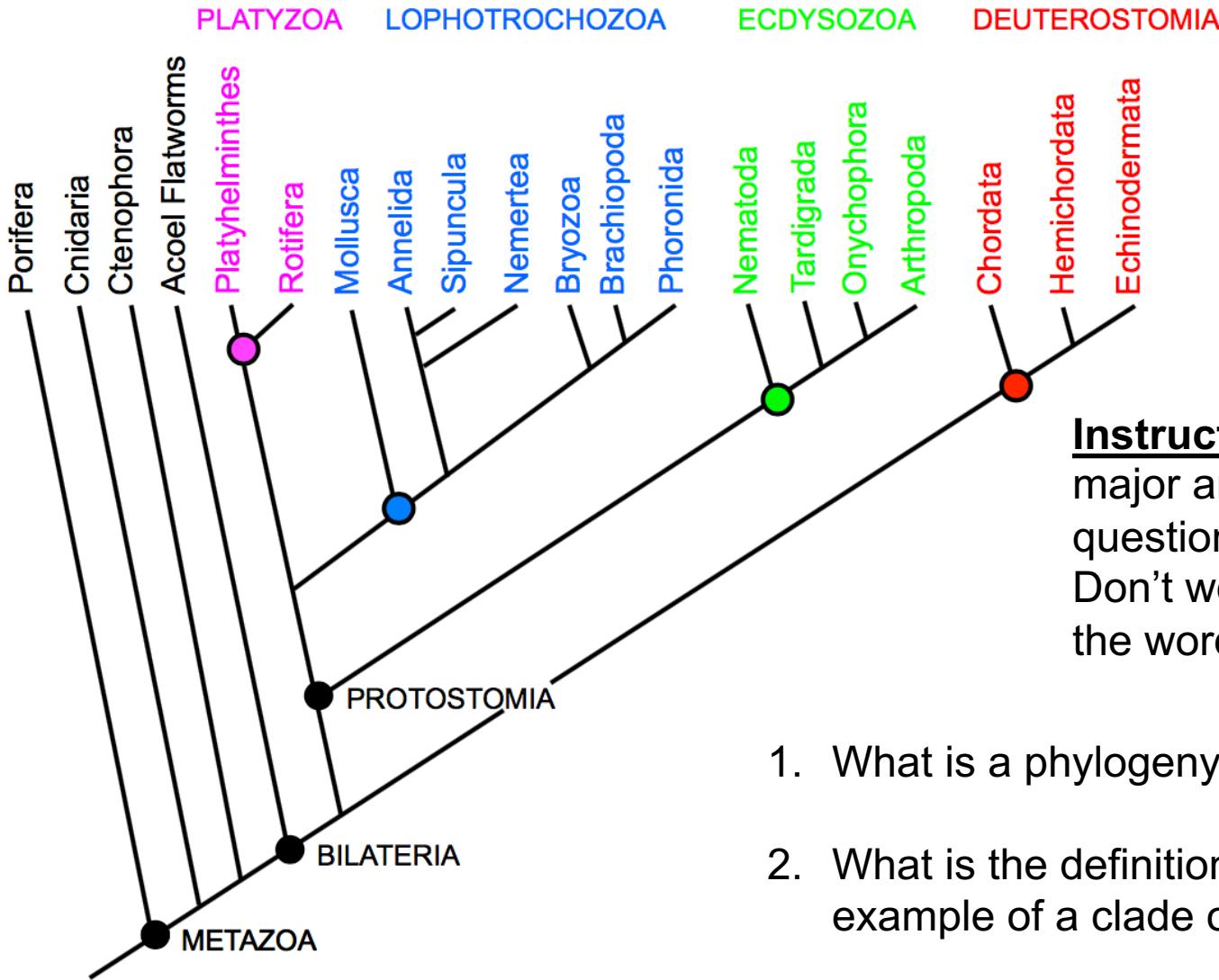
