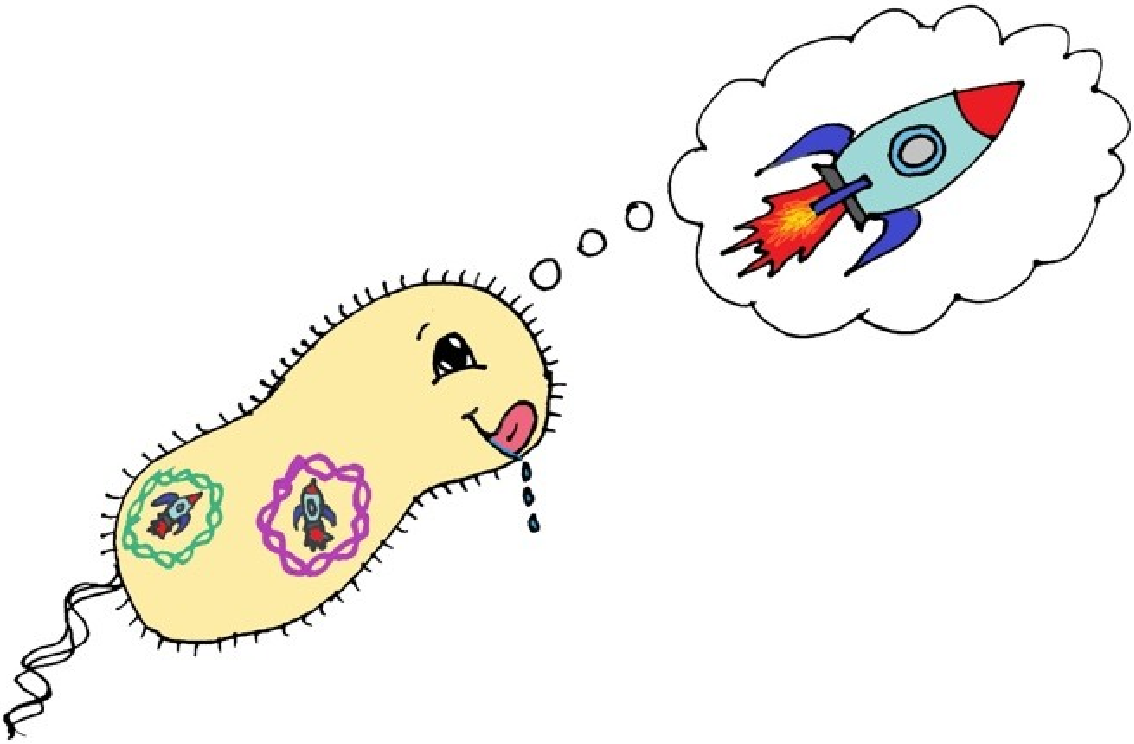
Microbial Organelles and Compartments

Daddy, birds fly, fish swim underwater,
and cheetahs run much faster than I can!
But is there anything bacteria do that I can't?



Rocket fuel for breakfast? Well, someone has to eat it!

