. 4 Centers for Disease Control and Prevention. “Meningococcal: Who Needs to Be Vaccinated?” http://www.cdc.gov/vaccines/vpd-vac/...-vaccinate.htm. Accessed September 12, 2016.

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 8.7: Biogeochemical Cycles is shared under a CC BY license and was authored, remixed, and/or curated by OpenStax.

CHAPTER OVERVIEW

7: How Microbes Grow

5.1: How Microbes Grow

Thumbnail: False color time-lapse video of E. coli colony growing on microscope slide. (CC BY-SA 4.0 International; Stewart EJ, Madden R, Paul G, Taddei F via wikipedia).

7: How Microbes Grow is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by LibreTexts.

5.1: How Microbes Grow

skills to develop

- Define the generation time for growth based on binary fission
- Identify and describe the activities of microorganisms undergoing typical phases of binary fission (simple cell division) in a growth curve
- Explain several laboratory methods used to determine viable and total cell counts in populations undergoing exponential growth
- Describe examples of cell division not involving binary fission, such as budding or fragmentation
- Describe the formation and characteristics of biofilms
- Identify health risks associated with biofilms and how they are addressed
- Describe quorum sensing and its role in cell-to-cell communication and coordination of cellular activities

Clinical Focus box: PART 1

Jeni, a 24-year-old pregnant woman in her second trimester, visits a clinic with complaints of high fever, 38.9 °C (102 °F), fatigue, and muscle aches—typical flu-like signs and symptoms. Jeni exercises regularly and follows a nutritious diet with emphasis on organic foods, including raw milk that she purchases from a local farmer's market. All of her immunizations are up to date. However, the health-care provider who sees Jeni is concerned and orders a blood sample to be sent for testing by the microbiology laboratory.

Exercise 5.1.1

Why is the health-care provider concerned about Jeni's signs and symptoms?

The bacterial cell cycle involves the formation of new cells through the replication of DNA and partitioning of cellular components into two daughter cells. In prokaryotes, reproduction is always asexual, although extensive genetic recombination in the form of horizontal gene transfer takes place, as will be explored in a different chapter. Most bacteria have a single circular chromosome; however, some exceptions exist. For example, *Borrelia burgdorferi*, the causative agent of Lyme disease, has a linear chromosome.

Binary Fission

The most common mechanism of cell replication in bacteria is a process called binary fission, which is depicted in Figure 5.1.1:. Before dividing, the cell grows and increases its number of cellular components. Next, the replication of DNA starts at a location on the circular chromosome called the origin of replication, where the chromosome is attached to the inner cell membrane. Replication continues in opposite directions along the chromosome until the terminus is reached.

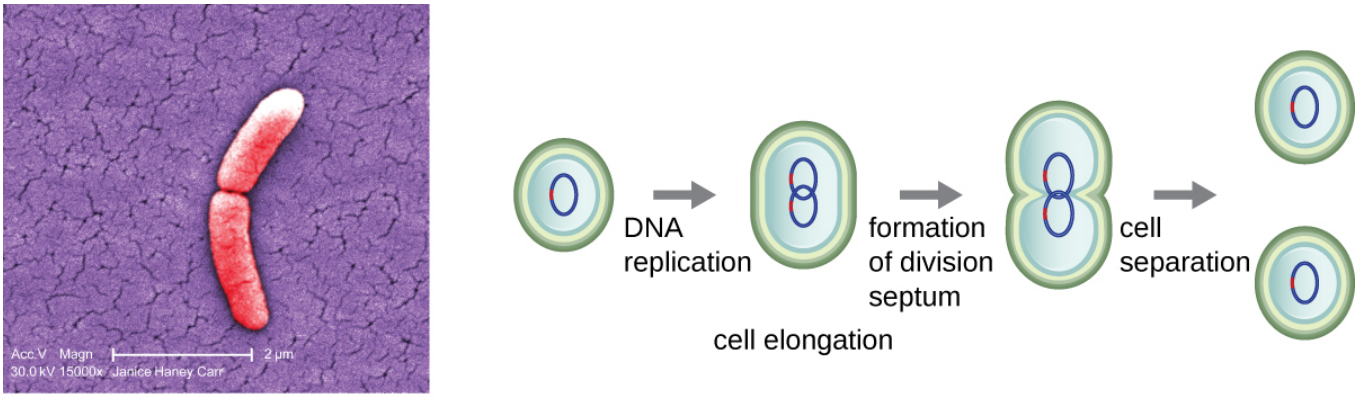


Figure 5.1.1: (a) The electron micrograph depicts two cells of Salmonella typhimurium after a binary fission event. (b) Binary fission in bacteria starts with the replication of DNA as the cell elongates. A division septum forms in the center of the cell. Two daughter cells of similar size form and separate, each receiving a copy of the original chromosome. (credit a: modification of work by Centers for Disease Control and Prevention).

The center of the enlarged cell constricts until two daughter cells are formed, each offspring receiving a complete copy of the parental genome and a division of the cytoplasm (cytokinesis). This process of cytokinesis and cell division is directed by a protein called FtsZ. FtsZ assembles into a Z ring on the cytoplasmic membrane (Figure 5.1.2). The Z ring is anchored by FtsZ-binding proteins and defines the division plane between the two daughter cells. Additional proteins required for cell division are added to the Z ring to form a structure called the divisome. The divisome activates to produce a peptidoglycan cell wall and build a septum that divides the two daughter cells. The daughter cells are separated by the division septum, where all of the cells' outer layers (the cell wall and outer membranes, if present) must be remodeled to complete division. For example, we know that specific enzymes break bonds between the monomers in peptidoglycans and allow addition of new subunits along the division septum.

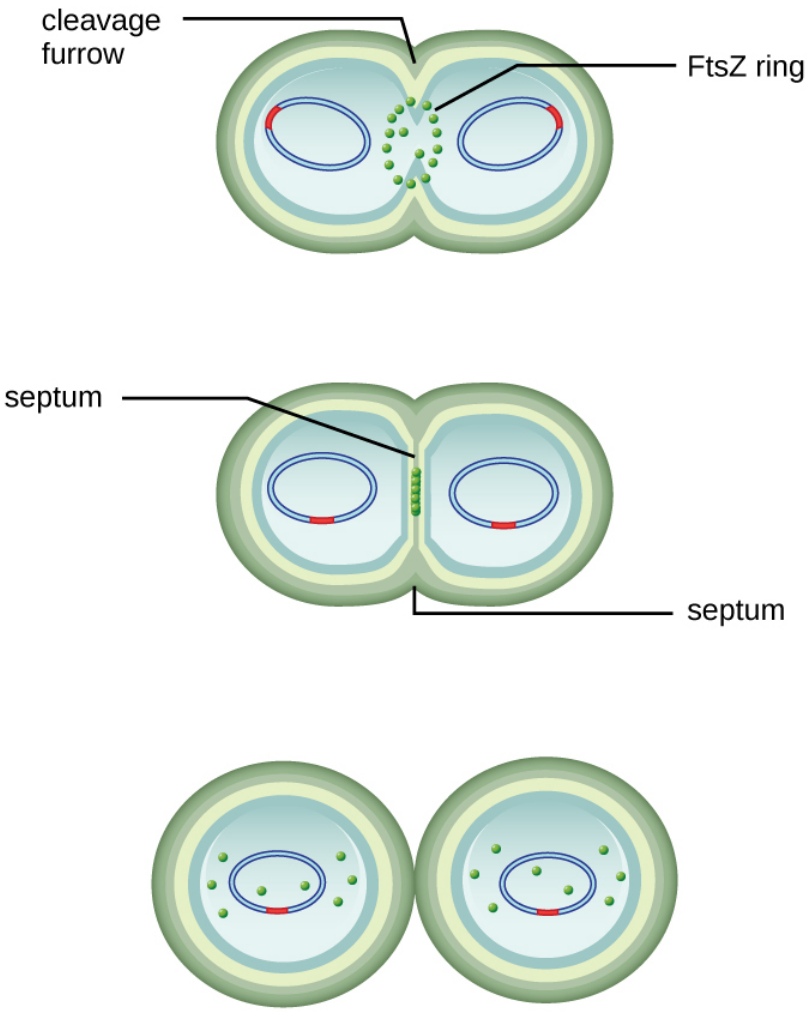


Figure 5.1.2: FtsZ proteins assemble to form a Z ring that is anchored to the plasma membrane. The Z ring pinches the cell envelope to separate the cytoplasm of the new cells.

Exercise 5.1.2

What is the name of the protein that assembles into a Z ring to initiate cytokinesis and cell division?

Generation Time

In eukaryotic organisms, the generation time is the time between the same points of the life cycle in two successive generations. For example, the typical generation time for the human population is 25 years. This definition is not practical for bacteria, which may reproduce rapidly or remain dormant for thousands of years. In prokaryotes (Bacteria and Archaea), the generation time is also called the doubling time and is defined as the time it takes for the population to double through one round of binary fission. Bacterial doubling times vary enormously. Whereas *Escherichia coli* can double in as little as 20 minutes under optimal growth conditions in the laboratory, bacteria of the same species may need several days to double in especially harsh environments. Most pathogens grow rapidly, like *E. coli*, but there are exceptions. For example, *Mycobacterium tuberculosis*, the causative agent of

tuberculosis, has a generation time of between 15 and 20 hours. On the other hand, *M. leprae*, which causes Hansen's disease (leprosy), grows much more slowly, with a doubling time of 14 days.

CALCULATING NUMBER OF CELLS

It is possible to predict the number of cells in a population when they divide by binary fission at a constant rate. As an example, consider what happens if a single cell divides every 30 minutes for 24 hours. The diagram in Figure 5.1.3 shows the increase in cell numbers for the first three generations.

The number of cells increases exponentially and can be expressed as 2^n, where n is the number of generations. If cells divide every 30 minutes, after 24 hours, 48 divisions would have taken place. If we apply the formula 2^n, where n is equal to 48, the single cell would give rise to 2^{48} or 281,474,976,710,656 cells at 48 generations (24 hours). When dealing with such huge numbers, it is more practical to use scientific notation. Therefore, we express the number of cells as 2.8×10^{14} cells.

In our example, we used one cell as the initial number of cells. For any number of starting cells, the formula is adapted as follows:

$$N_n = N_0 2^n \tag{5.1.1}$$

N_n is the number of cells at any generation n, N_0 is the initial number of cells, and n is the number of generations.

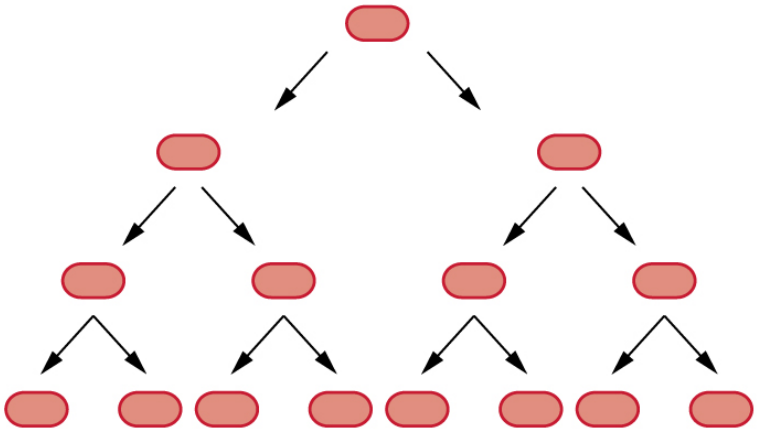
Number of generations (n)	Number of cells	Each division adds two new cells
0	1	
1	2	
2	4	
3	8	

Figure 5.1.3: *The parental cell divides and gives rise to two daughter cells. Each of the daughter cells, in turn, divides, giving a total of four cells in the second generation and eight cells in the third generation. Each division doubles the number of cells.*

Exercise 5.1.3

With a doubling time of 30 minutes and a starting population size of 1×10^5 cells, how many cells will be present after 2 hours, assuming no cell death?

The Growth Curve

Microorganisms grown in closed culture (also known as a batch culture), in which no nutrients are added and most waste is not removed, follow a reproducible growth pattern referred to as the growth curve. An example of a batch culture in nature is a pond in which a small number of cells grow in a closed environment. The culture density is defined as the number of cells per unit volume. In a closed environment, the culture density is also a measure of the number of cells in the population. Infections of the body do not always follow the growth curve, but correlations can exist depending upon the site and type of infection. When the number of live cells is plotted against time, distinct phases can be observed in the curve (Figure 5.1.4).