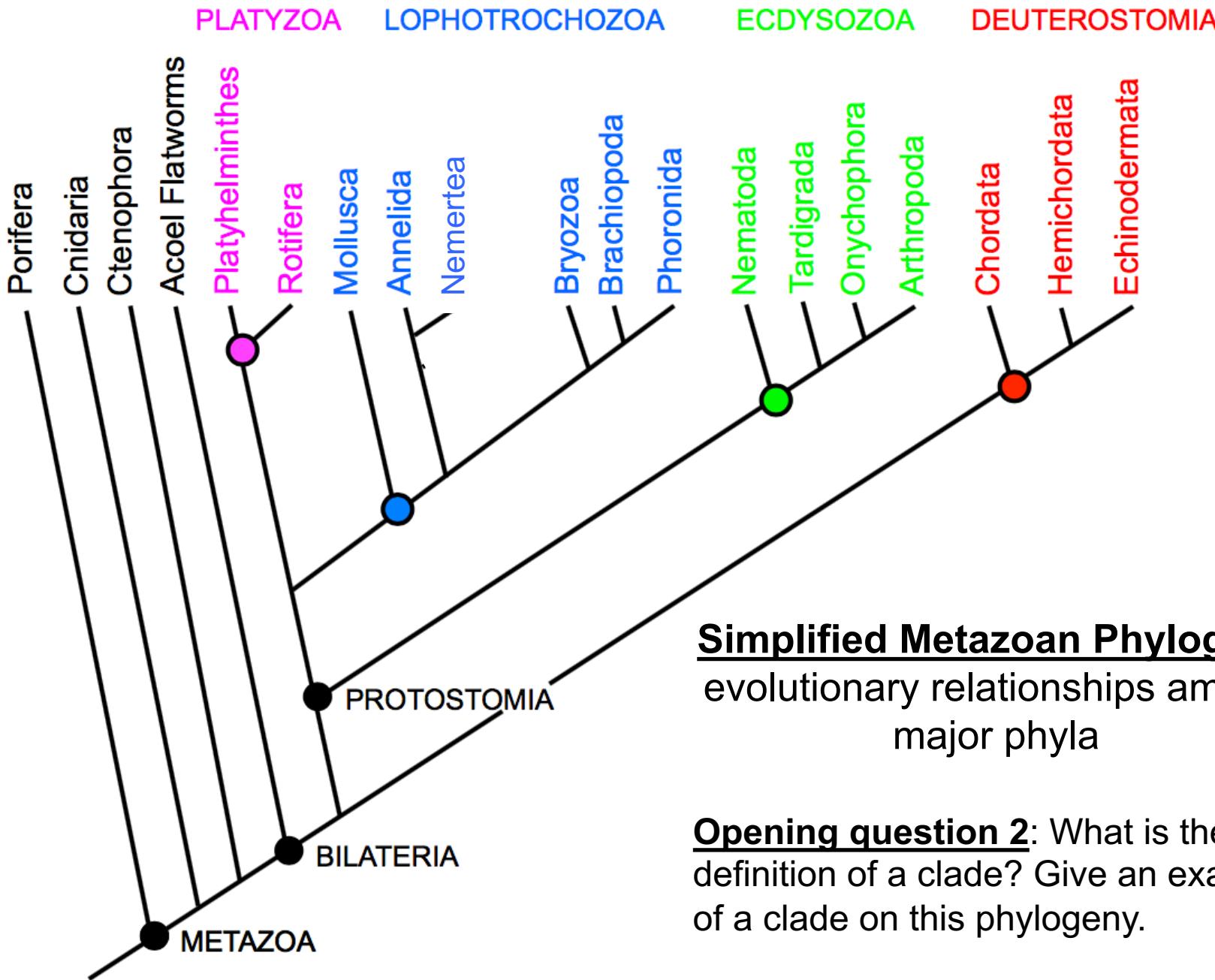