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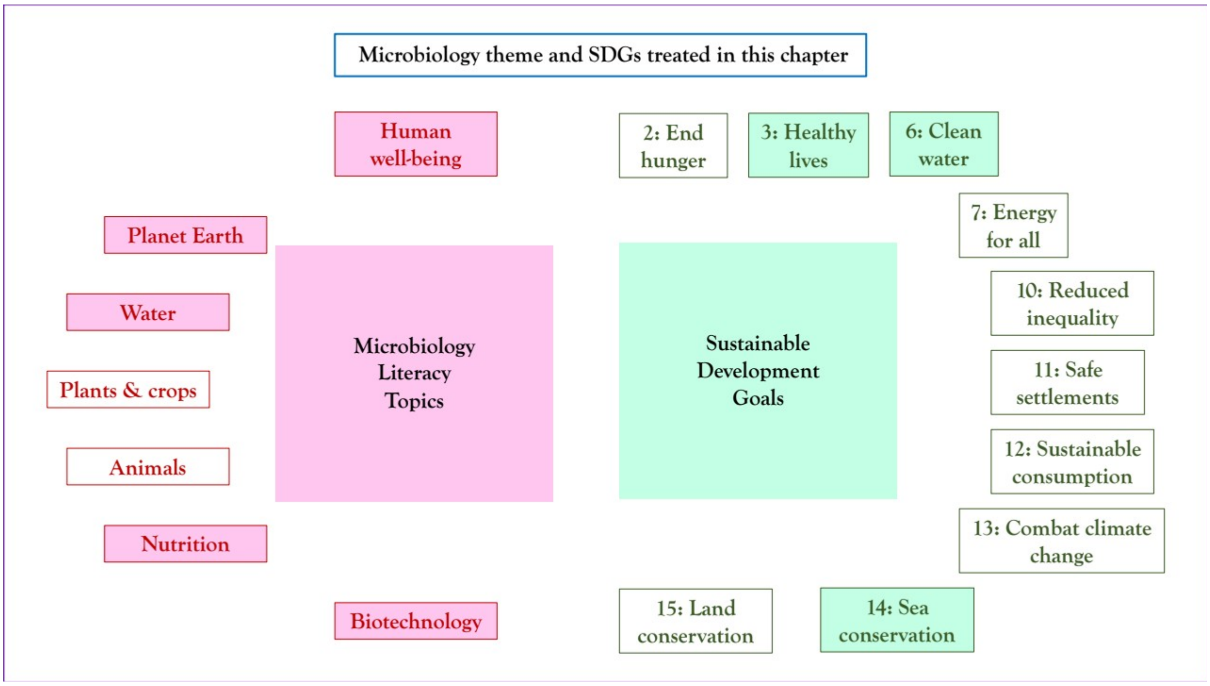
Storyline

Most people think microbes are 'simple': little more than unorganized bags of molecules. Yet microbes have had billions more years to evolve than we have and, as a result, have developed much complexity and some incredible 'superpowers'. Among their amazing abilities, bacteria can sense and swim towards the poles, grow by harvesting sunlight at incredibly low intensities, or eat toxic compounds like rocket fuel. All of these abilities and many others depend on organelles, i.e. miniature 'organs' or 'compartments', within their cells that perform specialized tasks separated from the rest of the cell. Organelles are highly diverse in size, structure, and function with different types of bacteria possessing distinct organelles. But collectively, they help bacteria adapt to almost every environment on earth and perform important functions such as nutrient recycling and pollutant removal. Like bacteria, microbial eukaryotes make diverse organelles too – some of which were originally derived from bacteria – that are critical their complex lifestyles. But whereas it was once thought that organelles originated in eukaryotes, we now know that they evolved first in bacteria.

The Microbiology and Societal Context

The microbiology: cell structure; microbial classification; nutritional strategies; evolution of complex life; primary production; nitrogen cycling. *Sustainability issues*: biodiversity, health, water quality.



Organelles and Compartments: The Microbiology

1. Microbes benefit from separating their functions into different compartments. All cells contain a membrane-enclosed cytoplasm containing important molecules such as proteins and DNA. The cytoplasm of most cells appears to be subdivided into different compartments with distinct functions. In some cases, these compartments are called organelles, i.e. enclosed compartments that perform specific functions. Just as the human body separates functions between organs, organelles enable cells to separate and regulate chemical processes; they help avoid chaos in the cell. As an example from everyday life, we can take the case of the two goals located at either ends of a football/hockey pitch, i.e. separated and precisely placed to enable opposing teams to develop the creative attack strategies to score that we enjoy so much. Now imagine that the goals would be randomly moved around during the game: chaos would result, play strategies would serve no purpose, and goal scoring would be a random, essentially accidental event.

Each organelle contains a distinct set of metabolites (i.e. small molecules), enzymes, and regulators that together coordinate a specific function. As summarized in Box 1, these functions range from energy conservation in the **mitochondria**, to information storage and coordination in the **nucleus**, to roles in other processes such as storage, transport, and detoxification. This compartmentation can also serve a range of specific purposes. First, organelles can increase the efficiency of metabolic processes by increasing the local concentrations of molecules or enzymes involved; for example, photosynthetic bacteria enhance the efficiency of carbon fixation by concentrating the gas carbon dioxide in **carboxysomes**. In addition, organelles can increase the surface area through which reactions can occur, for example mitochondria and **thylakoids** which contain extensive membrane folds where respiration and photosynthesis can occur. Organelles are also used to physically separate and confine reactive metabolites (e.g. hydrazine, aldehydes, and peroxides) from sensitive molecules such as DNA.