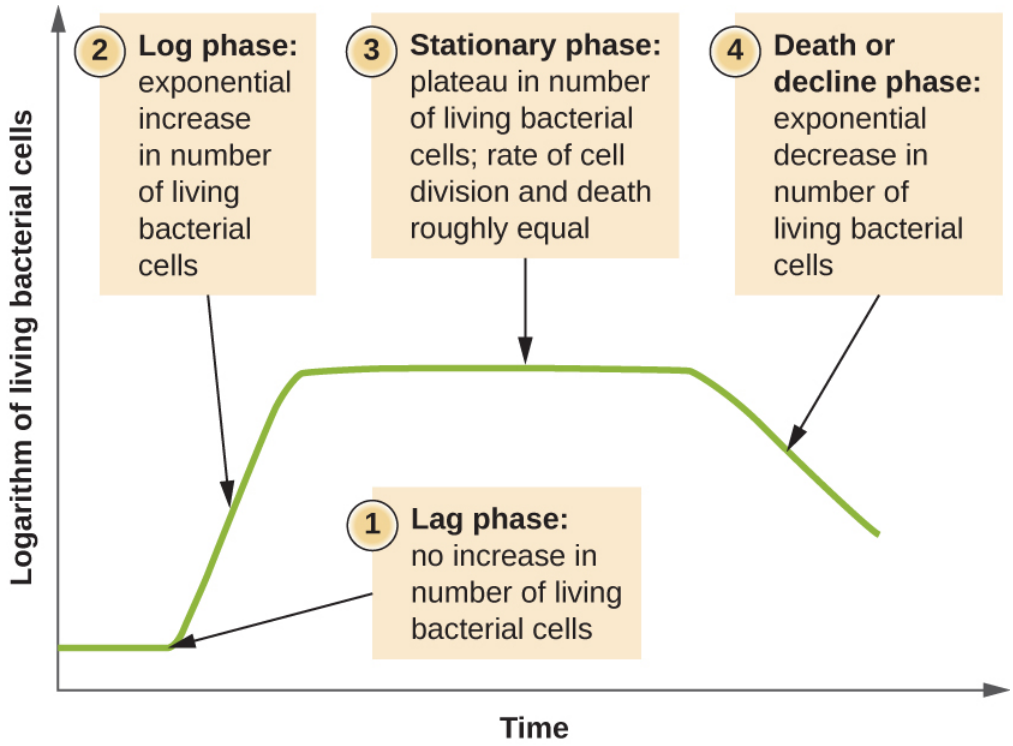


Figure 5.1.4: The growth curve of a bacterial culture is represented by the logarithm of the number of live cells plotted as a function of time. The graph can be divided into four phases according to the slope, each of which matches events in the cell. The four phases are lag, log, stationary, and death.

The Lag Phase

The beginning of the growth curve represents a small number of cells, referred to as an inoculum, that are added to a fresh culture medium, a nutritional broth that supports growth. The initial phase of the growth curve is called the lag phase, during which cells are gearing up for the next phase of growth. The number of cells does not change during the lag phase; however, cells grow larger and are metabolically active, synthesizing proteins needed to grow within the medium. If any cells were damaged or shocked during the transfer to the new medium, repair takes place during the lag phase. The duration of the lag phase is determined by many factors, including the species and genetic make-up of the cells, the composition of the medium, and the size of the original inoculum.

The Log Phase

In the logarithmic (log) growth phase, sometimes called exponential growth phase, the cells are actively dividing by binary fission and their number increases exponentially. For any given bacterial species, the generation time under specific growth conditions (nutrients, temperature, pH, and so forth) is genetically determined, and this generation time is called the intrinsic growth rate. During the log phase, the relationship between time and number of cells is not linear but exponential; however, the growth curve is often plotted on a semilogarithmic graph, as shown in Figure 5.1.5, which gives the appearance of a linear relationship.

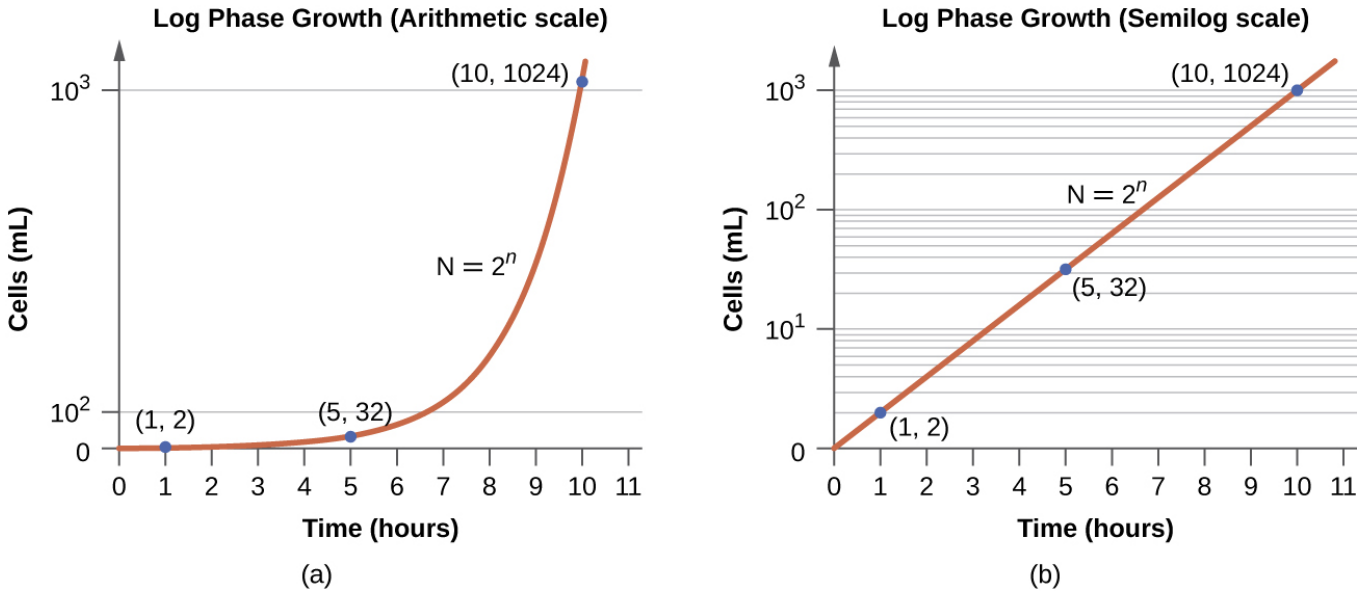


Figure 5.1.5: Both graphs illustrate population growth during the log phase for a bacterial sample with an initial population of one cell and a doubling time of 1 hour. (a) When plotted on an arithmetic scale, the growth rate resembles a curve. (b) When plotted on a semilogarithmic scale (meaning the values on the y-axis are logarithmic), the growth rate appears linear.

Cells in the log phase show constant growth rate and uniform metabolic activity. For this reason, cells in the log phase are preferentially used for industrial applications and research work. The log phase is also the stage where bacteria are the most susceptible to the action of disinfectants and common antibiotics that affect protein, DNA, and cell-wall synthesis.

Stationary Phase

As the number of cells increases through the log phase, several factors contribute to a slowing of the growth rate. Waste products accumulate and nutrients are gradually used up. In addition, gradual depletion of oxygen begins to limit aerobic cell growth. This combination of unfavorable conditions slows and finally stalls population growth. The total number of live cells reaches a plateau referred to as the stationary phase (Figure 5.1.4). In this phase, the number of new cells created by cell division is now equivalent to the number of cells dying; thus, the total population of living cells is relatively stagnant. The culture density in a stationary culture is constant. The culture's carrying capacity, or maximum culture density, depends on the types of microorganisms in the culture and the specific conditions of the culture; however, carrying capacity is constant for a given organism grown under the same conditions.

During the stationary phase, cells switch to a survival mode of metabolism. As growth slows, so too does the synthesis of peptidoglycans, proteins, and nucleic-acids; thus, stationary cultures are less susceptible to antibiotics that disrupt these processes. In bacteria capable of producing endospores, many cells undergo sporulation during the stationary phase. Secondary metabolites, including antibiotics, are synthesized in the stationary phase. In certain pathogenic bacteria, the stationary phase is also associated with the expression of virulence factors, products that contribute to a microbe's ability to survive, reproduce, and cause disease in a host organism. For example, quorum sensing in *Staphylococcus aureus* initiates the production of enzymes that can break down human tissue and cellular debris, clearing the way for bacteria to spread to new tissue where nutrients are more plentiful.

The Death Phase

As a culture medium accumulates toxic waste and nutrients are exhausted, cells die in greater and greater numbers. Soon, the number of dying cells exceeds the number of dividing cells, leading to an exponential decrease in the number of cells (Figure 5.1.4). This is the aptly named death phase, sometimes called the decline phase. Many cells lyse and release nutrients into the medium, allowing surviving cells to maintain viability and form endospores. A few cells, the so-called persisters, are characterized by a slow metabolic rate. Persister cells are medically important because they are associated with certain chronic infections, such as tuberculosis, that do not respond to antibiotic treatment.

Sustaining Microbial Growth

The growth pattern shown in Figure 5.1.4 takes place in a closed environment; nutrients are not added and waste and dead cells are not removed. In many cases, though, it is advantageous to maintain cells in the logarithmic phase of growth. One example is in

industries that harvest microbial products. A chemostat (Figure 5.1.6) is used to maintain a continuous culture in which nutrients are supplied at a steady rate. A controlled amount of air is mixed in for aerobic processes. Bacterial suspension is removed at the same rate as nutrients flow in to maintain an optimal growth environment.

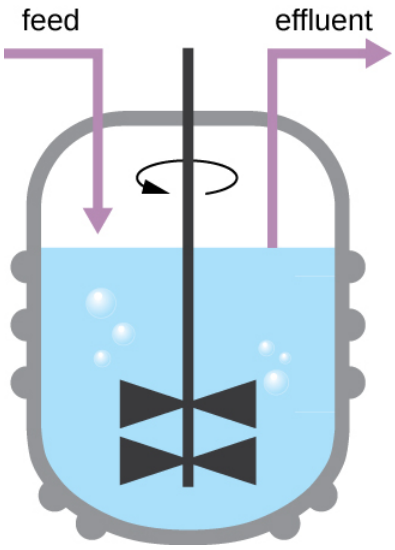


Figure 5.1.6: A chemostat is a culture vessel fitted with an opening to add nutrients (feed) and an outlet to remove contents (effluent), effectively diluting toxic wastes and dead cells. The addition and removal of fluids is adjusted to maintain the culture in the logarithmic phase of growth. If aerobic bacteria are grown, suitable oxygen levels are maintained.

Exercise 5.1.4

1. During which phase does growth occur at the fastest rate?
2. Name two factors that limit microbial growth.

Measurement of Bacterial Growth

Estimating the number of bacterial cells in a sample, known as a bacterial count, is a common task performed by microbiologists. The number of bacteria in a clinical sample serves as an indication of the extent of an infection. Quality control of drinking water, food, medication, and even cosmetics relies on estimates of bacterial counts to detect contamination and prevent the spread of disease. Two major approaches are used to measure cell number. The direct methods involve counting cells, whereas the indirect methods depend on the measurement of cell presence or activity without actually counting individual cells. Both direct and indirect methods have advantages and disadvantages for specific applications.

Direct Cell Count

Direct cell count refers to counting the cells in a liquid culture or colonies on a plate. It is a direct way of estimating how many organisms are present in a sample. Let's look first at a simple and fast method that requires only a specialized slide and a compound microscope.

The simplest way to count bacteria is called the direct microscopic cell count, which involves transferring a known volume of a culture to a calibrated slide and counting the cells under a light microscope. The calibrated slide is called a Petroff-Hausser chamber (Figure 5.1.7) and is similar to a hemocytometer used to count red blood cells. The central area of the counting chamber is etched into squares of various sizes. A sample of the culture suspension is added to the chamber under a coverslip that is placed at a specific height from the surface of the grid. It is possible to estimate the concentration of cells in the original sample by counting individual cells in a number of squares and determining the volume of the sample observed. The area of the squares and the height at which the coverslip is positioned are specified for the chamber. The concentration must be corrected for dilution if the sample was diluted before enumeration.

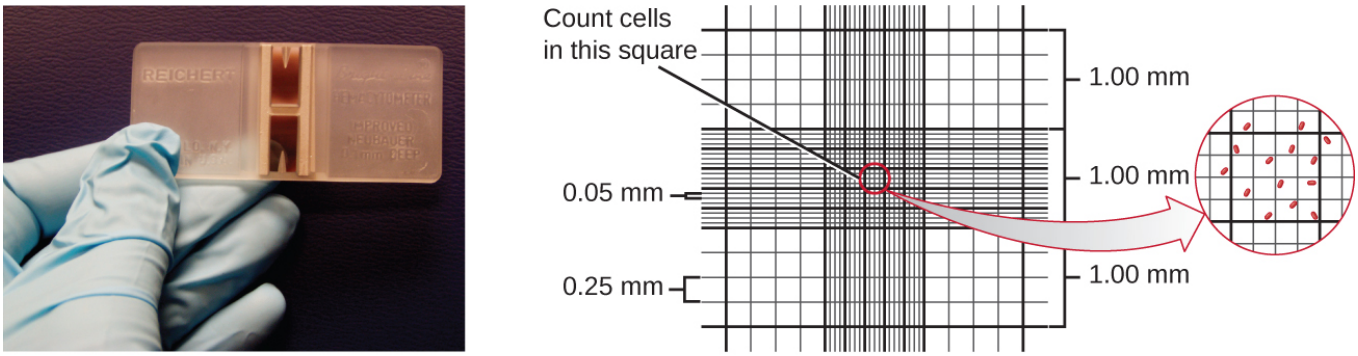


Figure 5.1.7: *(a) A Petroff-Hausser chamber is a special slide designed for counting the bacterial cells in a measured volume of a sample. A grid is etched on the slide to facilitate precision in counting. (b) This diagram illustrates the grid of a Petroff-Hausser chamber, which is made up of squares of known areas. The enlarged view shows the square within which bacteria (red cells) are counted. If the coverslip is 0.2 mm above the grid and the square has an area of 0.04 mm^2, then the volume is 0.008 mm^3, or 0.000008 mL. Since there are 10 cells inside the square, the density of bacteria is 10 cells/0.000008 mL, which equates to 1,250,000 cells/mL. (credit a: modification of work by Jeffrey M. Vinocur)*

Cells in several small squares must be counted and the average taken to obtain a reliable measurement. The advantages of the chamber are that the method is easy to use, relatively fast, and inexpensive. On the downside, the counting chamber does not work well with dilute cultures because there may not be enough cells to count.