# Opening Thought Questions – 2/7



**Instructions:** This is a phylogeny of the major animal phyla. Think about these questions and write a brief response. Don't worry if you don't understand all of the words or names on this slide!

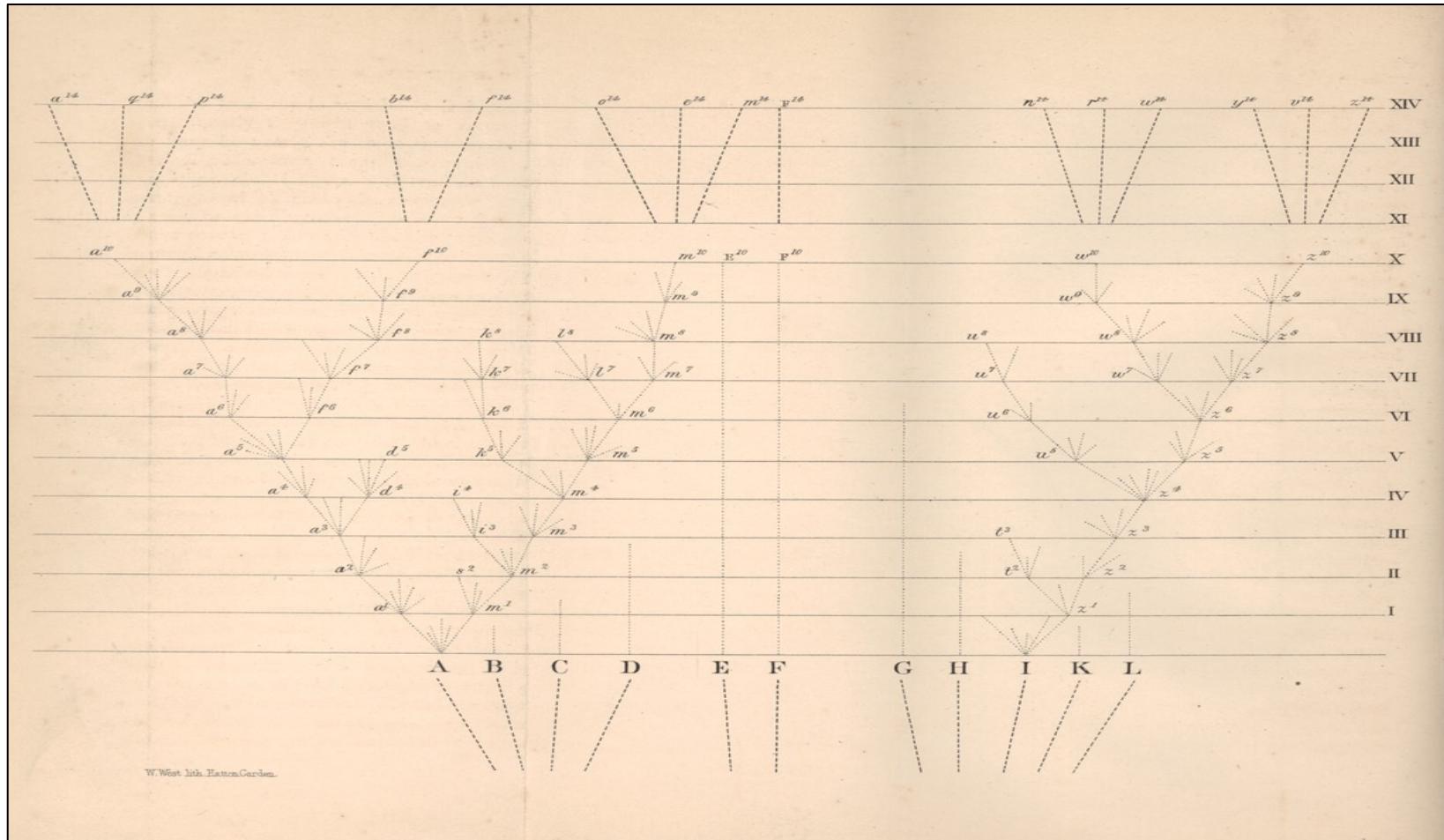
1. What is a phylogeny?
2. What is the definition of a clade? Give an example of a clade on this phylogeny.



