

INTIMATE STRANGERS: MICROBIAL PARTNERS IN THE NATURAL WORLD

SPRING 2020 🔘

OLLI

LECTURE 2: MICROBIAL EVOLUTION

MICROBIAL LIFE AS WE KNOW IT

THE BEGINNING

EARLY MICROBIAL COMMUNITIES

THE MICROBIAL REPERTOIRE EXPANDS

MAJOR MICROBIAL INVENTIONS

OXYGENIC PHOTOSYNTHESIS EVOLUTION OF EUKARYØTES

COLONIZING DRY LANDS

LIFE AS WE KNOW IT (LAWKI): LESSONS FROM MICROBES

- W. MARTIN ET AL. (DÜSSELDORF, GERMANY, 2016) → ANALYZED OVER 6 MILLION GENES FROM MICROBES AND GROUPED THEM INTO FAMILIES
- ONLY 355 GENE FAMILIES ARE PRESENT IN ALL ORGANISMS SAMPLED → THEY WERE PRESENT IN THE COMMON ANCESTOR
- ABOUT 100 OF THESE ARE INVOLVED IN PROTEIN TRANSLATION
- ANOTHER CA. 100 ARE INVOLVED IN DNA REPLICATION, MAINTENANCE AND REPAIR; AND RNA SYNTHESIS
- IMPLIES A VERY SOPHISTICATED GENETIC SYSTEM

• THIS IS STILL A VERY COMPLICATED ORGANISM!

DARWIN'S THOUGHTS

- "ALL ORGANIC BEINGS THAT HAVE LIVED ON EARTH COULD BE DESCENDED FROM SOME PRIMORDIAL FORM", IN THE ORIGIN OF SPECIES (1859)
- "THE INTIMATE RELATIONSHIP BETWEEN THE VITAL PHENOMENA WITH CHEMISTRY AND ITS LAWS MAKES THE IDEA OF SPONTANEOUS GENERATION CONCEIVABLE", IN NOTEBOOK 1937 (WHILE ON THE BEAGLE)
- IN A FAMOUS LETTER SENT IN 1 FEBRUARY 1871 TO HIS FRIEND, THE ENGLISH BOTANIST AND EXPLORER JOSEPH D. HOOKER, CHARLES DARWIN SUGGESTED THAT THE ORIGINAL SPARK OF LIFE MAY HAVE BEGUN IN A "WARM LITTLE POND, WITH ALL SORTS OF AMMONIA AND PHOSPHORIC SALTS, LIGHT, HEAT, ELECTRICITY, &C., PRESENT, THAT A PROTEINE (SIC) COMPOUND WAS CHEMICALLY FORMED READY TO UNDERGO STILL MORE COMPLEX CHANGES."

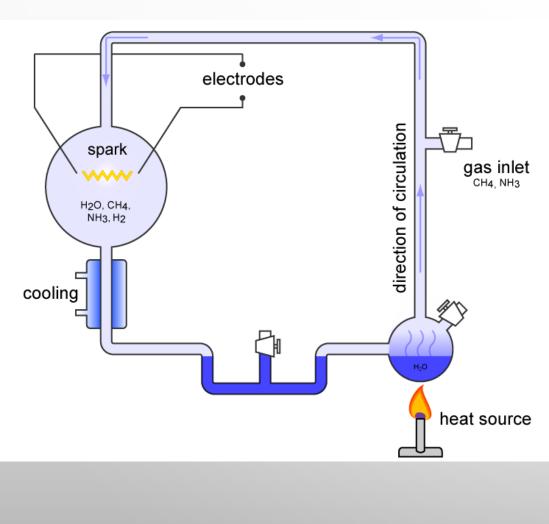
ALEXANDER OPARIN (1894-1980)



- IN 1924 HE PUT FORWARD A HYPOTHESIS SUGGESTING THAT LIFE ON EARTH DEVELOPED THROUGH A GRADUAL CHEMICAL
 EVOLUTION OF CARBON-BASED MOLECULES IN <u>THE EARTH'S PRIMORDIAL</u> <u>SOUP</u>
- THERE IS NO FUNDAMENTAL DIFFERENCE BETWEEN A LIVING ORGANISM AND LIFELESS MATTER
- EARLY EARTH HAD AN ATMOSPHERE CONTAINING METHANE, AMMONIA, HYDROGEN AND WATER VAPOR
- THERE WERE ONLY DILUTE SOLUTIONS
 OF SIMPLE ORGANIC MOLECULES
- GRADUALLY COMPLEXITY WILL ARRIVE



ABIOGENESIS OF ORGANIC COMPOUNDS



- IN 1952, CHEMISTS STANLEY MILLER AND HAROLD UREY
- WATER (H₂O), METHANE (CH₄), AMMONIA (NH₃) AND HYDROGEN (H₂)
- AMINO ACIDS AND OTHER ORGANIC MOLECULES
- BUT WE NOW KNOW THAT THE EARLY ATMOSPHERE CONSISTED MOSTLY OF NITROGEN AND CO2, WITH SMALL AMOUNTS OF HYDROGEN, WATER AND METHANE
- 2017, CZECH REPUBLIC: NH₃ + CO + H₂O → ALL OF THE RNA NUCLEOBASES—URACIL, CYTOSINE, ADENINE AND GUANINE. ALSO UREA AND THE SIMPLE AMINO ACIDS; ALSO ALCOHOLS, ORGANIC ACIDS, SIMPLE LIPIDS, ETC
- ADDING IRON AND CARBONATE MINERALS, ENRICHED FOR AMINO ACIDS

THE SOLAR SYSTEM (CA. 5 Ga [BILLION YEARS AGO])

In the early universe, vast molecular clouds of dust and gas condensed to form a protostar, surrounded by a protoplanetary disk.

EARTH FORMS (CA. 4.5 GA)

Tiny dust grains, consisting of silicate minerals coated with ice, stuck together and assembled into larger particles.