Using a counting chamber does not necessarily yield an accurate count of the number of live cells because it is not always possible to distinguish between live cells, dead cells, and debris of the same size under the microscope. However, newly developed fluorescence staining techniques make it possible to distinguish viable and dead bacteria. These viability stains (or live stains) bind to nucleic acids, but the primary and secondary stains differ in their ability to cross the cytoplasmic membrane. The primary stain, which fluoresces green, can penetrate intact cytoplasmic membranes, staining both live and dead cells. The secondary stain, which fluoresces red, can stain a cell only if the cytoplasmic membrane is considerably damaged. Thus, live cells fluoresce green because they only absorb the green stain, whereas dead cells appear red because the red stain displaces the green stain on their nucleic acids (Figure 5.1.8).

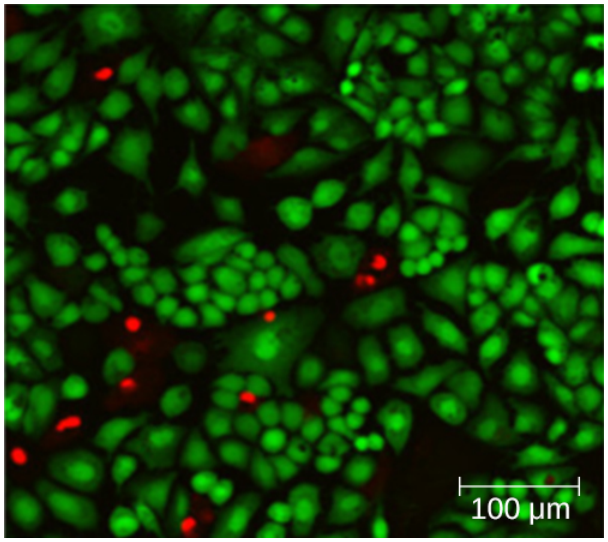


Figure 5.1.8: *Fluorescence staining can be used to differentiate between viable and dead bacterial cells in a sample for purposes of counting. Viable cells are stained green, whereas dead cells are stained red. (credit: modification of work by Panseri S, Cunha C, D'Alessandro T, Sandri M, Giavaresi G, Maracci M, Hung CT, Tampieri A)*

Another technique uses an electronic cell counting device (Coulter counter) to detect and count the changes in electrical resistance in a saline solution. A glass tube with a small opening is immersed in an electrolyte solution. A first electrode is suspended in the glass tube. A second electrode is located outside of the tube. As cells are drawn through the small aperture in the glass tube, they briefly change the resistance measured between the two electrodes and the change is recorded by an electronic sensor (Figure

5.1.9); each resistance change represents a cell. The method is rapid and accurate within a range of concentrations; however, if the culture is too concentrated, more than one cell may pass through the aperture at any given time and skew the results. This method also does not differentiate between live and dead cells.

Direct counts provide an estimate of the total number of cells in a sample. However, in many situations, it is important to know the number of live, or viable, cells. Counts of live cells are needed when assessing the extent of an infection, the effectiveness of antimicrobial compounds and medication, or contamination of food and water.

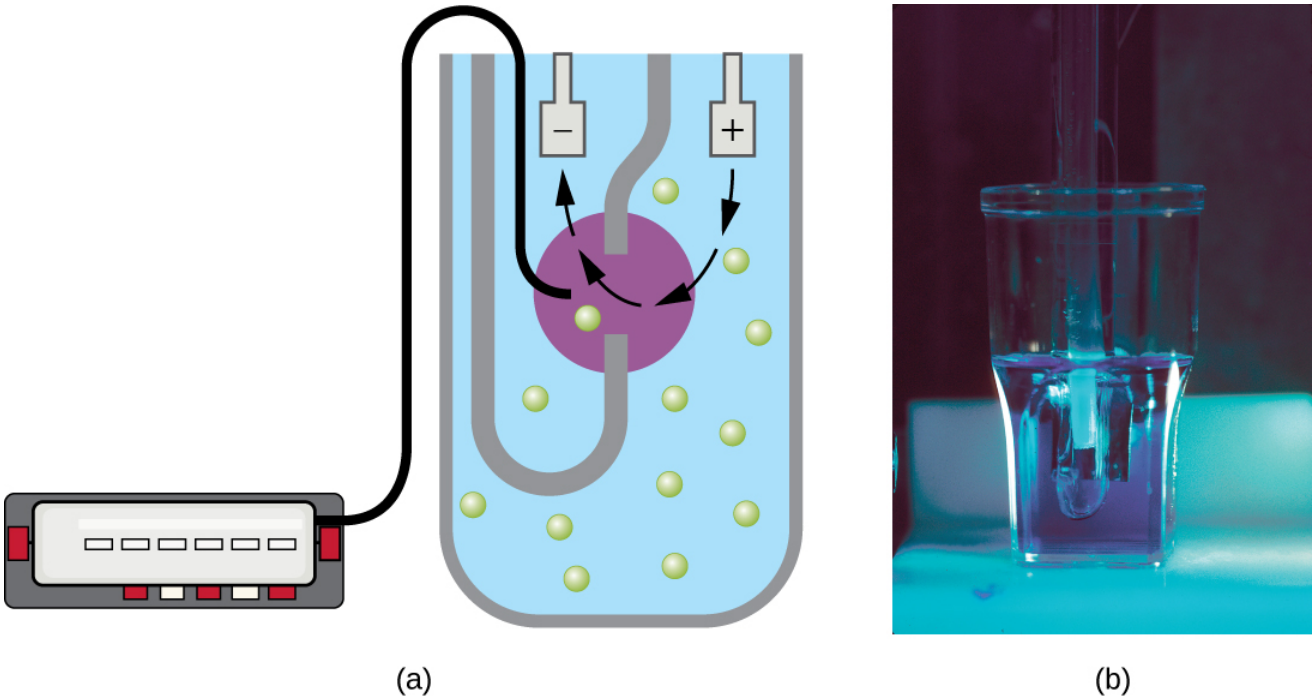


Figure 5.1.9: *A Coulter counter is an electronic device that counts cells. It measures the change in resistance in an electrolyte solution that takes place when a cell passes through a small opening in the inside container wall. A detector automatically counts the number of cells passing through the opening. (credit b: modification of work by National Institutes of Health)*

Exercise 5.1.5

1. Why would you count the number of cells in more than one square in the Petroff-Hausser chamber to estimate cell numbers?
2. In the viability staining method, why do dead cells appear red?

Plate Count

The viable plate count, or simply plate count, is a count of viable or live cells. It is based on the principle that viable cells replicate and give rise to visible colonies when incubated under suitable conditions for the specimen. The results are usually expressed as colony-forming units per milliliter (CFU/mL) rather than cells per milliliter because more than one cell may have landed on the same spot to give rise to a single colony. Furthermore, samples of bacteria that grow in clusters or chains are difficult to disperse and a single colony may represent several cells. Some cells are described as viable but nonculturable and will not form colonies on solid media. For all these reasons, the viable plate count is considered a low estimate of the actual number of live cells. These limitations do not detract from the usefulness of the method, which provides estimates of live bacterial numbers.

Microbiologists typically count plates with 30–300 colonies. Samples with too few colonies (<30) do not give statistically reliable numbers, and overcrowded plates (>300 colonies) make it difficult to accurately count individual colonies. Also, counts in this range minimize occurrences of more than one bacterial cell forming a single colony. Thus, the calculated CFU is closer to the true number of live bacteria in the population.

There are two common approaches to inoculating plates for viable counts: the pour plate and the spread plate methods. Although the final inoculation procedure differs between these two methods, they both start with a serial dilution of the culture.

Serial Dilution

The serial dilution of a culture is an important first step before proceeding to either the pour plate or spread plate method. The goal of the serial dilution process is to obtain plates with CFUs in the range of 30–300, and the process usually involves several dilutions in multiples of 10 to simplify calculation. The number of serial dilutions is chosen according to a preliminary estimate of the culture density. Figure 5.1.10 illustrates the serial dilution method.

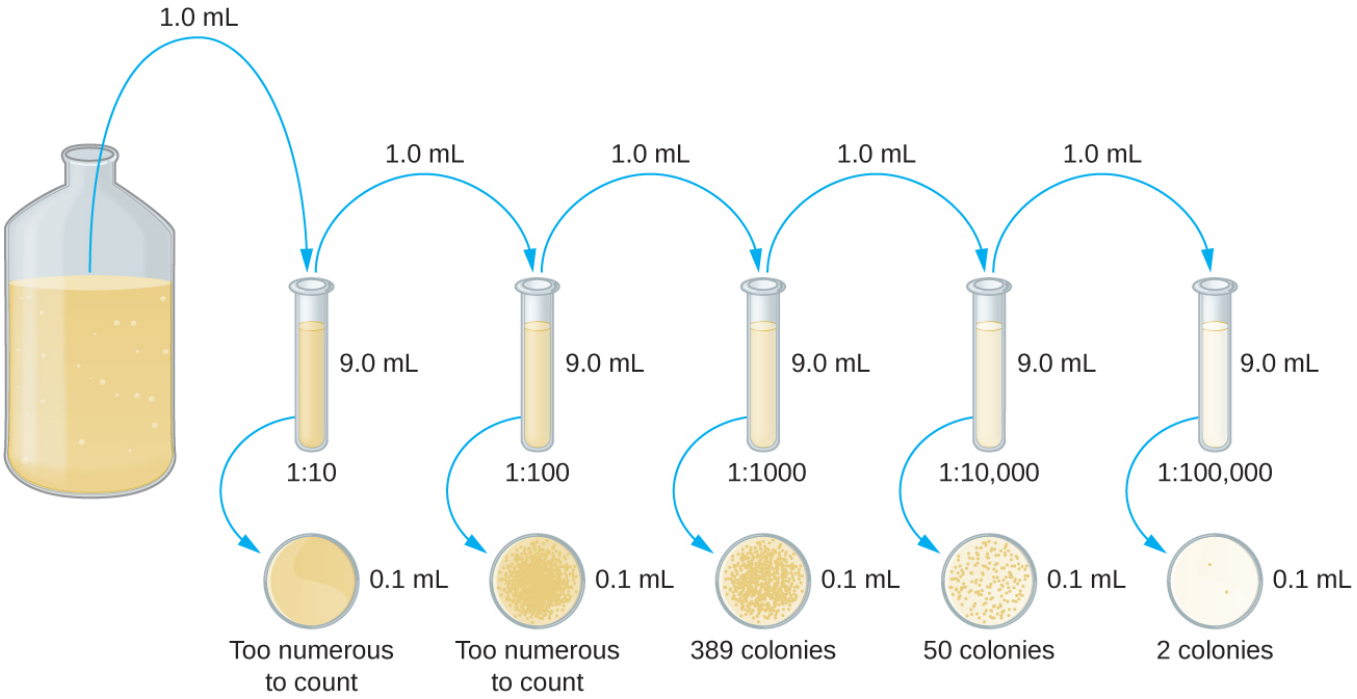


Figure 5.1.10: Serial dilution involves diluting a fixed volume of cells mixed with dilution solution using the previous dilution as an inoculum. The result is dilution of the original culture by an exponentially growing factor. (credit: modification of work by "Leberechtc"/Wikimedia Commons)

A fixed volume of the original culture, 1.0 mL, is added to and thoroughly mixed with the first dilution tube solution, which contains 9.0 mL of sterile broth. This step represents a dilution factor of 10, or 1:10, compared with the original culture. From this first dilution, the same volume, 1.0 mL, is withdrawn and mixed with a fresh tube of 9.0 mL of dilution solution. The dilution factor is now 1:100 compared with the original culture. This process continues until a series of dilutions is produced that will bracket the desired cell concentration for accurate counting. From each tube, a sample is plated on solid medium using either the pour plate method (Figure 5.1.11) or the spread plate method (Figure 5.1.12). The plates are incubated until colonies appear. Two to three plates are usually prepared from each dilution and the numbers of colonies counted on each plate are averaged. In all cases, thorough mixing of samples with the dilution medium (to ensure the cell distribution in the tube is random) is paramount to obtaining reliable results.

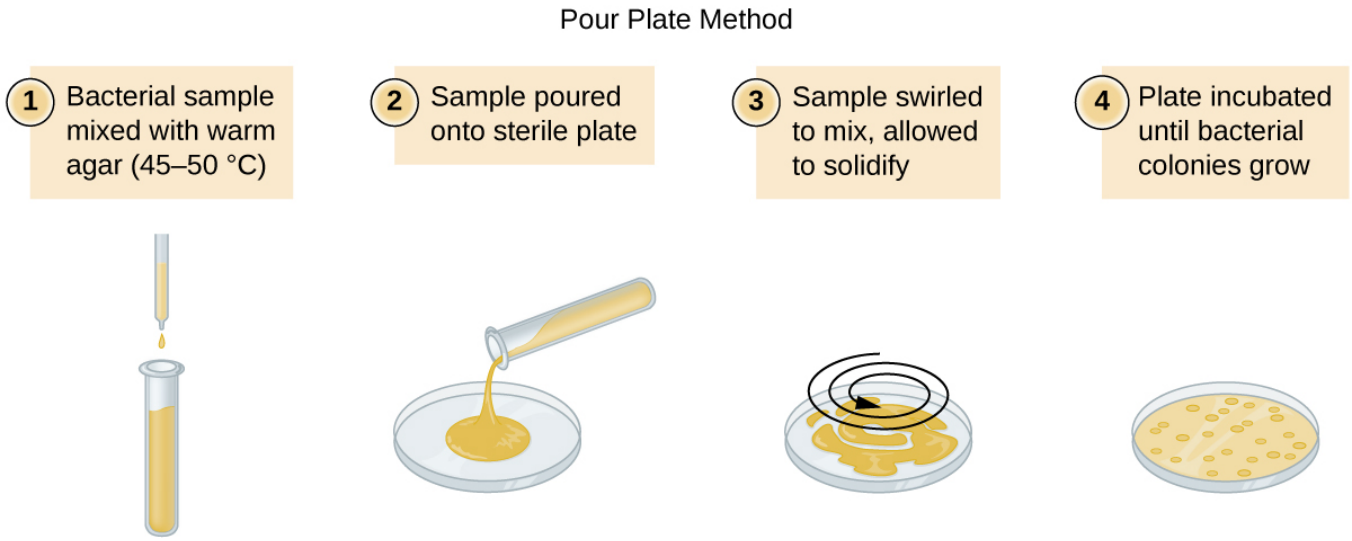


Figure 5.1.11: *In the pour plate method of cell counting, the sample is mixed in liquid warm agar (45–50 °C) poured into a sterile Petri dish and further mixed by swirling. This process is repeated for each serial dilution prepared. The resulting colonies are counted and provide an estimate of the number of cells in the original volume sampled.*

The dilution factor is used to calculate the number of cells in the original cell culture. In our example, an average of 50 colonies was counted on the plates obtained from the 1:10,000 dilution. Because only 0.1 mL of suspension was pipetted on the plate, the multiplier required to reconstitute the original concentration is 10 × 10,000. The number of CFU per mL is equal to 50 × 100 × 10,000 = 5,000,000. The number of bacteria in the culture is estimated as 5 million cells/mL. The colony count obtained from the 1:1000 dilution was 389, well below the expected 500 for a 10-fold difference in dilutions. This highlights the issue of inaccuracy when colony counts are greater than 300 and more than one bacterial cell grows into a single colony.