**Opening question 2:** What is the definition of a clade? Give an example of a clade on this phylogeny.

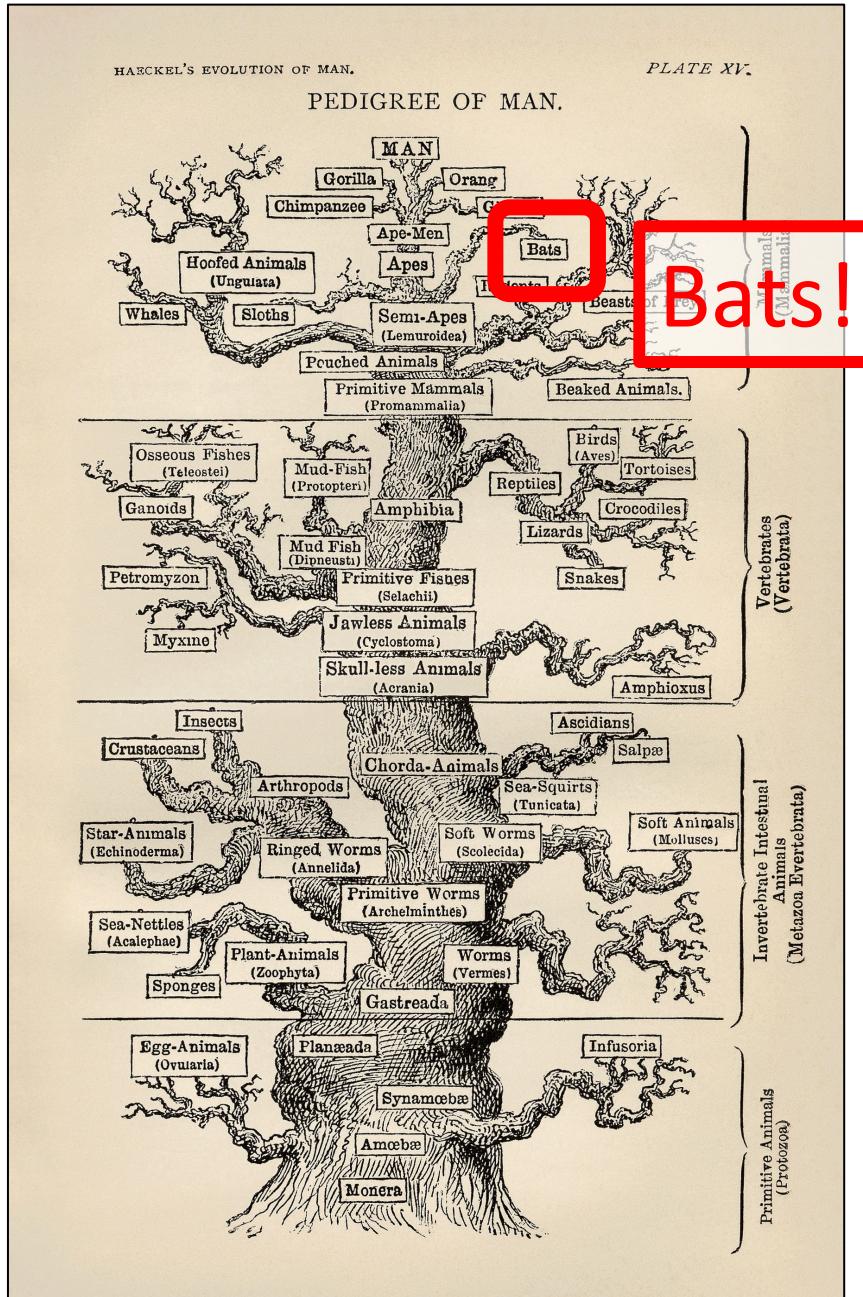
# Charles Darwin: 1859

“On the Origin of Species”



“As buds give rise by growth to fresh buds,  
and these, if vigorous, branch out and  
overtop on all sides many a feebler branch,  
so by generation I believe it has been with  
the great Tree of Life, which fills with its  
dead and broken branches the crust of the  
earth, and covers the surface with its ever  
branching and beautiful ramifications.”