EARLY EVENTS IN EARTH'S HISTORY

- BY ABOUT 4.4 GA, THE MOON-FORMING IMPACT TURNED THE EARTH INTO A BALL OF BOILING LAVA
- MAGMA OCEANS WITH TEMPERATURES OVER 2,000°K FORCED ALL WATER FROM EARLY ACCRETION INTO THE GAS PHASE
- ALL EARLY ACCRETED CARBON WAS CONVERTED TO ATMOSPHERIC CARBON DIOXIDE (CO₂)
- BY 4.2 TO 4.3 GA, THE EARTH HAD COOLED SUFFICIENTLY ENOUGH THAT A SOLID CRUST BEGAN FORMING AND WATER BEGAN CONDENSING INTO OCEANS
- THE FIRST SIGNS OF LIFE APPEAR AS CARBON ISOTOPE SIGNATURES IN ROCKS CA. 4 BILLION YEARS OF AGE
- THUS, SOMEWHERE ON THE OCEAN-COVERED EARLY EARTH AND IN A NARROW WINDOW OF TIME OF ONLY ABOUT 200 MILLION YEARS, LIFE CAME INTO EXISTENCE

EARLY EARTH (CA. 4 BILLION YEARS AGO)

The first land was probably volcanic, forming island arcs in a vast ocean.

Ponds or lakes in volcanic regions were likely environments for jump-starting life.

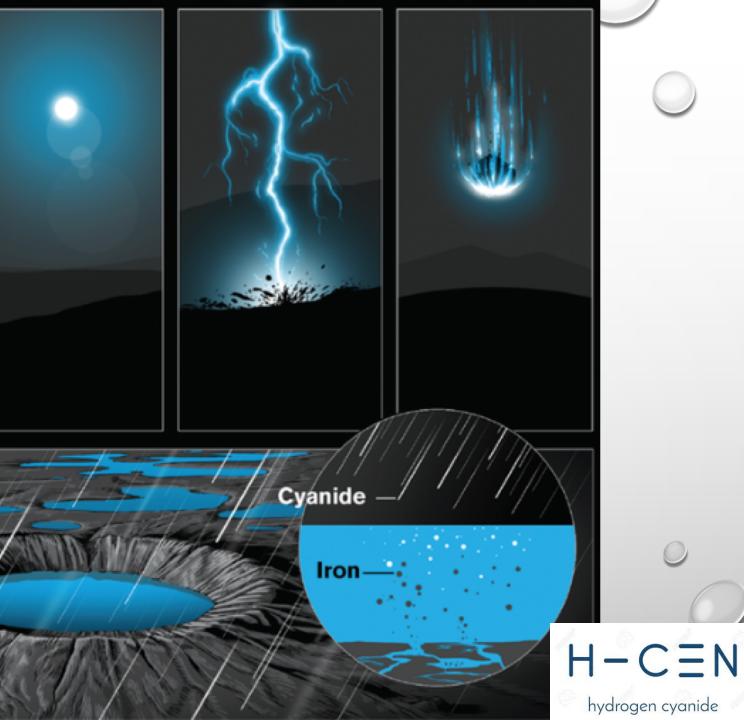


The early atmosphere had no oxygen. It consisted mainly of nitrogen and carbon dioxide, with smaller amounts of hydrogen, water and methane.

Lightning, asteroid impacts and ultraviolet light from the sun acted on the atmosphere to generate hydrogen cyanide, a compound of hydrogen, carbon and nitrogen.

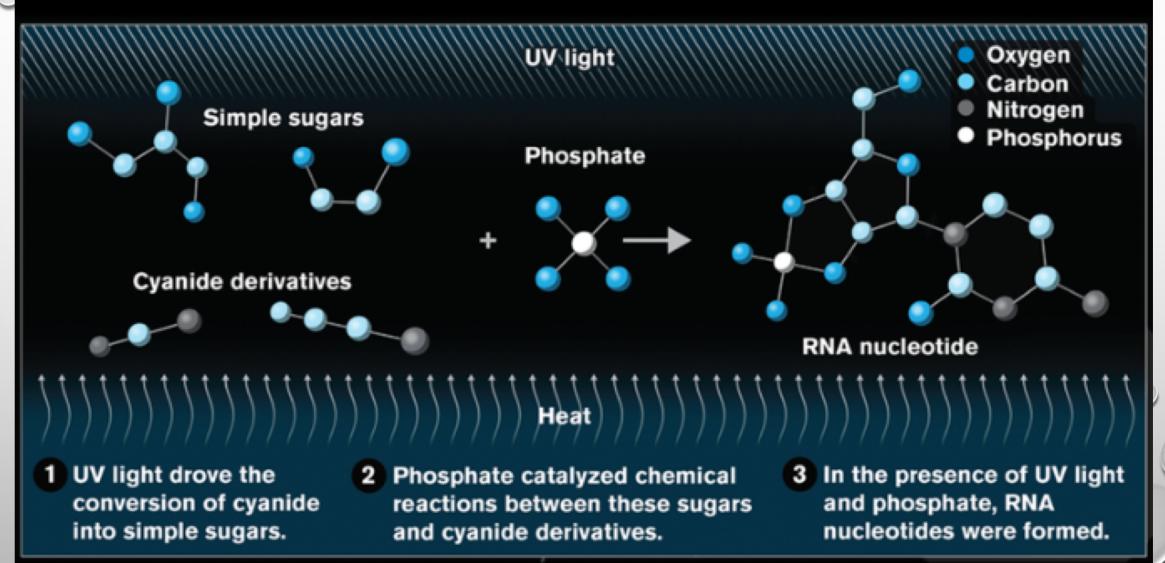
Raining into volcanic or crater lakes, the cyanide reacted with iron brought up by water circulating through rocks.

The resulting iron-cyanide compounds accumulated over time, building up into a concentrated stew of reactive chemicals.

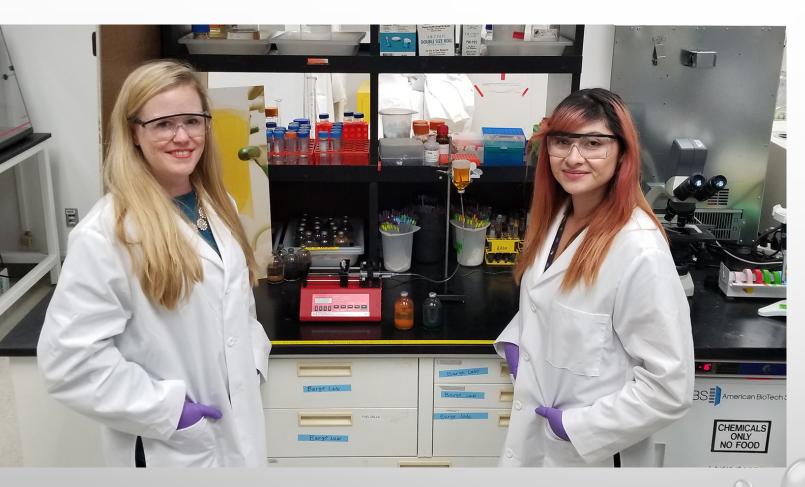


Life as we know it requires RNA. Some scientists believe that RNA emerged directly from these reactive chemicals, nudged along by dynamic forces in the environment.