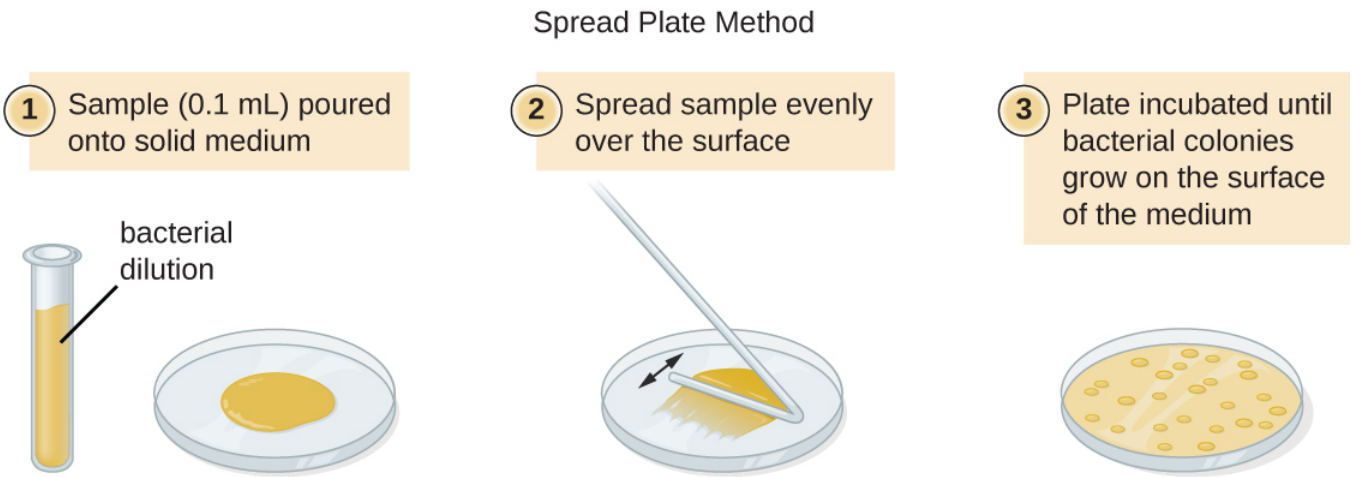


Figure 5.1.12: In the spread plate method of cell counting, the sample is poured onto solid agar and then spread using a sterile spreader. This process is repeated for each serial dilution prepared. The resulting colonies are counted and provide an estimate of the number of cells in the original volume samples.

A very dilute sample—drinking water, for example—may not contain enough organisms to use either of the plate count methods described. In such cases, the original sample must be concentrated rather than diluted before plating. This can be accomplished using a modification of the plate count technique called the membrane filtration technique. Known volumes are vacuum-filtered aseptically through a membrane with a pore size small enough to trap microorganisms. The membrane is transferred to a Petri plate containing an appropriate growth medium. Colonies are counted after incubation. Calculation of the cell density is made by dividing the cell count by the volume of filtered liquid.

Watch this video for demonstrations of serial dilutions and spread plate techniques.

The Most Probable Number

The number of microorganisms in dilute samples is usually too low to be detected by the plate count methods described thus far. For these specimens, microbiologists routinely use the most probable number (MPN) method, a statistical procedure for estimating of the number of viable microorganisms in a sample. Often used for water and food samples, the MPN method evaluates detectable growth by observing changes in turbidity or color due to metabolic activity.

A typical application of MPN method is the estimation of the number of coliforms in a sample of pond water. Coliforms are gram-negative rod bacteria that ferment lactose. The presence of coliforms in water is considered a sign of contamination by fecal matter. For the method illustrated in Figure 5.1.13, a series of three dilutions of the water sample is tested by inoculating five lactose broth tubes with 10 mL of sample, five lactose broth tubes with 1 mL of sample, and five lactose broth tubes with 0.1 mL of sample. The lactose broth tubes contain a pH indicator that changes color from red to yellow when the lactose is fermented. After inoculation and incubation, the tubes are examined for an indication of coliform growth by a color change in media from red to yellow. The first set of tubes (10-mL sample) showed growth in all the tubes; the second set of tubes (1 mL) showed growth in two tubes out of five; in the third set of tubes, no growth is observed in any of the tubes (0.1-mL dilution). The numbers 5, 2, and 0 are compared with Figure B1 in Appendix B, which has been constructed using a probability model of the sampling procedure. From our reading of the table, we conclude that 49 is the most probable number of bacteria per 100 mL of pond water.

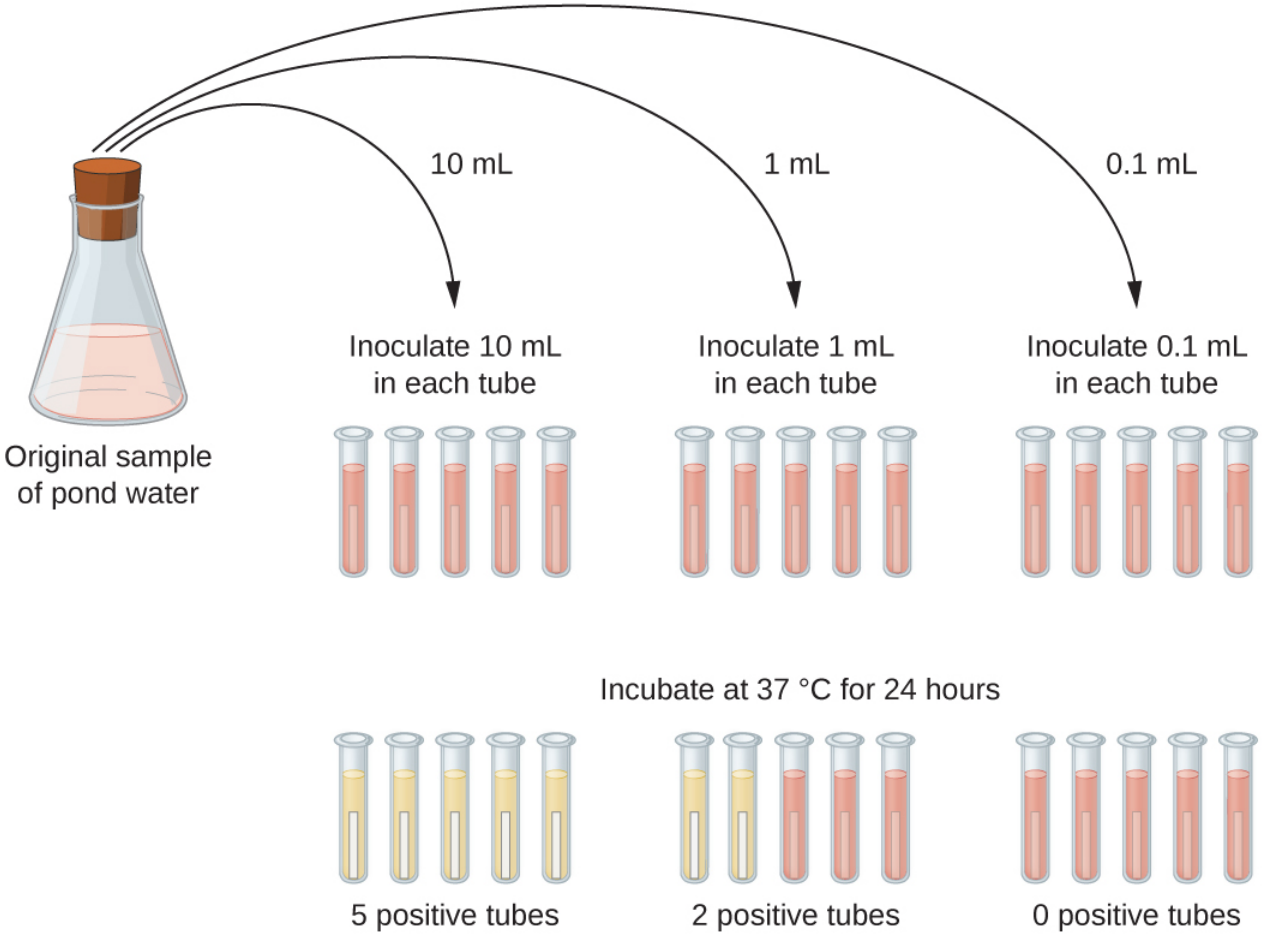


Figure 5.1.13: *In the most probable number method, sets of five lactose broth tubes are inoculated with three different volumes of pond water: 10 mL, 1 mL, and 0.1mL. Bacterial growth is assessed through a change in the color of the broth from red to yellow as lactose is fermented.*

Exercise 5.1.6

1. What is a colony-forming unit?
2. What two methods are frequently used to estimate bacterial numbers in water samples?

Indirect Cell Counts

Besides direct methods of counting cells, other methods, based on an indirect detection of cell density, are commonly used to estimate and compare cell densities in a culture. The foremost approach is to measure the turbidity (cloudiness) of a sample of bacteria in a liquid suspension. The laboratory instrument used to measure turbidity is called a spectrophotometer (Figure 5.1.14). In a spectrophotometer, a light beam is transmitted through a bacterial suspension, the light passing through the suspension is measured by a detector, and the amount of light passing through the sample and reaching the detector is converted to either percent transmission or a logarithmic value called absorbance (optical density). As the numbers of bacteria in a suspension increase, the turbidity also increases and causes less light to reach the detector. The decrease in light passing through the sample and reaching the detector is associated with a decrease in percent transmission and increase in absorbance measured by the spectrophotometer.

Measuring turbidity is a fast method to estimate cell density as long as there are enough cells in a sample to produce turbidity. It is possible to correlate turbidity readings to the actual number of cells by performing a viable plate count of samples taken from cultures having a range of absorbance values. Using these values, a calibration curve is generated by plotting turbidity as a function of cell density. Once the calibration curve has been produced, it can be used to estimate cell counts for all samples obtained or cultured under similar conditions and with densities within the range of values used to construct the curve.

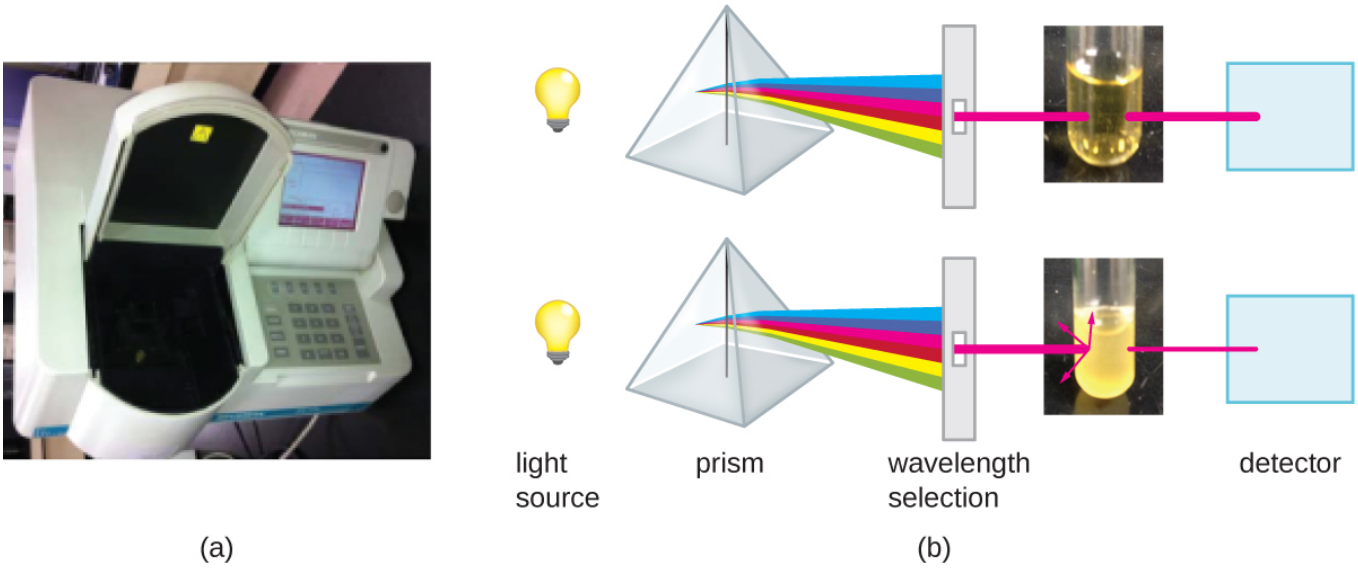


Figure 5.1.14: *(a) A spectrophotometer is commonly used to measure the turbidity of a bacterial cell suspension as an indirect measure of cell density. (b) A spectrophotometer works by splitting white light from a source into a spectrum. The spectrophotometer allows choice of the wavelength of light to use for the measurement. The optical density (turbidity) of the sample will depend on the wavelength, so once one wavelength is chosen, it must be used consistently. The filtered light passes through the sample (or a control with only medium) and the light intensity is measured by a detector. The light passing into a suspension of bacteria is scattered by the cells in such a way that some fraction of it never reaches the detector. This scattering happens to a far lesser degree in the control tube with only the medium. (credit a: modification of work by Hwang HS, Kim MS; credit b "test tube photos": modification of work by Suzanne Wakim)*

Measuring dry weight of a culture sample is another indirect method of evaluating culture density without directly measuring cell counts. The cell suspension used for weighing must be concentrated by filtration or centrifugation, washed, and then dried before the measurements are taken. The degree of drying must be standardized to account for residual water content. This method is especially useful for filamentous microorganisms, which are difficult to enumerate by direct or viable plate count.