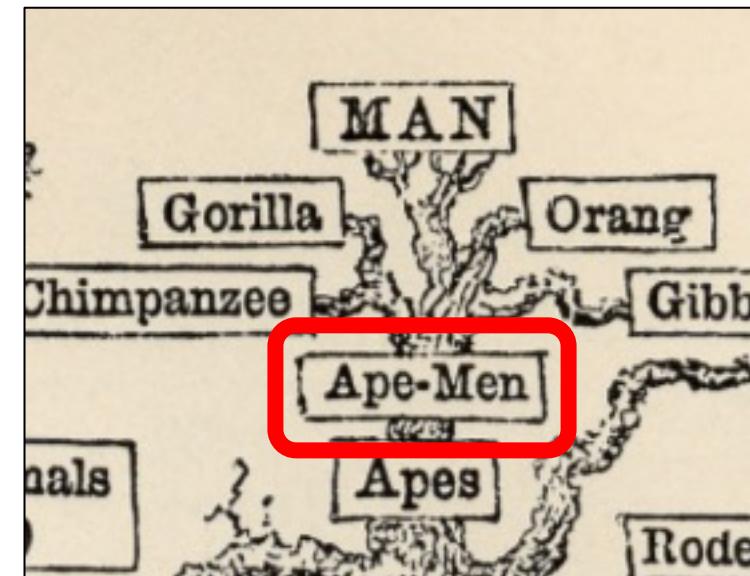
-- *Darwin, “On the Origin of Species”*



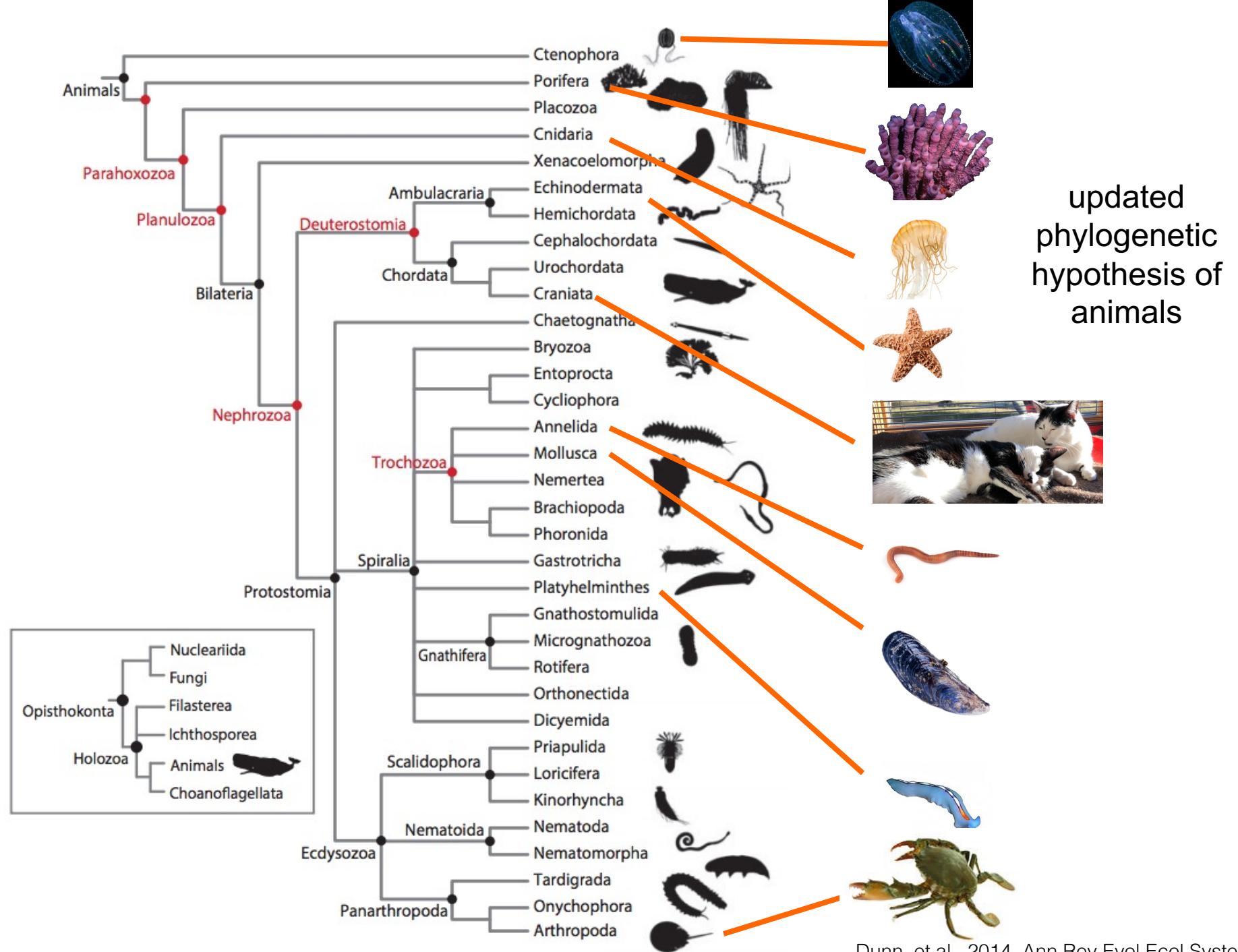