Nucleotides, the building blocks of RNA, eventually formed, then joined together to make strands of RNA. Some stages in this process are still not well understood.



ABIOGENESIS OF ORGANIC COMPOUNDS AROUND HYDROTHERMAL VENTS



- FEBRUARY 2019. DR LAURIE BARGE ET AL, JET PROPULSION LAB, PASADENA
- RE-CREATED HYDROTHERMAL VENT ENVIRONMENT IN THE LAB: WATER, MINERALS AND THE "PRECURSOR"
 MOLECULES PYRUVATE AND
 AMMONIA; HEAT TO 70°C; ADJUST PH;
 REMOVE O2 AND ADD IRON
 HYDROXIDE
- DETECTED AMINO ACIDS AND LACTIC
 ACID
- FIRST TIME AN ENVIRONMENT VERY
 SIMILAR TO A HYDROTHERMAL VENT
 DRIVES AN ORGANIC REACTION



MAKING NUCLEIC ACIDS IN THE PREBIOTIC WORLD

Monomers will base pair with a single stranded template and self ligate.

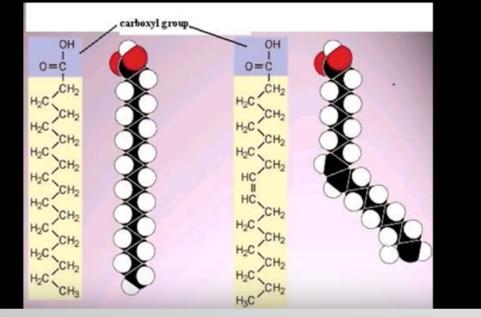
Covalent Bond Ligation Hydrogen Bonds Base Pair

They can also polymerize in solution, and spontaneously form new templates, or extend existing templates.

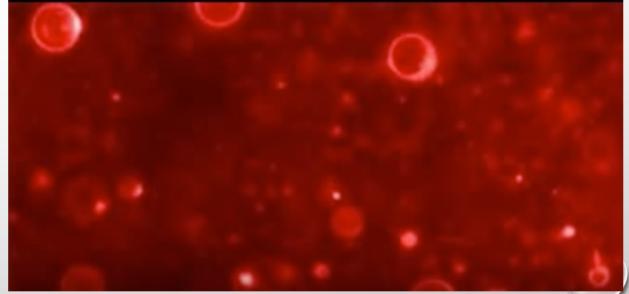
No special sequences are required, it's just chemistry.

ISOLATING FROM THE ENVIRONMENT – THE MAKINGS OF A 'MEMBRANE'

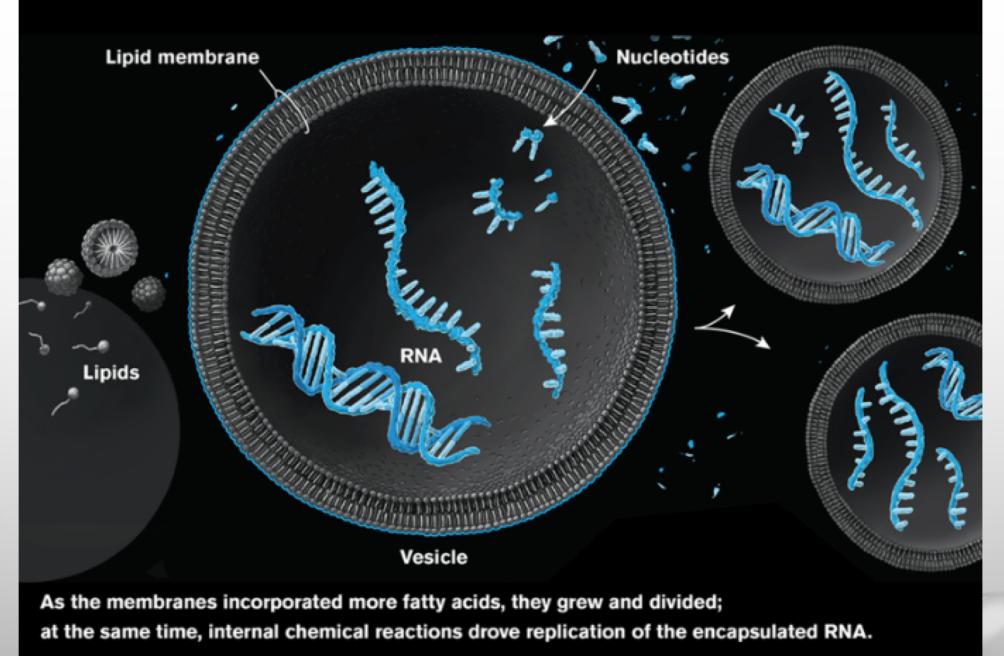
The pre-biotic environment contained many simple fatty acids



SPONTANEOUSLY form stable vesicles.

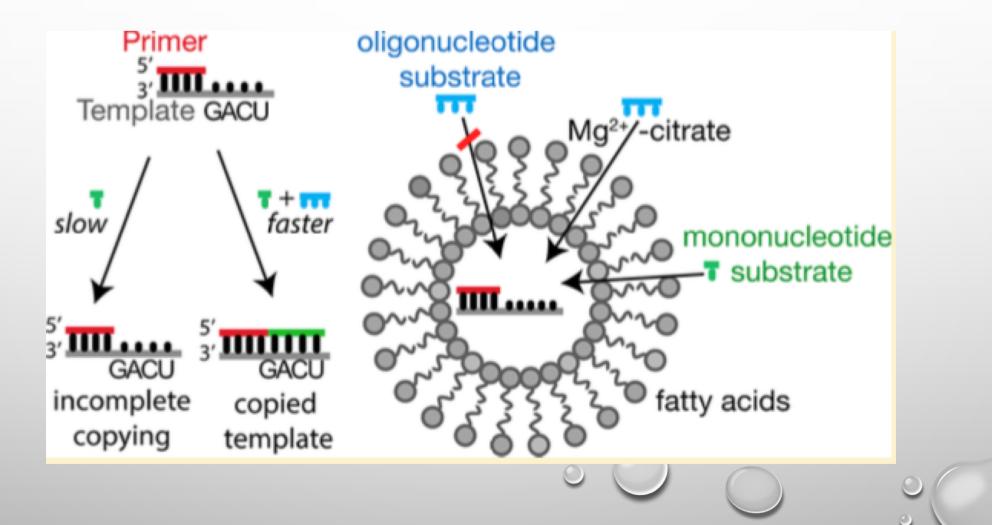


Once RNA was made, some strands of it became enclosed within tiny vesicles formed by the spontaneous assembly of fatty acids (lipids) into membranes, creating the first protocells.