As we have seen, methods to estimate viable cell numbers can be labor intensive and take time because cells must be grown. Recently, indirect ways of measuring live cells have been developed that are both fast and easy to implement. These methods measure cell activity by following the production of metabolic products or disappearance of reactants. Adenosine triphosphate (ATP) formation, biosynthesis of proteins and nucleic acids, and consumption of oxygen can all be monitored to estimate the number of cells.

Exercise 5.1.7

1. What is the purpose of a calibration curve when estimating cell count from turbidity measurements?

2. What are the newer indirect methods of counting live cells?

Alternative Patterns of Cell Division

Binary fission is the most common pattern of cell division in prokaryotes, but it is not the only one. Other mechanisms usually involve asymmetrical division (as in budding) or production of spores in aerial filaments.

In some cyanobacteria, many nucleoids may accumulate in an enlarged round cell or along a filament, leading to the generation of many new cells at once. The new cells often split from the parent filament and float away in a process called fragmentation (Figure 5.1.15). Fragmentation is commonly observed in the Actinomycetes, a group of gram-positive, anaerobic bacteria commonly found in soil. Another curious example of cell division in prokaryotes, reminiscent of live birth in animals, is exhibited by the giant bacterium *Epulopiscium*. Several daughter cells grow fully in the parent cell, which eventually disintegrates, releasing the new cells to the environment. Other species may form a long narrow extension at one pole in a process called budding. The tip of the extension swells and forms a smaller cell, the bud that eventually detaches from the parent cell. Budding is most common in yeast (Figure 5.1.15), but it is also observed in prosthecate bacteria and some cyanobacteria.

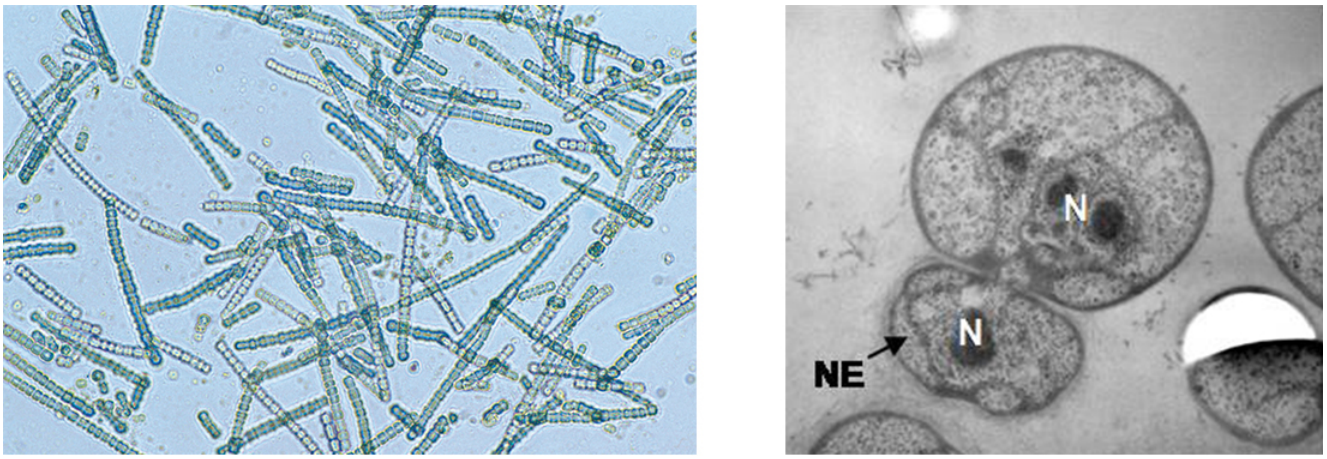


Figure 5.1.15: (a) Filamentous cyanobacteria, like those pictured here, replicate by fragmentation. (b) In this electron micrograph, cells of the bacterium Gemmata obscuriglobus are budding. The larger cell is the mother cell. Labels indicate the nucleoids (N) and the still-forming nuclear envelope (NE) of the daughter cell. (credit a: modification of work by CSIRO; credit b: modification of work by Kuo-Chang Lee, Rick I Webb and John A Fuerst)

The soil bacteria *Actinomyces* grow in long filaments divided by septa, similar to the mycelia seen in fungi, resulting in long cells with multiple nucleoids. Environmental signals, probably related to low nutrient availability, lead to the formation of aerial filaments. Within these aerial filaments, elongated cells divide simultaneously. The new cells, which contain a single nucleoid, develop into spores that give rise to new colonies.

Exercise 5.1.8

Identify at least one difference between fragmentation and budding.

Biofilms

In nature, microorganisms grow mainly in biofilms, complex and dynamic ecosystems that form on a variety of environmental surfaces, from industrial conduits and water treatment pipelines to rocks in river beds. Biofilms are not restricted to solid surface substrates, however. Almost any surface in a liquid environment containing some minimal nutrients will eventually develop a biofilm. Microbial mats that float on water, for example, are biofilms that contain large populations of photosynthetic microorganisms. Biofilms found in the human mouth may contain hundreds of bacterial species. Regardless of the environment where they occur, biofilms are not random collections of microorganisms; rather, they are highly structured communities that provide a selective advantage to their constituent microorganisms.

Biofilm Structure

Observations using confocal microscopy have shown that environmental conditions influence the overall structure of biofilms. Filamentous biofilms called streamers form in rapidly flowing water, such as freshwater streams, eddies, and specially designed laboratory flow cells that replicate growth conditions in fast-moving fluids. The streamers are anchored to the substrate by a "head" and the "tail" floats downstream in the current. In still or slow-moving water, biofilms mainly assume a mushroom-like shape. The structure of biofilms may also change with other environmental conditions such as nutrient availability.

Detailed observations of biofilms under confocal laser and scanning electron microscopes reveal clusters of microorganisms embedded in a matrix interspersed with open water channels. The extracellular matrix consists of extracellular polymeric substances (EPS) secreted by the organisms in the biofilm. The extracellular matrix represents a large fraction of the biofilm, accounting for 50%–90% of the total dry mass. The properties of the EPS vary according to the resident organisms and environmental conditions.

EPS is a hydrated gel composed primarily of polysaccharides and containing other macromolecules such as proteins, nucleic acids, and lipids. It plays a key role in maintaining the integrity and function of the biofilm. Channels in the EPS allow movement of nutrients, waste, and gases throughout the biofilm. This keeps the cells hydrated, preventing desiccation. EPS also shelters organisms in the biofilm from predation by other microbes or cells (e.g., protozoans, white blood cells in the human body).

Biofilm Formation

Free-floating microbial cells that live in an aquatic environment are called planktonic cells. The formation of a biofilm essentially involves the attachment of planktonic cells to a substrate, where they become sessile (attached to a surface). This occurs in stages, as depicted in Figure 5.1.16. The first stage involves the attachment of planktonic cells to a surface coated with a conditioning film of organic material. At this point, attachment to the substrate is reversible, but as cells express new phenotypes that facilitate the formation of EPS, they transition from a planktonic to a sessile lifestyle. The biofilm develops characteristic structures, including an extensive matrix and water channels. Appendages such as fimbriae, pili, and flagella interact with the EPS, and microscopy and genetic analysis suggest that such structures are required for the establishment of a mature biofilm. In the last stage of the biofilm life cycle, cells on the periphery of the biofilm revert to a planktonic lifestyle, sloughing off the mature biofilm to colonize new sites. This stage is referred to as dispersal.

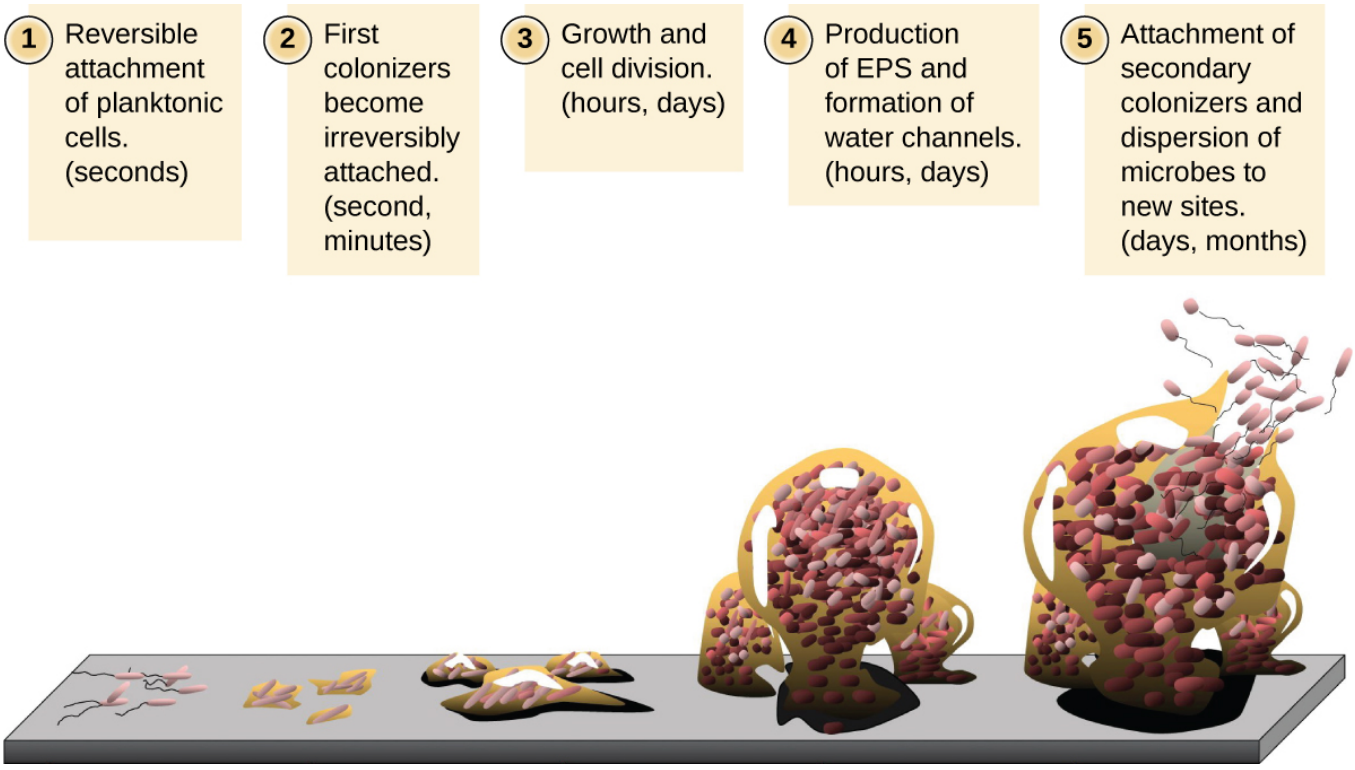


Figure 5.1.16: *Stages in the formation and life cycle of a biofilm. (credit: modification of work by Public Library of Science and American Society for Microbiology)*

Within a biofilm, different species of microorganisms establish metabolic collaborations in which the waste product of one organism becomes the nutrient for another. For example, aerobic microorganisms consume oxygen, creating anaerobic regions that promote the growth of anaerobes. This occurs in many polymicrobial infections that involve both aerobic and anaerobic pathogens.

The mechanism by which cells in a biofilm coordinate their activities in response to environmental stimuli is called quorum sensing. Quorum sensing—which can occur between cells of different species within a biofilm—enables microorganisms to detect their cell density through the release and binding of small, diffusible molecules called autoinducers. When the cell population reaches a critical threshold (a quorum), these autoinducers initiate a cascade of reactions that activate genes associated with cellular functions that are beneficial only when the population reaches a critical density. For example, in some pathogens, synthesis of virulence factors only begins when enough cells are present to overwhelm the immune defenses of the host. Although mostly studied in bacterial populations, quorum sensing takes place between bacteria and eukaryotes and between eukaryotic cells such as the fungus *Candida albicans*, a common member of the human microbiota that can cause infections in immunocompromised individuals.