# Ernst Haeckel

## 1879

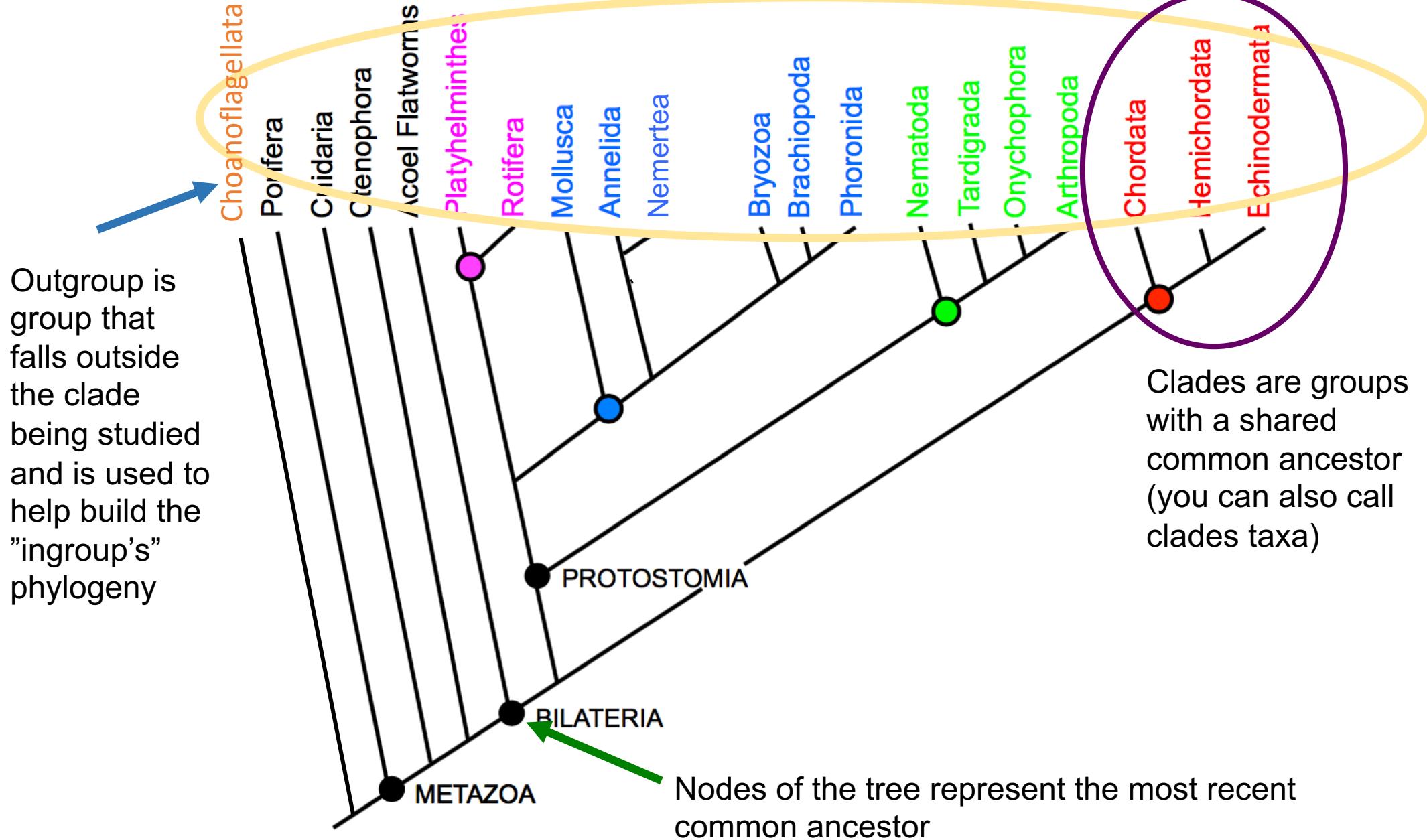
- "The Evolution of Man"