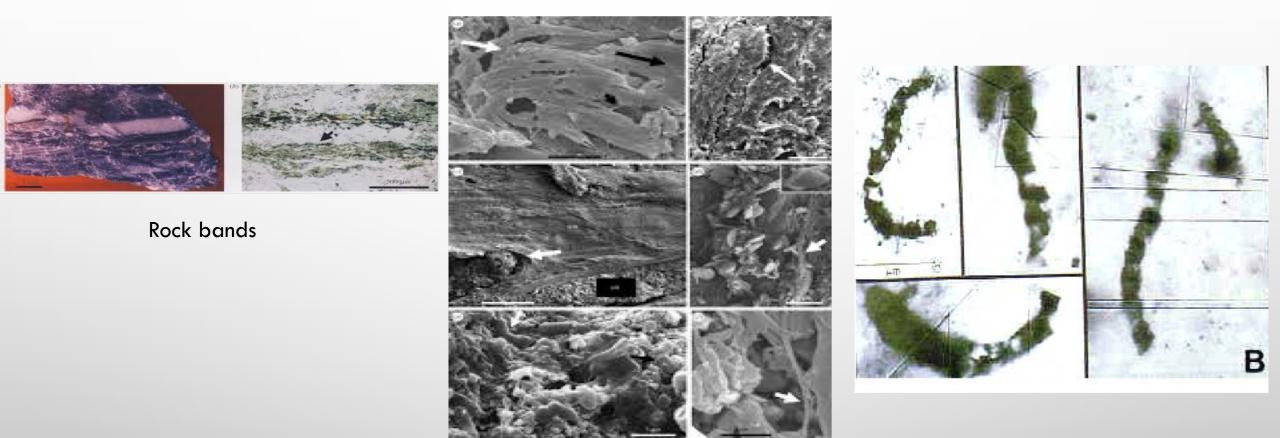


AND VALIDATION - SZOSTAK ET AL., J. AM. CHEM. SOC. 2018, 140, 5171-5178

COPYING OF MIXED-SEQUENCE RNA TEMPLATES INSIDE MODEL PROTOCELLS



3.5 BILLION-YEAR-OLD MICROBIAL MAT: SURFACE OF VOLCANIC LITTORAL SEDIMENT (WESTERN AUSTRALIA)



Micrographs

ANCIENT MICROBIAL LIFE



- IN 3.7 BILLION-YEAR-OLD ROCKS IN GREENLAND
- THE CONE-SHAPED
 STRUCTURES (ABOUT THE SIZE OF A QUARTER) MAY
 BE FOSSILIZED
 MICROBIAL MATS

WHAT ABOUT THE OTHER CA. 150 GENES?

- GENES POINTED QUITE PRECISELY TO AN ORGANISM THAT LIVED IN THE CONDITIONS FOUND IN DEEP SEA VENTS, THE GASSY, METAL-LADEN, INTENSELY HOT PLUMES CAUSED BY SEAWATER INTERACTING WITH MAGMA ERUPTING THROUGH THE OCEAN FLOOR
- ANAEROBIC
- SOURCE OF CARBON: CO₂
- IN THE PRESENCE OF H₂, CAN CONVERT TO METHYL GROUP (CH₃⁻) AND CARBON MONOXIDE (CO)
- IN TURN CONVERTS TO ACETATE, THAT FEEDS INTO CENTRAL METABOLISM
- THESE ARE SUBSTRATES FOR THE MAKING OF BIOCHEMICAL COMPOUNDS (SUGARS, AMINO ACIDS, ETC.)
- SOURCE OF ENERGY: CO2 + 4 $H_2 \rightarrow CH4 + 2 H_2O$

WHAT OTHER PHYSIOLOGIES CAN ARISE?

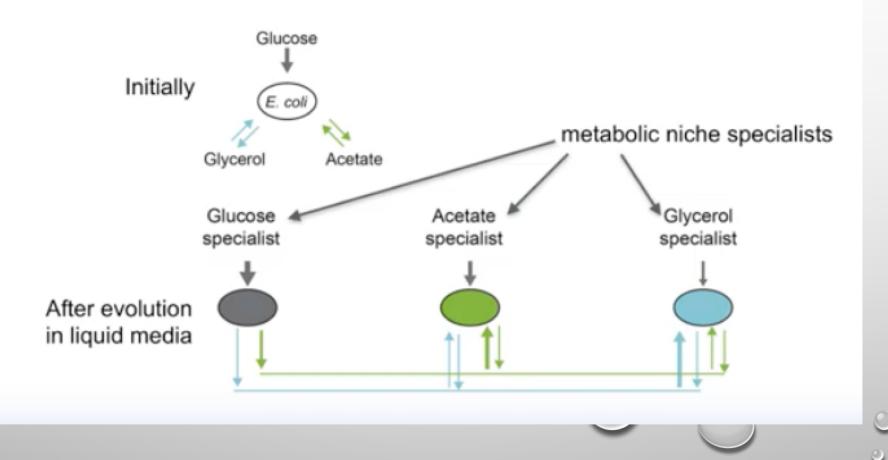
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- ORGANISMS NEED A SOURCE OF CARBON AND A SOURCE OF ENERGY
- SOURCE OF CARBON: CO2
- SOURCE OF ENERGY:
 - OXIDATION, E.G. H₂ (HYDROGEN), H₂S (HYDROGEN SULFIDE), NH₃ (AMMONIA), FE ²⁺ (FERROUS IRON), VARIOUS SULFUR, IRON AND NITROGEN COMPOUNDS
- CHEMOLITHOAUTOTROPHS: MICROBES THAT UTILIZE CHEMICALS (CHEMO) FROM THE BEDROCK (LITHO) AS AN ENERGY SOURCE FOR MAKING THEIR OWN (AUTO) FOOD (TROPH)