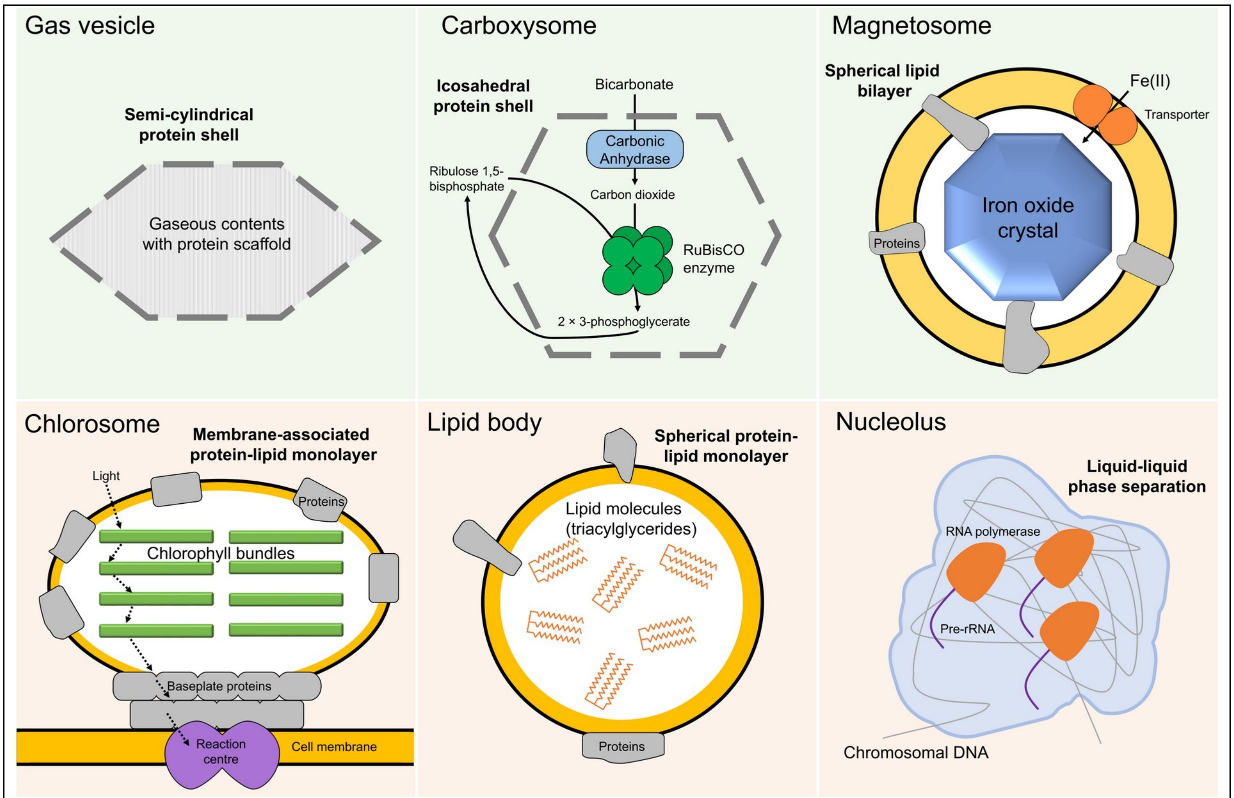
Organelle	Primary function	Distribution
Anammoxosome	Anaerobic oxidation of ammonium	Planctomycetes
Carboxysome	Concentration and fixation of carbon dioxide	Cyanobacteria, Proteobacteria
Chromatophore	Light harvesting and energy conversion	Proteobacteria
Chloroplasts	Light harvesting and conversion, carbon fixation	Plants (bacteria-derived)
Chlorosome	Light harvesting and energy conversion	Chlorobia
Gas vesicle	Accumulation of gases for buoyancy	Diverse bacteria, archaea
Golgi apparatus	Transport and control of vesicles	Eukaryotes
Lipid bodies	Storage of lipids as energy reserves	Diverse bacteria, archaea
Magnetosome	Formation of iron crystals for magnetoreception	Proteobacteria, Nitrospirae
Metabolosome	Alcohol metabolism and aldehyde detoxification	Diverse bacteria, archaea
Mitochondria	Aerobic respiration	Eukaryotes (bacteria-derived)
Nanocompartment	Contains iron and oxidative stress enzymes	Diverse bacteria. archaea
Nucleolus	Synthesis of ribosomal RNAs	Diverse bacteria, eukaryotes
Nucleus	DNA storage, gene expression, coordination	Eukaryotes
Peroxisome	Lipid metabolism and peroxide detoxification	Eukaryotes
Thylakoid	Light harvesting and energy conversion	Cyanobacteria, plants, algae
Vacuole	Storage of metabolites or waste products	Diverse bacteria, eukaryotes