The signaling molecules in quorum sensing belong to two major classes. Gram-negative bacteria communicate mainly using N-acylated homoserine lactones, whereas gram-positive bacteria mostly use small peptides (Figure 5.1.17). In all cases, the first step in quorum sensing consists of the binding of the autoinducer to its specific receptor only when a threshold concentration of signaling molecules is reached. Once binding to the receptor takes place, a cascade of signaling events leads to changes in gene expression. The result is the activation of biological responses linked to quorum sensing, notably an increase in the production of signaling molecules themselves, hence the term autoinducer.

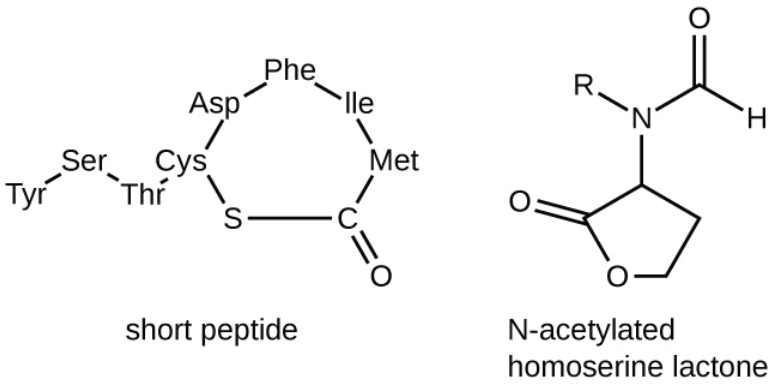


Figure 5.1.17: Short peptides in gram-positive bacteria and N-acetylated homoserine lactones in gram-negative bacteria act as autoinducers in quorum sensing and mediate the coordinated response of bacterial cells. The R side chain of the N-acetylated homoserine lactone is specific for the species of gram-negative bacteria. Some secreted homoserine lactones are recognized by more than one species.

Biofilms and Human Health

The human body harbors many types of biofilms, some beneficial and some harmful. For example, the layers of normal microbiota lining the intestinal and respiratory mucosa play a role in warding off infections by pathogens. However, other biofilms in the body can have a detrimental effect on health. For example, the plaque that forms on teeth is a biofilm that can contribute to dental and periodontal disease. Biofilms can also form in wounds, sometimes causing serious infections that can spread. The bacterium *Pseudomonas aeruginosa* often colonizes biofilms in the airways of patients with cystic fibrosis, causing chronic and sometimes fatal infections of the lungs. Biofilms can also form on medical devices used in or on the body, causing infections in patients with in-dwelling catheters, artificial joints, or contact lenses.

Pathogens embedded within biofilms exhibit a higher resistance to antibiotics than their free-floating counterparts. Several hypotheses have been proposed to explain why. Cells in the deep layers of a biofilm are metabolically inactive and may be less susceptible to the action of antibiotics that disrupt metabolic activities. The EPS may also slow the diffusion of antibiotics and antiseptics, preventing them from reaching cells in the deeper layers of the biofilm. Phenotypic changes may also contribute to the increased resistance exhibited by bacterial cells in biofilms. For example, the increased production of efflux pumps, membrane-embedded proteins that actively extrude antibiotics out of bacterial cells, have been shown to be an important mechanism of

antibiotic resistance among biofilm-associated bacteria. Finally, biofilms provide an ideal environment for the exchange of extrachromosomal DNA, which often includes genes that confer antibiotic resistance.

Exercise 5.1.9

1. What is the matrix of a biofilm composed of?
2. What is the role of quorum sensing in a biofilm?

Key Concepts and Summary

- Most bacterial cells divide by **binary fission**. **Generation time** in bacterial growth is defined as the **doubling time**of the population.
- Cells in a closed system follow a pattern of growth with four phases: **lag**, **logarithmic (exponential)**, **stationary**, and **death**.
- Cells can be counted by **direct viable cell count**. The **pour plate** and **spread plate** methods are used to plate **serial dilutions** into or onto, respectively, agar to allow counting of viable cells that give rise to **colony-forming units**. **Membrane filtration** is used to count live cells in dilute solutions. The **most probable cell number (MPN)**method allows estimation of cell numbers in cultures without using solid media.
- Indirect methods can be used to estimate **culture density** by measuring **turbidity** of a culture or live cell density by measuring metabolic activity.
- Other patterns of cell division include multiple nucleoid formation in cells; asymmetric division, as in **budding**; and the formation of hyphae and terminal spores.
- **Biofilms** are communities of microorganisms enmeshed in a matrix of **extracellular polymeric substance**. The formation of a biofilm occurs when **planktonic** cells attach to a substrate and become **sessile**. Cells in biofilms coordinate their activity by communicating through **quorum sensing**.
- Biofilms are commonly found on surfaces in nature and in the human body, where they may be beneficial or cause severe infections. Pathogens associated with biofilms are often more resistant to antibiotics and disinfectants.

Multiple Choice

Which of the following methods would be used to measure the concentration of bacterial contamination in processed peanut butter?

A. turbidity measurement
B. total plate count
C. dry weight measurement
D. direct counting of bacteria on a calibrated slide under the microscope

---

B

In which phase would you expect to observe the most endospores in a *Bacillus* cell culture?

A. death phase
B. lag phase
C. log phase
D. log, lag, and death phases would all have roughly the same number of endospores.

A

During which phase would penicillin, an antibiotic that inhibits cell-wall synthesis, be most effective?

A. death phase
B. lag phase
C. log phase
D. stationary phase

C

Which of the following is the best definition of generation time in a bacterium?

A. the length of time it takes to reach the log phase
B. the length of time it takes for a population of cells to double
C. the time it takes to reach stationary phase
D. the length of time of the exponential phase

B

What is the function of the Z ring in binary fission?

A. It controls the replication of DNA.
B. It forms a contractile ring at the septum.
C. It separates the newly synthesized DNA molecules.
D. It mediates the addition of new peptidoglycan subunits.

B

If a culture starts with 50 cells, how many cells will be present after five generations with no cell death?

A. 200
B. 400
C. 1600
D. 3200

C

Filamentous cyanobacteria often divide by which of the following?

A. budding
B. mitosis
C. fragmentation
D. formation of endospores

C

Which is a reason for antimicrobial resistance being higher in a biofilm than in free-floating bacterial cells?

A. The EPS allows faster diffusion of chemicals in the biofilm.
B. Cells are more metabolically active at the base of a biofilm.
C. Cells are metabolically inactive at the base of a biofilm.
D. The structure of a biofilm favors the survival of antibiotic resistant cells.

C

Quorum sensing is used by bacterial cells to determine which of the following?

A. the size of the population
B. the availability of nutrients
C. the speed of water flow
D. the density of the population

D

Which of the following statements about autoinducers is incorrect?

A. They bind directly to DNA to activate transcription.
B. They can activate the cell that secreted them.
C. N-acylated homoserine lactones are autoinducers in gram-negative cells.
D. Autoinducers may stimulate the production of virulence factors.

A

Fill in the Blank

Direct count of total cells can be performed using a _____ or a _____.

hemocytometer, Petroff-Hausser counting chamber

The _____ method allows direct count of total cells growing on solid medium.

plate count

A statistical estimate of the number of live cells in a liquid is usually done by _____.

most probable number

For this indirect method of estimating the growth of a culture, you measure _____ using a spectrophotometer.

turbidity

Active growth of a culture may be estimated indirectly by measuring the following products of cell metabolism: _____ or _____.

ATP, acid from fermentation

Matching

Match the definition with the name of the growth phase in the growth curve.

___Number of dying cells is higher than the number of cells dividing	A. Lag phase
___Number of new cells equal to number of dying cells	B. Log phase
___New enzymes to use available nutrients are induced	C. Stationary phase
___Binary fission is occurring at maximum rate	D. Death phase

D, C, A, B

Short Answer

Why is it important to measure the transmission of light through a control tube with only broth in it when making turbidity measures of bacterial cultures?

In terms of counting cells, what does a plating method accomplish that an electronic cell counting method does not?

Order the following stages of the development of a biofilm from the earliest to the last step.

1. secretion of EPS
2. reversible attachment
3. dispersal
4. formation of water channels
5. irreversible attachment

Infections among hospitalized patients are often related to the presence of a medical device in the patient. Which conditions favor the formation of biofilms on in-dwelling catheters and prostheses?

Critical Thinking

A patient in the hospital has an intravenous catheter inserted to allow for the delivery of medications, fluids, and electrolytes. Four days after the catheter is inserted, the patient develops a fever and an infection in the skin around the catheter. Blood cultures reveal that the patient has a blood-borne infection. Tests in the clinical laboratory identify the blood-borne pathogen as *Staphylococcus epidermidis*, and antibiotic susceptibility tests are performed to provide doctors with essential information for selecting the best drug for treatment of the infection. Antibacterial chemotherapy is initiated and delivered through the intravenous catheter that was originally inserted into the patient. Within 7 days, the skin infection is gone, blood cultures are negative for *S. epidermidis*, and the antibacterial chemotherapy is discontinued. However, 2 days after discontinuing the antibacterial chemotherapy, the patient develops another fever and skin infection and the blood cultures are positive for the same strain of *S. epidermidis* that had been isolated the previous week. This time, doctors remove the intravenous catheter and administer oral antibiotics, which successfully treat both the skin and blood-borne infection caused by *S. epidermidis*. Furthermore, the infection does not return after discontinuing the oral antibacterial chemotherapy. What are some possible reasons why intravenous chemotherapy failed to completely cure the patient despite laboratory tests showing the bacterial strain was susceptible to the prescribed antibiotic? Why might the second round of antibiotic therapy have been more successful? Justify your answers.

Why are autoinducers small molecules?

Refer to Figure B1 in Appendix B. If the results from a pond water sample were recorded as 3, 2, 1, what would be the MPN of bacteria in 100 mL of pond water?

Refer to Figure. Why does turbidity lose reliability at high cell concentrations when the culture reaches the stationary phase?

Contributor

- Template:ContribOpenSTAXMicrobiology

This page titled 5.1: How Microbes Grow is shared under a CC BY-NC-SA license and was authored, remixed, and/or curated by OpenStax.

CHAPTER OVERVIEW

Back Matter

Index

Glossary

Detailed Licensing

Index

A

A site
Protein Synthesis (Translation)
activator
Operon Theory
active site
8.1: Energy, Matter, and Enzymes
Adenosine triphosphate
8.1: Energy, Matter, and Enzymes
aerobic respiration
8.3: Cellular Respiration
alarmones
Operon Theory
allosteric inhibitor
8.1: Energy, Matter, and Enzymes
allosteric inhibitors
8.1: Energy, Matter, and Enzymes
allosteric sites
8.1: Energy, Matter, and Enzymes
Ames test
Mutations
Anabolism
8.1: Energy, Matter, and Enzymes
anaerobic respiration
8.3: Cellular Respiration
anoxygenic photosynthesis
8.6: Photosynthesis and the Importance of Light
anticodon
Protein Synthesis (Translation)
apoenzyme
8.1: Energy, Matter, and Enzymes
astrobiology
1: Life and Earth
1.1: Daisyworld
1.1: What is life?
ATP
8.1: Energy, Matter, and Enzymes
ATP synthase
8.3: Cellular Respiration
attachment
3.3B: The Viral Life Cycle
attenuation
Operon Theory
autotrophs
8.1: Energy, Matter, and Enzymes
auxotrophs
Mutations

B

binary fission
5.1: How Microbes Grow
Biofilms
5.1: How Microbes Grow
Biofundamentals
1.1: What is life?
biogeochemical cycle
8.7: Biogeochemical Cycles
Bioremediation
8.7: Biogeochemical Cycles
biosynthesis
3.3B: The Viral Life Cycle

C

CAP
Operon Theory
capsid
3.3A: Viruses
capsule
3.1: Unique Characteristics of Prokaryotic Cells
carbon cycle
8.7: Biogeochemical Cycles
Catabolism
8.1: Energy, Matter, and Enzymes
8.5: Catabolism of Lipids and Proteins
catabolite activator protein
Operon Theory
catalysts
8.1: Energy, Matter, and Enzymes
cell envelope
3.1: Unique Characteristics of Prokaryotic Cells
cell morphology
3.1: Unique Characteristics of Prokaryotic Cells
cell wall
3.1: Unique Characteristics of Prokaryotic Cells
3.2: Unique Characteristics of Eukaryotic Cells
cellular arrangement
3.1: Unique Characteristics of Prokaryotic Cells
Central Dogma
What Are Genes?
Centrosomes
3.2: Unique Characteristics of Eukaryotic Cells
charged tRNA
Protein Synthesis (Translation)
chemiosmosis
8.3: Cellular Respiration
Chemotrophs
8.1: Energy, Matter, and Enzymes
cilia
3.2: Unique Characteristics of Eukaryotic Cells
Coenzymes
8.1: Energy, Matter, and Enzymes
cofactor
8.1: Energy, Matter, and Enzymes
cognate amino acid
Protein Synthesis (Translation)
Competitive inhibitors
8.1: Energy, Matter, and Enzymes
complex
3.3A: Viruses
conjugation
How Asexual Prokaryotes Achieve Genetic Diversity
conjugation pilus
How Asexual Prokaryotes Achieve Genetic Diversity
constitutively expressed
Operon Theory
cyclic photophosphorylation
8.6: Photosynthesis and the Importance of Light
cytoskeleton
3.2: Unique Characteristics of Eukaryotic Cells

D

dark repair
Mutations
death
5.1: How Microbes Grow
degenerate
Protein Synthesis (Translation)
direct viable cell count
5.1: How Microbes Grow
doubling time
5.1: How Microbes Grow