"Primary" succession by evolution of niche specialists





BECOMING FOOD

 THESE CHEMOLITHOAUTOTROPHS IN TURN BECOME FOOD → HETEROTROPHS: THE SOURCE OF CARBON IS ORGANIC MOLECULES

• OPARIN'S OCEAN CAN NOW HAPPEN! IT CAN BE RESTOCKED, REGENERATED

ORGANISMS THAT EAT ORGANICS CAN NOW ARISE AND THRIVE

THE MICROBIAL COMMUNITY EXPANDS - CHEMO

Energy source	Oxidizing donor source	Carbon source	Name	
Breaking Chemical Compounds <i>Chemo-</i>	Organic <i>-organo-</i>	Organic - <i>heterotroph</i>	Chemoorganoheterotroph	
		Carbon dioxide <i>-autotroph</i>	Chemoorganoautotroph	
	Inorganic <i>-litho-</i> *	Organic - <i>heterotroph</i>	Chemolithoheterotroph	
		Carbon dioxide -autotroph	Chemolithoautotroph	0 (

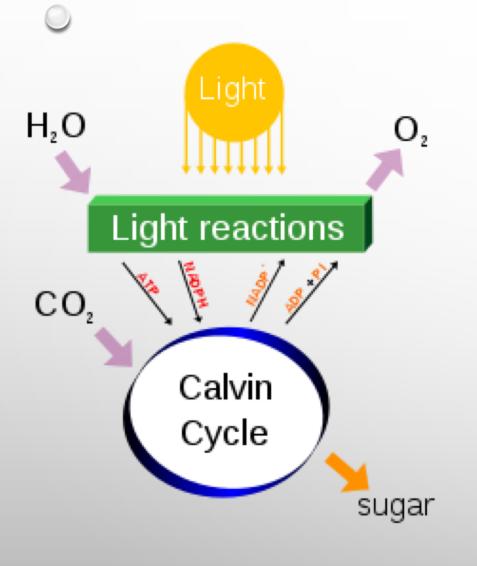
- ADAPTATIONS:
 - MORE EFFICIENT CATALYSTS → COLDER ENVIRONMENTS
 - NEWER SOURCES OF ENERGY (SOMEONE'S METABOLIC WASTE BECOMES SOMEONE'S BONANZA)
 - ACCUMULATING ORGANIC
 MATERIAL PAVED THE WAY FOR
 CHEMOORGANOTROPHS AND
 HETEROTROPHS

THE MICROBIAL COMMUNITY EXPANDS – ANOXYGENIC PHOTOSYNTHESIS

- CA. 3.5 BILLION YEARS OLD
- CAPABLE OF SYNTHESIZING THEIR OWN FOOD FROM INORGANIC SUBSTANCES USING LIGHT AS AN ENERGY SOURCE

- ADAPTATIONS:
 - SPECIALIZED PIGMENTS THAT ALLOW THEM TO CAPTURE ENERGY FROM THE SUN TO OXIDIZE HYDROGEN SULFIDE, (ELEMENTAL SULFUR AS WASTE PRODUCT)
 - USE CO₂ AS CARBON SOURCE

OXYGENIC PHOTOSYNTHESIS – THE GAME CHANGER



- CA. 2.8 BILLION YEARS AGO \rightarrow CYANOBACTERIA
- SYNTHESIZE FOOD DIRECTLY FROM CARBON DIOXIDE AND WATER USING ENERGY FROM LIGHT

 $\frac{\text{CO}_2}{\text{carbon}} + \frac{2\text{H}_2\text{O}}{\text{water}} + \frac{\text{photons}}{\text{light energy}} \rightarrow \underbrace{[\text{CH}_2\text{O}]}_{\text{carbohydrate}} + \underbrace{\text{O}_2}_{\text{oxygen}} + \frac{\text{H}_2\text{O}}{\text{water}}$

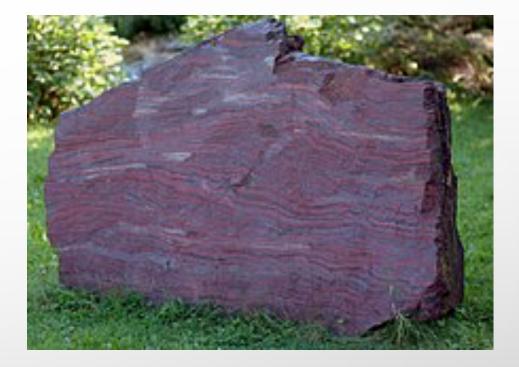
- LIGHT-DEPENDENT STAGE PHOTOSYNTHESIS 1: CHLOROPHYLL CAPTURES LIGHT, USES THE ENERGY TO SYNTHESIZE ATP
- 2 H₂O + 2 NADP⁺ + 3 ADP + 3 P₁ + LIGHT \rightarrow 2 NADPH + 2 H⁺ + 3 ATP + O_2^{\prime}

• LIGHT-INDEPENDENT STAGE – PHOTOSYNTHESIS 2: ATP IS USED TO INCORPORATE CO₂ INTO SUGARS

• 3 CO₂ + 9 ATP + 6 NADPH + 6 H⁺ \rightarrow C₃H₆O₃-PHOSPHATE + 9 ADP + 8 P₁ + 6 NADP⁺ + 3 H₂O

OXYGEN MAKES AN APPEARANCE

- IN THE ABSENCE OF OXYGEN, THE EARTH'S IRON WAS IN THE REDUCED FORM DISSOLVED IN THE OCEANS (OCEANS WERE PROBABLY ORANGE THEN, NOT BLUE AS TODAY)
- THE OXYGEN PRODUCED BY THE CYANOBACTERIA
 WOULD HAVE IMMEDIATELY REACTED WITH THE IRON
 COMPOUNDS AND OXIDIZED THEM
- THESE WERE NOT VERY SOLUBLE IN WATER AT ALL → THEY PRECIPITATED, RAINING DOWN ON THE OCEAN
 FLOOR AND LEADING TO BANDED IRON FORMATIONS
- ONLY AFTER THE IRON WAS DEPLETED, COULD OXYGEN
 BEGIN ACCUMULATING IN THE ATMOSPHERE



2.1-billion-year-old rock showing banded iron formation. A major source of iron ore

PROBLEMS WITH OXYGEN

- OXYGEN IS A VERY REACTIVE CHEMICAL SPECIES → PEROXIDES (H₂O₂), HYDROXYL RADICALS ('OH), SUPEROXIDE
- THESE ARE ALL VERY TOXIC TO CELLS
- PROBABLY WIDE EXTINCTION OF MICROBES NOT ABLE TO ADAPT TO INCREASING O2
- THIS MAY HAVE LED TO THE OPENING OF ECOLOGICAL NICHES
- ADAPTING TO THE PRESENCE OF OXYGEN DEMANDS A MAJOR GENETIC INVESTMENT
- FOR REFERENCE: E. COLI HAS 100 GENES OR MORE (OF CA. 4000 GENES) DEVOTED TO COPING WITH OXIDATIVE STRESS AND OXIDATIVE CELL DAMAGE