Summary of the function and distribution of organelles in microorganisms. This list is not exhaustive and only covers the diverse organelles mentioned in this lesson.

2. Bacteria, archaea, and eukaryotes all make organelles. It has long been recognized that eukaryotes – spanning various unicellular and multicellular species – are compartmented. The defining feature of eukaryotes is their nucleus that stores genetic information and regulates gene expression, unlike bacteria and archaea. Most eukaryotes, including microorganisms such as the budding yeast *Saccharomyces cerevisiae*, also contain multiple other organelles with roles in processes such as energy conservation (e.g. mitochondria), transport (e.g. **Golgi apparatus**), storage (e.g. **vacuoles**), and detoxification (e.g. **peroxisomes**). Though organelles were once thought to be defining traits of eukaryotes, it is now recognized that bacteria and archaea were in fact the first to produce organelles. Far from the classical view that bacterial cells are little more than 'bags of molecules', recent advances in microscopy have uncovered exquisite organization in these cells. The compartments produced by bacteria and archaea are generally distinct from those of eukaryotes. Some organelles are quite widespread, for example **lipid bodies** that store lipids (primarily triacylglycerides) that are used as food reserves when bacteria or archaea experience starvation. Others perform specialized functions in a restricted few species, for example **anammoxosomes** that allow bacteria exclusively within the lineage Planctomycetes to grow through anaerobic ammonium oxidation (anammox).

3. Microbial organelles are structurally and functionally diverse. Microbes produce diverse organelles that differ in both their interior and exterior contents. The lumen (i.e. interior) of an organelle has a distinct molecular composition to the surrounding cytosol and typically defines its function. Some organelles are relatively simple in content. For example, **gas vesicles** are essentially hollow gas stores acting as air bubbles that allow bacteria and archaea to stay buoyant in water. However, many organelles such as mitochondria, thylakoids, and anammoxosomes, have complex structures and highly specialized proteomes (i.e. the composition of proteins held within them). The boundary around an organelle physically separates it from the cytosol. Most organelles, including the **nucleus** are bounded by a lipid membrane. However, some organelles are instead defined by a protein shell (e.g. gas vesicles), a lipid-protein monolayer (e.g. lipid bodies), or alternatively liquid-liquid phase separation (e.g. **nucleolus**). Reflecting their diverse structures, organelles are created in a range of ways: some form from invaginations of the cell membrane, others undergo binary fission during cell division, and others form through phase separation. The structure and functions of six diverse bacterial organelles are summarized below.