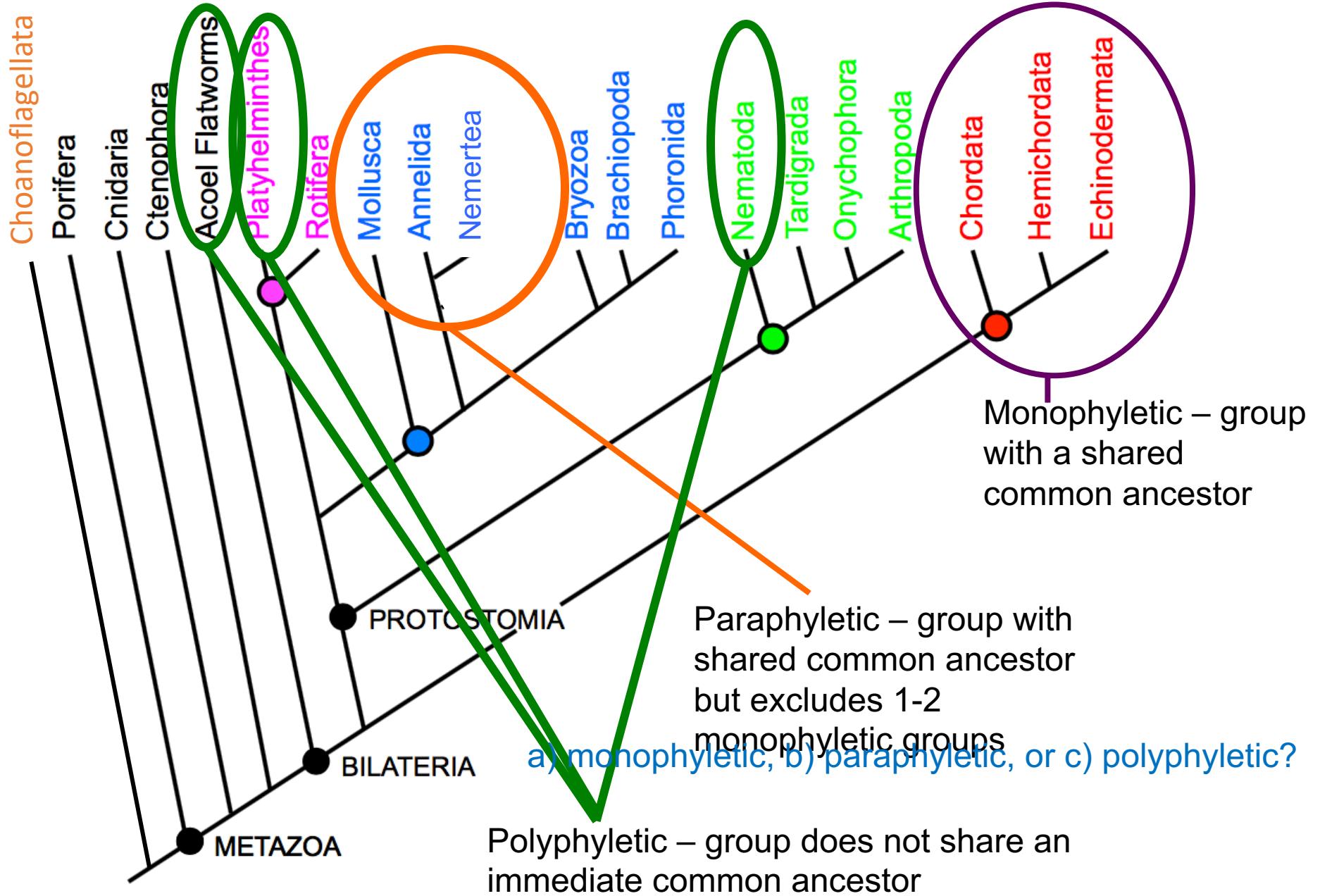


# Phylogenetic Trees

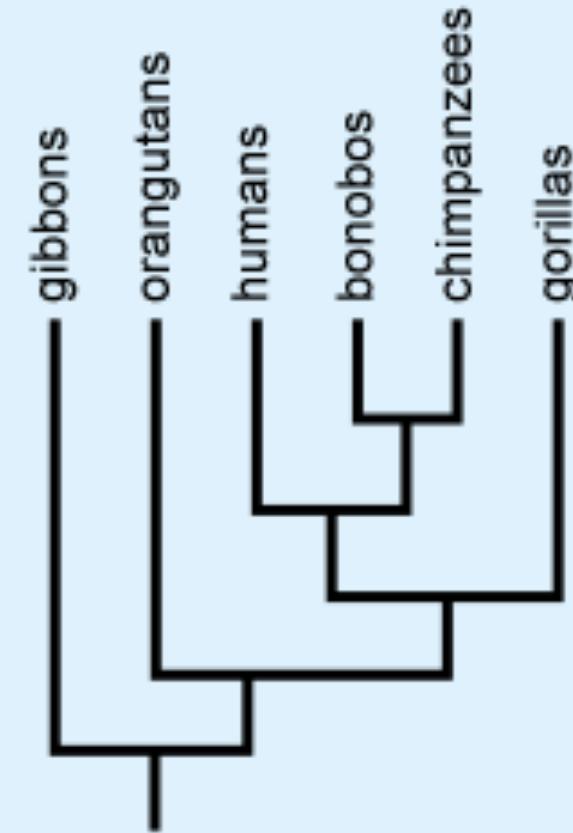