THE GOOD SIDE OF OXYGEN – AEROBIC RESPIRATION

- IN THE ABSENCE OF OXYGEN, EXTRACTING ENERGY FROM ORGANIC MATTER IS NOT VERY EFFICIENT
 - LOWER ENERGY YIELDS
 - BY-PRODUCTS: ALCOHOL (YEAST, TO OUR DELIGHT), METHANE (COW BELCHING, SWAMPS), ACETIC ACID
- IN THE PRESENCE OF OXYGEN, RESPIRATION IS A VERY EFFICIENT PROCESS
 - HIGHER ENERGY YIELDS: CA. 10-FOLD HIGHER
 - END PRODUCTS: H₂O AND CO₂

OXYGEN ACCUMULATES IN THE ATMOSPHERE

 OXYGEN OXIDIZED ATMOSPHERIC METHANE (A STRONG GREENHOUSE GAS) TO CARBON DIOXIDE (A WEAKER ONE) AND WATER. THIS WEAKENED THE GREENHOUSE EFFECT OF THE EARTH'S ATMOSPHERE, CAUSING PLANETARY COOLING. THIS MAY HAVE TRIGGERED A SERIES OF ICE AGES KNOWN AS THE HURONIAN GLACIATION, BRACKETING AN AGE RANGE OF 2.45–2.22 GA

 FORMATION OF OZONE (O₃): EARTH IS BOMBARDED BY INTENSE AMOUNT OF ULTRAVIOLET RADIATION, THAT CAUSES SEVERE DAMAGE TO DNA AND IS LETHAL TO CELLS. O₂ IN THE ATMOSPHERE IS CONVERTED TO O₃ WHICH STRONGLY ABSORBS UV, PROTECTING EARTH. THIS PROCESS RENDERED THE EARTH'S SURFACE POTENTIALLY INHABITABLE

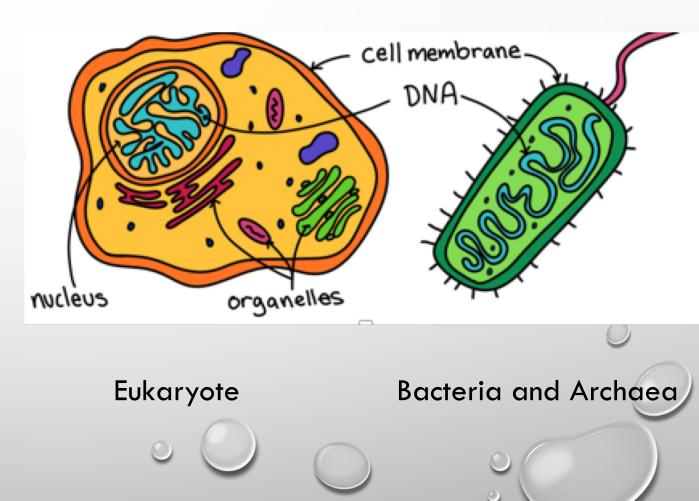


Stages 5 1 2 3 4 0.5 0.4 Atmosphere PO2 (atm) 0.3 0.2 0.1 2 0 3.8 3 Ga 0 2 The upper red and lower green lines represent the range of the estimates

Stage 1 (3.85–2.45 Ga): Practically no O_2 in the atmosphere. The oceans were largely anoxic with the possible exception of O_2 in the shallow oceans. **Stage 2** (2.45–1.85 Ga): O₂ produced, but absorbed in oceans and seabed rock. **Stage 3** (1.85–0.85 Ga): O₂ starts to gas out of the oceans, but is absorbed by land surfaces. No significant change in oxygen level. Stages 4 and 5 (0.85 Gapresent): Other O₂ reservoirs filled; gas accumulates in atmosphere

AND...

- OXYGEN MAY HAVE HAD MOMENTOUS IMPORTANCE IN THE NEXT BIG EVOLUTIONARY INVENTION, THE EUKARYOTIC CELL
- EUKARYOTIC CELL:
 - NUCLEUS WHERE GENETIC MATERIAL IS
 FOUND, SURROUNDED BY MEMBRANE
 - OTHER MEMBRANE-BOUND STRUCTURES (MITOCHONDRIA, CHLOROPLASTS)
 - CYTOSKELETON: A SYSTEM OF TUBULES AND FILAMENTS THAT PROVIDE STRUCTURE TO THE CELL
 - CAN SEXUALLY REPRODUCE, ALTHOUGH THEY NOT ALWAYS DO SO; THEY CAN ALSO REPRODUCE CLONALLY BY MITOSIS



ORIGIN OF EUKARYOTES

The ENDOSYMBIOTIC THEORY

 Infoldings in the plasma membrane of an ancestral prokaryote gave rise to endomembrane components, including a nucleus and endoplasmic reticulum.

Nucleus

1

Proto-eukaryote

In a second endosymbiotic event, the early eukaryote consumed photosynthetic bacteria that evolved into chloroplasts.

Endoplasmic

reticulum

2

2 In a first endosymbiotic event, the ancestral eukaryote

consumed aerobic bacteria that evolved into mitochondria.

Photosynthetic bacterium

3

Aerobic

bacterium



Mitochondrion

eukaryote

Modern photosynthetic

Modern heterotrophic eukaryote



>2 BILLION YEARS AGO: EUKARYOTES

 OLDEST FOSSILS OF EUKARYOTES— THE PROTIST, GRYPANIA SPIRALIS.
 THESE FOSSILS WERE FOUND IN
 2.1-BILLION-YEAR-OLD BANDED
 IRON FORMATIONS IN MICHIGAN.
 BOTTOM IMAGE: GRYPANIA
 SPIRALIS RIBBONS ON GRAY, NELY LAMINATED, IRON-RICH SHALE (SLAB
 IS 9.0 CM ACROSS). EACH FOSSIL
 RIBBON IS ~0.5 TO 0.6 MM WIDE

DID OXYGEN PLAY A ROLE IN THE EVOLUTION OF EUKARYOTES?