E

E site
Protein Synthesis (Translation)
electron carriers
8.1: Energy, Matter, and Enzymes
electron transport system
8.3: Cellular Respiration
elongation
DNA Replication
Protein Synthesis (Translation)
RNA Transcription
endergonic reactions
8.1: Energy, Matter, and Enzymes
endocytosis
3.2: Unique Characteristics of Eukaryotic Cells
endomembrane
3.2: Unique Characteristics of Eukaryotic Cells
endospores
3.1: Unique Characteristics of Prokaryotic Cells
enzymes
8.1: Energy, Matter, and Enzymes
epigenetic regulation
Operon Theory
ETS
8.3: Cellular Respiration
exergonic reaction
8.1: Energy, Matter, and Enzymes
exocytosis
3.2: Unique Characteristics of Eukaryotic Cells
Extracellular Matrix
3.2: Unique Characteristics of Eukaryotic Cells
extracellular polymeric substance
5.1: How Microbes Grow

F

F plasmid
How Asexual Prokaryotes Achieve Genetic Diversity
F+ cell
How Asexual Prokaryotes Achieve Genetic Diversity
feedback inhibition
8.1: Energy, Matter, and Enzymes
feedbacks
1.1: Daisyworld

fermentation
8.4: Fermentation
fimbriae
3.1: Unique Characteristics of Prokaryotic Cells
flagella
3.1: Unique Characteristics of Prokaryotic Cells
frameshift mutation
Mutations
free ribosomes)
3.2: Unique Characteristics of Eukaryotic Cells

G
Gaia
1.1: Daisyworld
gene expression
Operon Theory
generalized
3.3B: The Viral Life Cycle
generalized transduction
How Asexual Prokaryotes Achieve Genetic Diversity
Generation time
5.1: How Microbes Grow
genes
What Are Genes?
genetic code
Protein Synthesis (Translation)
geobiology
1: Life and Earth
germinate
3.1: Unique Characteristics of Prokaryotic Cells
glycocalyx
3.1: Unique Characteristics of Prokaryotic Cells
glycolysis
8.2: Catabolism of Carbohydrates
Golgi apparatus
3.2: Unique Characteristics of Eukaryotic Cells

H
helical
3.3A: Viruses
helicase
DNA Replication
heterolactic fermentation
8.4: Fermentation
heterotrophs
8.1: Energy, Matter, and Enzymes
Hfr cell
How Asexual Prokaryotes Achieve Genetic Diversity
holoenzyme
8.1: Energy, Matter, and Enzymes
homolactic fermentation
8.4: Fermentation
Horizontal Gene Transfer
How Asexual Prokaryotes Achieve Genetic Diversity
host ranges
3.3A: Viruses

I
inclusions
3.1: Unique Characteristics of Prokaryotic Cells
induced fit
8.1: Energy, Matter, and Enzymes
induced mutations
Mutations
inducer
Operon Theory
inducible operon
Operon Theory
Initiation
Protein Synthesis (Translation)
initiation factors
Protein Synthesis (Translation)
initiation of replication
DNA Replication
initiation of transcription.
RNA Transcription
intermediate filaments
3.2: Unique Characteristics of Eukaryotic Cells
Ionizing radiation
Mutations

K
Krebs cycle
8.2: Catabolism of Carbohydrates

L
lag
5.1: How Microbes Grow
lagging strand
DNA Replication
latency
3.3B: The Viral Life Cycle
leading strand
DNA Replication
lipases
8.5: Catabolism of Lipids and Proteins
lithotrophs
8.1: Energy, Matter, and Enzymes
logarithmic
5.1: How Microbes Grow
lysogenic cycle
3.3B: The Viral Life Cycle
Lysosomes
3.2: Unique Characteristics of Eukaryotic Cells
lytic
3.3B: The Viral Life Cycle
lytic cycle
3.3B: The Viral Life Cycle

M
maturation
3.3B: The Viral Life Cycle
metabolism
8.1: Energy, Matter, and Enzymes
Methanogens
8.7: Biogeochemical Cycles
Microbial fermentation
8.4: Fermentation
Microbial Genetics
3: Genes to Enzymes
microtubules
3.2: Unique Characteristics of Eukaryotic Cells
missense mutation
Mutations
mitochondria
3.2: Unique Characteristics of Eukaryotic Cells
MPN
5.1: How Microbes Grow
mutagen
Mutations
mutation
Mutations

N
nitrogen cycle
8.7: Biogeochemical Cycles
Noncompetitive inhibitors
8.1: Energy, Matter, and Enzymes
Noncyclic photophosphorylation
8.6: Photosynthesis and the Importance of Light
Nonionizing radiation
Mutations
nonsense mutation
Mutations
nuclear envelope
3.2: Unique Characteristics of Eukaryotic Cells
nuclear membrane
3.2: Unique Characteristics of Eukaryotic Cells
nucleoid
3.1: Unique Characteristics of Prokaryotic Cells
nucleolus
3.2: Unique Characteristics of Eukaryotic Cells
nucleotide excision repair
Mutations
nucleus
3.2: Unique Characteristics of Eukaryotic Cells

O
operator
Operon Theory
operons
Operon Theory
Organotrophs
8.1: Energy, Matter, and Enzymes
origin of replication
DNA Replication
oxidative phosphorylation
8.3: Cellular Respiration
oxygenic photosynthesis
8.6: Photosynthesis and the Importance of Light

P
P site
Protein Synthesis (Translation)
penetration
3.3B: The Viral Life Cycle
peptidoglycan
3.1: Unique Characteristics of Prokaryotic Cells
Peritrichous
3.1: Unique Characteristics of Prokaryotic Cells

phagocytosis
3.2: Unique Characteristics of Eukaryotic Cells
phospholipases
8.5: Catabolism of Lipids and Proteins
photosynthesis
8.6: Photosynthesis and the Importance of Light
photosynthetic pigments
8.6: Photosynthesis and the Importance of Light
Photosystems
8.6: Photosynthesis and the Importance of Light
phototrophs
8.1: Energy, Matter, and Enzymes
Phylogenetic Trees
4.1: Phylogenetic Trees
4.2: Limitations of Phylogenetic Trees
pili
3.1: Unique Characteristics of Prokaryotic Cells
planktonic
5.1: How Microbes Grow
plasma membrane
3.1: Unique Characteristics of Prokaryotic Cells
plasmids
3.1: Unique Characteristics of Prokaryotic Cells
point mutation
Mutations
polycistronic
RNA Transcription
polycistronic mRNA
RNA Transcription
polyhedral
3.3A: Viruses
pour plate
5.1: How Microbes Grow
primer
DNA Replication
RNA Transcription
proteases
8.5: Catabolism of Lipids and Proteins
proton motive force
8.3: Cellular Respiration
pseudopeptidoglycan
3.1: Unique Characteristics of Prokaryotic Cells

Q

quorum sensing
5.1: How Microbes Grow

R

R plasmids
How Asexual Prokaryotes Achieve Genetic Diversity
redox reactions
8.1: Energy, Matter, and Enzymes
release
3.3B: The Viral Life Cycle
repressible operon
Operon Theory
repressor
Operon Theory
ribosomes
3.1: Unique Characteristics of Prokaryotic Cells
riboswitches
Operon Theory
RNA polymerase
RNA Transcription
RNA transcript
RNA Transcription
rough endoplasmic reticulum
3.2: Unique Characteristics of Eukaryotic Cells
runs
3.1: Unique Characteristics of Prokaryotic Cells

S

serial dilutions
5.1: How Microbes Grow
sessile
5.1: How Microbes Grow
Sigma Factor
Operon Theory
silent mutation
Mutations
slime layers
3.1: Unique Characteristics of Prokaryotic Cells
smooth endoplasmic reticulum
3.2: Unique Characteristics of Eukaryotic Cells
specialized transduction
How Asexual Prokaryotes Achieve Genetic Diversity
3.3B: The Viral Life Cycle
splicing
RNA Transcription
Spontaneous mutations
Mutations
sporulation
3.1: Unique Characteristics of Prokaryotic Cells
spread plate
5.1: How Microbes Grow
start codon
Protein Synthesis (Translation)
stationary
5.1: How Microbes Grow
stop codon
Protein Synthesis (Translation)
Substrates
8.1: Energy, Matter, and Enzymes
sulfur cycling
8.7: Biogeochemical Cycles
supercoiled
DNA Replication

T

telomerase
DNA Replication
Telomeres
DNA Replication
Termination
Protein Synthesis (Translation)
Termination of transcription
RNA Transcription
transcription factors
Operon Theory
transduction
How Asexual Prokaryotes Achieve Genetic Diversity
transformation
How Asexual Prokaryotes Achieve Genetic Diversity
translation
Protein Synthesis (Translation)
transposons
How Asexual Prokaryotes Achieve Genetic Diversity
tumbles
3.1: Unique Characteristics of Prokaryotic Cells

U

uncoating
3.3B: The Viral Life Cycle

V

Virions
3.3A: Viruses
viruses
3.3A: Viruses

X

xenobiotics
8.7: Biogeochemical Cycles

Z

Z ring
5.1: How Microbes Grow

Glossary

Sample Word 1 | Sample Definition 1

Detailed Licensing

Overview

Title: Text

Webpages: 43

Applicable Restrictions: Noncommercial

All licenses found:

- CC BY-NC-SA 4.0: 48.8% (21 pages)
- Undeclared: 32.6% (14 pages)
- CC BY 4.0: 18.6% (8 pages)

By Page

- Text - *CC BY-NC-SA 4.0*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Life and Earth - *CC BY-NC-SA 4.0*
    - 1.1: Daisyworld - *CC BY-NC-SA 4.0*
    - 1.2 Interactions Among Organisms - *Undeclared*
  - 2: What is life? - *Undeclared*
  - 3: Genes to Enzymes - *CC BY-NC-SA 4.0*
    - DNA Replication - *CC BY-NC-SA 4.0*
    - DNA, RNA, Genes and Chromosomes - *Undeclared*
    - How Asexual Prokaryotes Achieve Genetic Diversity - *CC BY-NC-SA 4.0*
    - Mutations - *CC BY-NC-SA 4.0*
    - Operon Theory - *CC BY-NC-SA 4.0*
    - Protein Synthesis (Translation) - *CC BY-NC-SA 4.0*
    - RNA Transcription - *CC BY-NC-SA 4.0*
    - What Are Genes? - *Undeclared*
  - 4: Tracing the History of Evolution - *Undeclared*
    - 4.1: Phylogenetic Trees - *CC BY-NC-SA 4.0*
    - 4.2: Limitations of Phylogenetic Trees - *CC BY-NC-SA 4.0*
    - 4.3: The Levels of Classification - *CC BY-NC-SA 4.0*
  - 5: Structure of life - *CC BY-NC-SA 4.0*
    - 3.1: Unique Characteristics of Prokaryotic Cells - *CC BY-NC-SA 4.0*
    - 3.2: Unique Characteristics of Eukaryotic Cells - *CC BY-NC-SA 4.0*
    - 3.3: Viruses - *CC BY-NC-SA 4.0*
      - 3.3A: Viruses - *CC BY-NC-SA 4.0*
      - 3.3B: The Viral Life Cycle - *CC BY-NC-SA 4.0*
  - 6: Microbial Metabolism - *CC BY 4.0*
    - 8.1: Energy, Matter, and Enzymes - *CC BY 4.0*
    - 8.2: Catabolism of Carbohydrates - *CC BY 4.0*
    - 8.3: Cellular Respiration - *CC BY 4.0*
    - 8.4: Fermentation - *CC BY 4.0*
    - 8.5: Catabolism of Lipids and Proteins - *CC BY 4.0*
    - 8.6: Photosynthesis and the Importance of Light - *CC BY 4.0*
    - 8.7: Biogeochemical Cycles - *CC BY 4.0*
  - 7: How Microbes Grow - *CC BY-NC-SA 4.0*
    - 5.1: How Microbes Grow - *CC BY-NC-SA 4.0*
  - Back Matter - *Undeclared*
    - Index - *Undeclared*
    - Glossary - *Undeclared*
    - Detailed Licensing - *Undeclared*

Index

A

A site
Protein Synthesis (Translation)
activator
Operon Theory
active site
8.1: Energy, Matter, and Enzymes
Adenosine triphosphate
8.1: Energy, Matter, and Enzymes
aerobic respiration
8.3: Cellular Respiration
alarmones
Operon Theory
allosteric inhibitor
8.1: Energy, Matter, and Enzymes
allosteric inhibitors
8.1: Energy, Matter, and Enzymes
allosteric sites
8.1: Energy, Matter, and Enzymes
Ames test
Mutations
Anabolism
8.1: Energy, Matter, and Enzymes
anaerobic respiration
8.3: Cellular Respiration
anoxygenic photosynthesis
8.6: Photosynthesis and the Importance of Light
anticodon
Protein Synthesis (Translation)
apoenzyme
8.1: Energy, Matter, and Enzymes
astrobiology
1: Life and Earth
1.1: Daisyworld
1.1: What is life?
ATP
8.1: Energy, Matter, and Enzymes
ATP synthase
8.3: Cellular Respiration
attachment
3.3B: The Viral Life Cycle
attenuation
Operon Theory
autotrophs
8.1: Energy, Matter, and Enzymes
auxotrophs
Mutations

B

binary fission
5.1: How Microbes Grow
Biofilms
5.1: How Microbes Grow
Biofundamentals
1.1: What is life?
biogeochemical cycle
8.7: Biogeochemical Cycles
Bioremediation
8.7: Biogeochemical Cycles
biosynthesis
3.3B: The Viral Life Cycle