4. Organelles enable bacteria to perform extraordinary functions. Bacteria perform numerous functions that eukaryotic life is incapable of. Among the most notable of these is their ability to grow on inorganic compounds, as opposed to organic foods like we do. For example, Planctomycetes are the only organisms that can grow anaerobically (i.e. without oxygen) using ammonium as their energy source. To do so, they react ammonium and nitrite to produce nitrogen gas and water within their anammoxosomes. In the process, they make and consume the toxic compound hydrazine, better known as rocket fuel (see cartoon). Bacteria also use a distinct class of organelles, called **metabolosomes**, to grow on challenging organic compounds such as ethanolamine and propanediol. Organelles also allow bacteria occupy ecological niches that eukaryotes cannot thrive in. For example, anaerobic bacteria called Chlorobia use special organelles called **chlorosomes** to capture light energy at extremely low intensities; this allows them to grow photosynthetically at much deeper depths in lakes than any plant or algae. Bacteria even use organelles to sense magnetic fields: they accumulate and crystallize iron in organelles called **magnetosomes**. They carefully orient these magnetosomes so they form a chain within the cell that acts like the needle of a compass. By becoming magnetic in this way, these bacteria in turn constrain their searches (via chemotaxis) for oxygenated environments.



Diverse structures and functions of organelles present in bacteria. Each of the organelles has a distinct boundary layer made from either a protein shell, a lipid bilayer, or a protein-lipid monolayer, or through liquid-liquid phase separation. Each organelle also has different luminal contents that reflect their function: gas vesicles are hollow stores are gas that provide buoyancy; carboxysomes provide a concentrated supply of carbon dioxide for the carbon-fixing enzyme RuBisCO; magnetosomes store iron oxide crystals that enable cells to orient to magnetic poles; chlorosomes contain chlorophyll bundles that capture and transmit light energy at low concentrations; lipid bodies store large quantities of triacylglycerides; and the nucleolus synthesizes ribosomal RNA using chromosomal DNA as a template. Adapted from Greening and Lithgow, Nature Reviews Microbiology 2020.

5. Organelles are broadly environmentally, medically, and industrially significant. Microbial organelles are critical for numerous processes that contribute to global nutrient cycling, including photosynthesis and carbon fixation. The three most abundant lineages of photosynthetic bacteria – the Cyanobacteria, Proteobacteria, and the Chlorobia – have each evolved distinct organelles to harvest light energy using photosynthetic pigments (e.g. chlorophylls).

Likewise, by providing a concentrated supply of carbon dioxide, carboxysomes greatly enhance the notoriously inefficient process of carbon fixation performed by the enzyme RuBisCO. Photosynthetic bacteria are critical for the productivity of marine and freshwater systems, in turn supporting marine biodiversity and fisheries. They are also useful biotechnologically and some are even consumed as food (e.g. spirulina). Anaerobic ammonium oxidation, mediated by the anammoxosome, is also a critical process in the global nitrogen cycle and is often promoted by wastewater treatment plants to remove excess nitrogen pollution. Thus, the organelles of bacteria promote important ecosystem services (including supporting, regulatory, and provisioning services). Yet some deadly pathogens also depend on organelles to cause disease. For example, the causative agent of tuberculosis (*Mycobacterium tuberculosis*) has recently been shown to use ultrasmall protein-bounded organelles called **nanocompartments** to survive against the human body's immune defenses during infection.

6. Some eukaryote organelles are derived from bacteria. Two of the most important organelles in eukaryotes were originally derived from bacteria: mitochondria which mediate respiration in most eukaryotes and **chloroplasts** that mediate photosynthesis in plants and algae. It is now widely accepted that the first eukaryote resulted from the engulfment of a bacterial cell (to form mitochondria) by an archaeal cell (which formed the cytoplasm); these became strictly dependent on each other (i.e. obligate mutualistic) through metabolic interactions. This process is termed endosymbiosis. In a later endosymbiotic event, the eukaryotic ancestor of plants and algae engulfed a photosynthetic Cyanobacteria that became a chloroplast. Each eukaryotic cell can contain numerous mitochondria and chloroplasts, thereby multiplying their capacity for energy conservation compared to bacteria. In turn, these organelles have facilitated increases in the cell size and organismal complexity of eukaryotes. Modern-day mitochondria and chloroplasts still contain remnant genomes of their bacterial ancestors. Thus, in addition to forming the first organelles, bacteria continue to be a key part of us through our mitochondria.