THE CASE FOR A CELL NUCLEUS

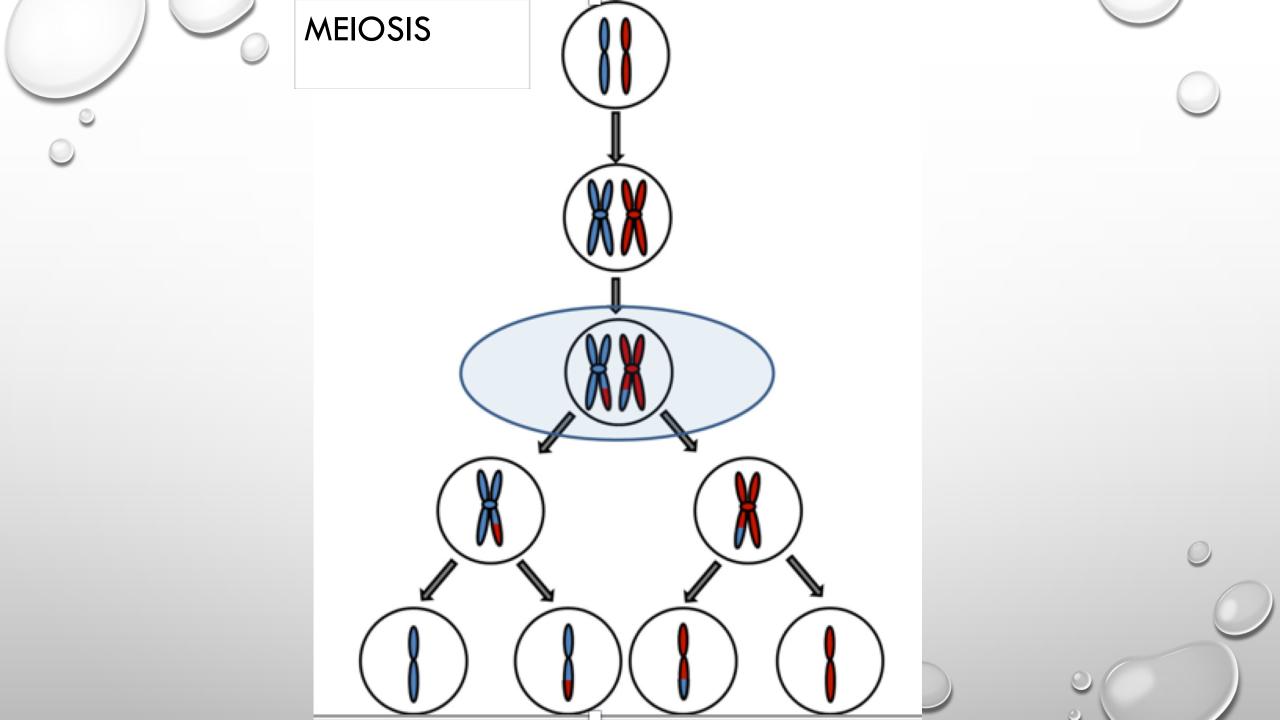
- EUKARYOTES BENEFITTED FROM THE HIGH-ENERGY GAIN OF AEROBIC METABOLISM, ALLOWING FURTHER CELLULAR COMPLEXITY AND LARGER SIZE
- BUT HIGH-ENERGY METABOLISM (BOTH AEROBIC RESPIRATION AND PHOTOSYNTHESIS) REQUIRES OXYGEN, WHICH IS VERY REACTIVE
- THIS LEADS TO INCREASED INTERNAL ROS (REACTIVE OXYGEN SPECIES) PRODUCTION
- THE NUCLEAR ENVELOPE MIGHT HAVE DEVELOPED TO PROTECT THE HOST GENOME FROM
 OXIDATIVE STRESS DUE TO ROS

 IT MAY NOT BE THE WHOLE STORY; FOR EXAMPLE, A NUCLEAR MEMBRANE WOULD ISOLATE THE RESIDENT GENETIC MATERIAL FROM DELETERIOUS INTRUSIONS OF ALIEN DNA

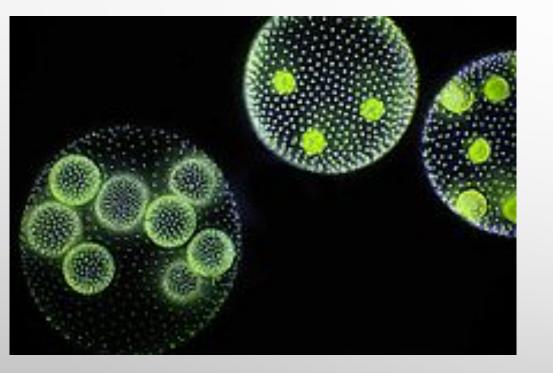
DID OXYGEN PLAY A ROLE IN THE EVOLUTION OF EUKARYOTES?

THE CASE FOR SEX

- MITOSIS (CLONAL REPRODUCTION) AND MEIOSIS (SEX) PROBABLY EVOLVED CONCURRENTLY IN EARLY EUKARYOTES
- SEXUAL REPRODUCTION IS THE PROCESS BY WHICH THE GENOMES OF TWO PARENTS ARE BROUGHT TOGETHER TO PRODUCE PROGENY THAT MAY CONTAIN RE-ASSORTED PORTIONS OF THE PARENTAL GENOMES
- BUT IT IS RISKY, AND TIME- AND ENERGY-CONSUMING
- WHY KEEP DOING IT?
- ONE POSSIBLE EXPLANATION: SEXUAL REPRODUCTION MAY BE A SUPERIOR NUCLEAR DNA REPAIR MECHANISM → BY PAIRING HOMOLOGOUS CHROMOSOMES, REPAIR OF DNA DAMAGED BY ROS WOULD BE ENHANCED



SOME EXPERIMENTAL VALIDATION – THE CASE OF VOLVOX



- GREEN ALGAE
- EACH MATURE VOLVOX COLONY IS COMPOSED OF UP TO THOUSANDS OF CELLS
- THE CELLS SWIM IN A COORDINATED FASHION, WITH DISTINCT ANTERIOR AND POSTERIOR POLES
- ASEXUAL REPRODUCTION IS MOST COMMONLY
 OBSERVED
- SEXUAL REPRODUCTION CAN BE TRIGGERED BY
 OXIDATIVE STRESS

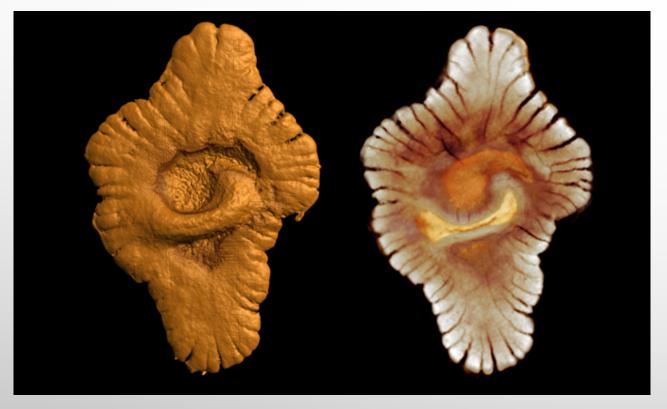
DID OXYGEN PLAY A ROLE IN THE EVOLUTION OF EUKARYOTES?