C

CAP
Operon Theory
capsid
3.3A: Viruses
capsule
3.1: Unique Characteristics of Prokaryotic Cells
carbon cycle
8.7: Biogeochemical Cycles
Catabolism
8.1: Energy, Matter, and Enzymes
8.5: Catabolism of Lipids and Proteins
catabolite activator protein
Operon Theory
catalysts
8.1: Energy, Matter, and Enzymes
cell envelope
3.1: Unique Characteristics of Prokaryotic Cells
cell morphology
3.1: Unique Characteristics of Prokaryotic Cells
cell wall
3.1: Unique Characteristics of Prokaryotic Cells
3.2: Unique Characteristics of Eukaryotic Cells
cellular arrangement
3.1: Unique Characteristics of Prokaryotic Cells
Central Dogma
What Are Genes?
Centrosomes
3.2: Unique Characteristics of Eukaryotic Cells
charged tRNA
Protein Synthesis (Translation)
chemiosmosis
8.3: Cellular Respiration
Chemotrophs
8.1: Energy, Matter, and Enzymes
cilia
3.2: Unique Characteristics of Eukaryotic Cells
Coenzymes
8.1: Energy, Matter, and Enzymes
cofactor
8.1: Energy, Matter, and Enzymes
cognate amino acid
Protein Synthesis (Translation)
Competitive inhibitors
8.1: Energy, Matter, and Enzymes
complex
3.3A: Viruses
conjugation
How Asexual Prokaryotes Achieve Genetic Diversity
conjugation pilus
How Asexual Prokaryotes Achieve Genetic Diversity
constitutively expressed
Operon Theory
cyclic photophosphorylation
8.6: Photosynthesis and the Importance of Light
cytoskeleton
3.2: Unique Characteristics of Eukaryotic Cells

D

dark repair
Mutations
death
5.1: How Microbes Grow
degenerate
Protein Synthesis (Translation)
direct viable cell count
5.1: How Microbes Grow
doubling time
5.1: How Microbes Grow

E

E site
Protein Synthesis (Translation)
electron carriers
8.1: Energy, Matter, and Enzymes
electron transport system
8.3: Cellular Respiration
elongation
DNA Replication
Protein Synthesis (Translation)
RNA Transcription
endergonic reactions
8.1: Energy, Matter, and Enzymes
endocytosis
3.2: Unique Characteristics of Eukaryotic Cells
endomembrane
3.2: Unique Characteristics of Eukaryotic Cells
endospores
3.1: Unique Characteristics of Prokaryotic Cells
enzymes
8.1: Energy, Matter, and Enzymes
epigenetic regulation
Operon Theory
ETS
8.3: Cellular Respiration
exergonic reaction
8.1: Energy, Matter, and Enzymes
exocytosis
3.2: Unique Characteristics of Eukaryotic Cells
Extracellular Matrix
3.2: Unique Characteristics of Eukaryotic Cells
extracellular polymeric substance
5.1: How Microbes Grow

F

F plasmid
How Asexual Prokaryotes Achieve Genetic Diversity
F+ cell
How Asexual Prokaryotes Achieve Genetic Diversity
feedback inhibition
8.1: Energy, Matter, and Enzymes
feedbacks
1.1: Daisyworld

fermentation
8.4: Fermentation
fimbriae
3.1: Unique Characteristics of Prokaryotic Cells
flagella
3.1: Unique Characteristics of Prokaryotic Cells
frameshift mutation
Mutations
free ribosomes)
3.2: Unique Characteristics of Eukaryotic Cells

G
Gaia
1.1: Daisyworld
gene expression
Operon Theory
generalized
3.3B: The Viral Life Cycle
generalized transduction
How Asexual Prokaryotes Achieve Genetic Diversity
Generation time
5.1: How Microbes Grow
genes
What Are Genes?
genetic code
Protein Synthesis (Translation)
geobiology
1: Life and Earth
germinate
3.1: Unique Characteristics of Prokaryotic Cells
glycocalyx
3.1: Unique Characteristics of Prokaryotic Cells
glycolysis
8.2: Catabolism of Carbohydrates
Golgi apparatus
3.2: Unique Characteristics of Eukaryotic Cells

H
helical
3.3A: Viruses
helicase
DNA Replication
heterolactic fermentation
8.4: Fermentation
heterotrophs
8.1: Energy, Matter, and Enzymes
Hfr cell
How Asexual Prokaryotes Achieve Genetic Diversity
holoenzyme
8.1: Energy, Matter, and Enzymes
homolactic fermentation
8.4: Fermentation
Horizontal Gene Transfer
How Asexual Prokaryotes Achieve Genetic Diversity
host ranges
3.3A: Viruses

I
inclusions
3.1: Unique Characteristics of Prokaryotic Cells
induced fit
8.1: Energy, Matter, and Enzymes
induced mutations
Mutations
inducer
Operon Theory
inducible operon
Operon Theory
Initiation
Protein Synthesis (Translation)
initiation factors
Protein Synthesis (Translation)
initiation of replication
DNA Replication
initiation of transcription.
RNA Transcription
intermediate filaments
3.2: Unique Characteristics of Eukaryotic Cells
Ionizing radiation
Mutations

K
Krebs cycle
8.2: Catabolism of Carbohydrates

L
lag
5.1: How Microbes Grow
lagging strand
DNA Replication
latency
3.3B: The Viral Life Cycle
leading strand
DNA Replication
lipases
8.5: Catabolism of Lipids and Proteins
lithotrophs
8.1: Energy, Matter, and Enzymes
logarithmic
5.1: How Microbes Grow
lysogenic cycle
3.3B: The Viral Life Cycle
Lysosomes
3.2: Unique Characteristics of Eukaryotic Cells
lytic
3.3B: The Viral Life Cycle
lytic cycle
3.3B: The Viral Life Cycle

M
maturation
3.3B: The Viral Life Cycle
metabolism
8.1: Energy, Matter, and Enzymes
Methanogens
8.7: Biogeochemical Cycles
Microbial fermentation
8.4: Fermentation
Microbial Genetics
3: Genes to Enzymes
microtubules
3.2: Unique Characteristics of Eukaryotic Cells
missense mutation
Mutations
mitochondria
3.2: Unique Characteristics of Eukaryotic Cells
MPN
5.1: How Microbes Grow
mutagen
Mutations
mutation
Mutations

N
nitrogen cycle
8.7: Biogeochemical Cycles
Noncompetitive inhibitors
8.1: Energy, Matter, and Enzymes
Noncyclic photophosphorylation
8.6: Photosynthesis and the Importance of Light
Nonionizing radiation
Mutations
nonsense mutation
Mutations
nuclear envelope
3.2: Unique Characteristics of Eukaryotic Cells
nuclear membrane
3.2: Unique Characteristics of Eukaryotic Cells
nucleoid
3.1: Unique Characteristics of Prokaryotic Cells
nucleolus
3.2: Unique Characteristics of Eukaryotic Cells
nucleotide excision repair
Mutations
nucleus
3.2: Unique Characteristics of Eukaryotic Cells

O
operator
Operon Theory
operons
Operon Theory
Organotrophs
8.1: Energy, Matter, and Enzymes
origin of replication
DNA Replication
oxidative phosphorylation
8.3: Cellular Respiration
oxygenic photosynthesis
8.6: Photosynthesis and the Importance of Light

P
P site
Protein Synthesis (Translation)
penetration
3.3B: The Viral Life Cycle
peptidoglycan
3.1: Unique Characteristics of Prokaryotic Cells
Peritrichous
3.1: Unique Characteristics of Prokaryotic Cells

phagocytosis
3.2: Unique Characteristics of Eukaryotic Cells
phospholipases
8.5: Catabolism of Lipids and Proteins
photosynthesis
8.6: Photosynthesis and the Importance of Light
photosynthetic pigments
8.6: Photosynthesis and the Importance of Light
Photosystems
8.6: Photosynthesis and the Importance of Light
phototrophs
8.1: Energy, Matter, and Enzymes
Phylogenetic Trees
4.1: Phylogenetic Trees
4.2: Limitations of Phylogenetic Trees
pili
3.1: Unique Characteristics of Prokaryotic Cells
planktonic
5.1: How Microbes Grow
plasma membrane
3.1: Unique Characteristics of Prokaryotic Cells
plasmids
3.1: Unique Characteristics of Prokaryotic Cells
point mutation
Mutations
polycistronic
RNA Transcription
polycistronic mRNA
RNA Transcription
polyhedral
3.3A: Viruses
pour plate
5.1: How Microbes Grow
primer
DNA Replication
RNA Transcription
proteases
8.5: Catabolism of Lipids and Proteins
proton motive force
8.3: Cellular Respiration
pseudopeptidoglycan
3.1: Unique Characteristics of Prokaryotic Cells

Q

quorum sensing
5.1: How Microbes Grow

R

R plasmids
How Asexual Prokaryotes Achieve Genetic Diversity
redox reactions
8.1: Energy, Matter, and Enzymes
release
3.3B: The Viral Life Cycle
repressible operon
Operon Theory
repressor
Operon Theory
ribosomes
3.1: Unique Characteristics of Prokaryotic Cells
riboswitches
Operon Theory
RNA polymerase
RNA Transcription
RNA transcript
RNA Transcription
rough endoplasmic reticulum
3.2: Unique Characteristics of Eukaryotic Cells
runs
3.1: Unique Characteristics of Prokaryotic Cells

S

serial dilutions
5.1: How Microbes Grow
sessile
5.1: How Microbes Grow
Sigma Factor
Operon Theory
silent mutation
Mutations
slime layers
3.1: Unique Characteristics of Prokaryotic Cells
smooth endoplasmic reticulum
3.2: Unique Characteristics of Eukaryotic Cells
specialized transduction
How Asexual Prokaryotes Achieve Genetic Diversity
3.3B: The Viral Life Cycle
splicing
RNA Transcription
Spontaneous mutations
Mutations
sporulation
3.1: Unique Characteristics of Prokaryotic Cells
spread plate
5.1: How Microbes Grow
start codon
Protein Synthesis (Translation)
stationary
5.1: How Microbes Grow
stop codon
Protein Synthesis (Translation)
Substrates
8.1: Energy, Matter, and Enzymes
sulfur cycling
8.7: Biogeochemical Cycles
supercoiled
DNA Replication

T

telomerase
DNA Replication
Telomeres
DNA Replication
Termination
Protein Synthesis (Translation)
Termination of transcription
RNA Transcription
transcription factors
Operon Theory
transduction
How Asexual Prokaryotes Achieve Genetic Diversity
transformation
How Asexual Prokaryotes Achieve Genetic Diversity
translation
Protein Synthesis (Translation)
transposons
How Asexual Prokaryotes Achieve Genetic Diversity
tumbles
3.1: Unique Characteristics of Prokaryotic Cells

U

uncoating
3.3B: The Viral Life Cycle

V

Virions
3.3A: Viruses
viruses
3.3A: Viruses

X

xenobiotics
8.7: Biogeochemical Cycles

Z

Z ring
5.1: How Microbes Grow

Glossary

Sample Word 1 | Sample Definition 1

Detailed Licensing

Overview

Title: Text

Webpages: 43

Applicable Restrictions: Noncommercial

All licenses found:

- CC BY-NC-SA 4.0: 48.8% (21 pages)
- Undeclared: 32.6% (14 pages)
- CC BY 4.0: 18.6% (8 pages)

By Page

- Text - *CC BY-NC-SA 4.0*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Life and Earth - *CC BY-NC-SA 4.0*
    - 1.1: Daisyworld - *CC BY-NC-SA 4.0*
    - 1.2 Interactions Among Organisms - *Undeclared*
  - 2: What is life? - *Undeclared*
  - 3: Genes to Enzymes - *CC BY-NC-SA 4.0*
    - DNA Replication - *CC BY-NC-SA 4.0*
    - DNA, RNA, Genes and Chromosomes - *Undeclared*
    - How Asexual Prokaryotes Achieve Genetic Diversity - *CC BY-NC-SA 4.0*
    - Mutations - *CC BY-NC-SA 4.0*
    - Operon Theory - *CC BY-NC-SA 4.0*
    - Protein Synthesis (Translation) - *CC BY-NC-SA 4.0*
    - RNA Transcription - *CC BY-NC-SA 4.0*
    - What Are Genes? - *Undeclared*
  - 4: Tracing the History of Evolution - *Undeclared*
    - 4.1: Phylogenetic Trees - *CC BY-NC-SA 4.0*
    - 4.2: Limitations of Phylogenetic Trees - *CC BY-NC-SA 4.0*
    - 4.3: The Levels of Classification - *CC BY-NC-SA 4.0*
  - 5: Structure of life - *CC BY-NC-SA 4.0*
    - 3.1: Unique Characteristics of Prokaryotic Cells - *CC BY-NC-SA 4.0*
    - 3.2: Unique Characteristics of Eukaryotic Cells - *CC BY-NC-SA 4.0*
    - 3.3: Viruses - *CC BY-NC-SA 4.0*
      - 3.3A: Viruses - *CC BY-NC-SA 4.0*
      - 3.3B: The Viral Life Cycle - *CC BY-NC-SA 4.0*
  - 6: Microbial Metabolism - *CC BY 4.0*
    - 8.1: Energy, Matter, and Enzymes - *CC BY 4.0*
    - 8.2: Catabolism of Carbohydrates - *CC BY 4.0*
    - 8.3: Cellular Respiration - *CC BY 4.0*
    - 8.4: Fermentation - *CC BY 4.0*
    - 8.5: Catabolism of Lipids and Proteins - *CC BY 4.0*
    - 8.6: Photosynthesis and the Importance of Light - *CC BY 4.0*
    - 8.7: Biogeochemical Cycles - *CC BY 4.0*
  - 7: How Microbes Grow - *CC BY-NC-SA 4.0*
    - 5.1: How Microbes Grow - *CC BY-NC-SA 4.0*
  - Back Matter - *Undeclared*
    - Index - *Undeclared*
    - Glossary - *Undeclared*
    - Detailed Licensing - *Undeclared*