7. Bacteria make nucleus-like compartments during viral infection. The defining feature that distinguishes eukaryotes from bacteria and archaea is their nucleus. Yet it was recently shown that, when bacteriophages (i.e. bacterial viruses) infect *Pseudomonas* cells, they form an organelle highly analogous to a nucleus. Here bacteriophages mediate rapid rates of nucleic acid synthesis to propagate. These nucleus-like structures selectively exclude cytoplasmic proteins and enable bacteriophages to evade bacterial immunity (i.e. CRISPR nucleases). However, the boundaries that distinguish eukaryotic nuclei from bacteriophage-induced bacterial nuclei differ, and these compartments are not evolutionarily related.

Relevance for Sustainable Development Goals and Grand Challenges

- **Goal 3 – Healthy lives:** Various human pathogens depend on organelles. For example, *Mycobacterium tuberculosis* uses nanocompartments to evade human host defences and survive oxidative stress. This contributes to the notorious persistence of this pathogen, which kills 1.5 million people each year. Likewise, all eukaryotic pathogens depend on organelles. For example, special organelles called hydrogenosomes enable protists such as *Trichomonas vaginalis* to perform anaerobic energy conservation and are the target of antiparasitic medicines, such as metronidazole.
- **Goal 6 – Clean water:** Organelles are critical for the activity of important bacteria in wastewater treatment plants. Most notably, the anammoxosome of Planctomycetes mediates the conversion of the dissolved waste nitrogen compounds ammonium and nitrite into inert nitrogen gas. These bacteria are increasingly used to increase the efficiency of nitrogen removal processes during wastewater treatment, as demonstrated by large-scale reactors in the Netherlands.
- **Goal 14 – Sea conservation:** Organelles mediate the light and dark reactions of photosynthesis in bacteria, algae, and plants. They therefore generate most of the biomass that supports food webs of global marine and freshwater ecosystems. Human activities, including eutrophication and global warming, are causing shifts in the dominant photosynthetic organisms and promote problematic, sometimes toxic algal blooms. A strong understanding of the cell biology and metabolism of these organisms is needed to predict and alleviate their responses to change.

Pupil Participation

1. ***Discussion topic:*** Class discussion on what bacterial superpowers impressed them the most.
2. ***Pupil stakeholder awareness (questions to ask)***
    a. What distinguishes eukaryotes from bacteria, given both contain organelles?
    b. What are the advantages of compartmenting processes? Are there any disadvantages?
    c. Name three ways that bacterial organelles are important for global nutrient cycling.
3. ***Exercises***
    a. Assembling cells using eukaryotes as a model system. https://www.wisc-online.com/learn/natural-science/life-science/mby3204/eukaryotic-cells-assembling-the-cell
    b. Describe three organelles present bacteria. What are their functions and how do they allow bacteria to adapt to their environment?
    c. Let's revisit the organelles in eukaryotes. Which eukaryotic organelles are related to bacteria or their organelles? And what are simply analogous?

The Evidence Base, Further Reading and Teaching Aids

Characteristics of eukaryotic organelles: https://www.youtube.com/watch?v=7FN1NBoV2u0
Bacterial organelles revise ideas about which came first:
https://www.quantamagazine.org/bacterial-organelles-revise-ideas-about-which-came-first-20190612/
Where did eukaryotic cells come from? A journey into endosymbiotic theory:
https://www.youtube.com/watch?v=4LhBZ2H5SwM

Greening, C. and Lithgow, T. (2020), *Formation and function of bacterial organelles.* Nature Reviews Microbiology 18, 677-689.
Murat, D., Bryne, M., Komeili, A. (2010), *Cell biology of prokaryotic organelles*. Cold Spring Harbour Perspectives in Biology 2, a000422.

Glossary

Carbon fixation –conversion of carbon dioxide into organic compounds (biomass)
Chemotaxis – movement of a microbe typically towards a preferred nutrient or resource
Cytoplasm – material enclosed by a cell membrane within a given cell (except the nucleus)
Ecosystem service – function performed by ecosystems that benefit humanity
Organelles – enclosed compartments that perform specific cellular functions
Phase separation – segregation of two liquids, for example oil and water
Photosynthesis – conversion of sunlight into usable energy (ATP) by bacteria, algae, and plants
Proteome – total protein content of a given cell or compartment
RuBisCO – enzyme that mediates fixation of carbon dioxide into organic carbon