THE CASE FOR MULTICELLULARITY

- TRADITION HAS IT THAT:
 - LOW LEVELS OF O₂ IN THE EARLY ATMOSPHERE KEPT CELLS SMALL AND ORGANISMS UNICELLULAR → TO GET ENOUGH OXYGEN, ORGANISMS NEEDED THE HIGHEST POSSIBLE RATIO OF SURFACE TO VOLUME
 - ONLY AFTER OXYGEN LEVELS STARTED RISING (ABOUT 1 BILLION YEARS AGO) COULD LARGER, MULTICELLULAR ORGANISMS ARISE
- BUT MULTICELLULARITY AROSE MUCH EARLIER THAN PREVIOUSLY THOUGHT, AND IT MAY NOT HAVE
 BEEN TOO DIFFICULT, IT AROSE MULTIPLE TIMES ACROSS MANY DIFFERENT LINEAGES

• SEE NEXT SLIDE

EARLIEST MULTICELLULAR FOSSIL



- 2.1-BILLION-YEAR-OLD FOSSIL
- FLAT DISCS ALMOST 5 INCHES ACROSS, WITH SCALLOPED EDGES AND RADIAL SLITS
- EITHER COMPLEX COLONIES OF SINGLE-CELLED ORGANISMS, OR EARLY ANIMALS

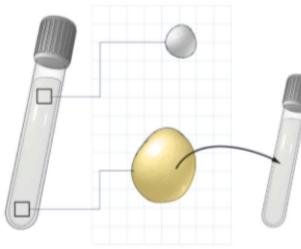


DID OXYGEN PLAY A ROLE?

- THE DRIVER MAY HAVE BEEN LOWER CONCENTRATIONS OF OXYGEN: LOW OXYGEN LEVELS WOULD FAVOR THE EVOLUTION OF MULTICELLULARITY IN ORGANISMS UTILIZING OXYGEN. LARGER, MULTICELLULAR ORGANISMS—WITH MULTIPLE FLAGELLA—WERE BETTER AT SWEEPING WATER PAST THEIR CELL MEMBRANES TO HARVEST OXYGEN. SCARCE NUTRIENTS WOULD HAVE HELPED DRIVE THE NEXT STEP, THE EVOLUTION OF SPECIALIZED CELL TYPES, BECAUSE MORE COMPLEX ORGANISMS CAN HARVEST FOOD MORE EFFICIENTLY
- GENETIC COMPARISONS BETWEEN SIMPLE MULTICELLULAR ORGANISMS AND THEIR SINGLE-CELLED RELATIVES REVEAL THAT MUCH OF THE MOLECULAR EQUIPMENT NEEDED FOR CELLS TO AGGREGATE AND COORDINATE THEIR ACTIVITIES MAY HAVE BEEN IN PLACE WELL BEFORE MULTICELLULARITY. THERE IS REPURPOSING OF EXISTING CAPABILITIES
- IN THE TEST TUBE, SINGLE-CELLED LIFE CAN EVOLVE THE BEGINNINGS OF MULTICELLULARITY IN JUST A FEW HUNDRED GENERATIONS

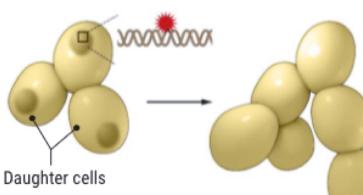
Multicellularity made easy

Researchers got single-cell yeast to evolve multicellularity in the lab, demonstrating the relative ease of the transition.



1 Selection

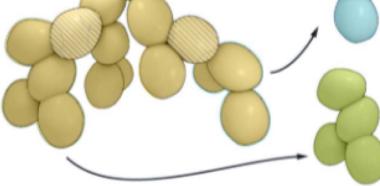
As single yeast cells grow, the larger ones sink faster. Only those cells are allowed to reproduce; repeated rounds of selection result in ever-bigger yeast.



2 Multicellularity

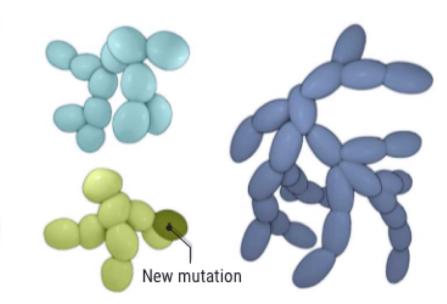
A single mutation causes a reproducing yeast's daughter cells to stick together. Branching snowflake structures

form.



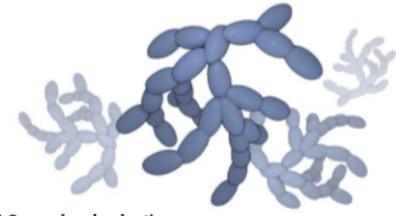
3 Differentiation

A few cells specialize to die early, releasing the cells at the tips of the snowflake to start new snowflakes.



4 Bottleneck

Each freed tip proliferates, and many varieties of multicellular snowflakes form.



5 Group-level selection

Some cell assemblages do better than others and thrive; others do not.

- ONCE ORGANISMS CROSS THE THRESHOLD TO MULTICELLULARITY, THEY RARELY TURN BACK
- SOME LINEAGES OF MICROBES TRIED IT MORE THAN ONCE; SOME DO IT REPEATEDLY
- THE LINEAGES LEADING TO PLANTS ON ONE HAND, AND ANIMALS ON THE OTHER, TRIED IT ONCE AND STUCK WITH IT

- THE MORE SPECIALIZED AND DEPENDENT ON ONE ANOTHER THE CELLS OF COMPLEX ORGANISMS BECOME, THE HARDER IT IS TO REVERT TO A SINGLE-CELL LIFESTYLE
- COOPER & WEST, 28 MAY 2018 IN NATURE ECOLOGY & EVOLUTION. "DIVISION OF LABOR IS NOT A CONSEQUENCE BUT A DRIVER" OF MORE COMPLEX ORGANISMS