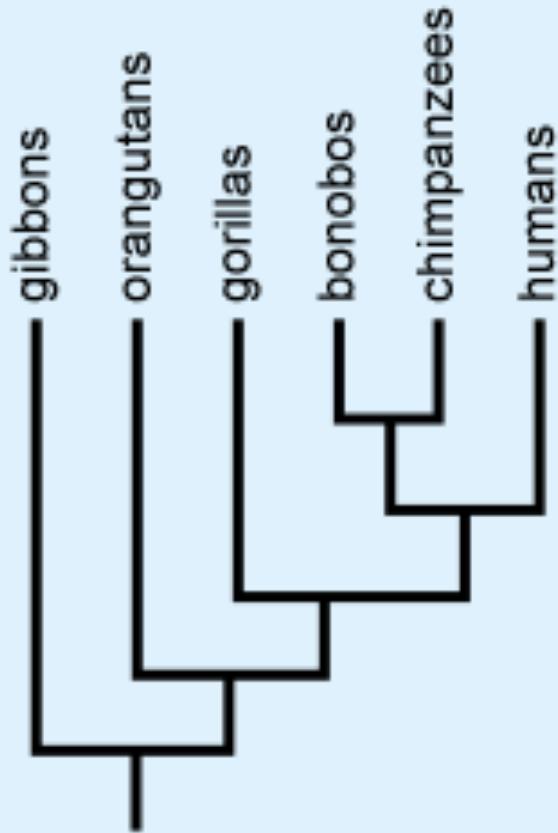


Tips of the tree are taxonomic groups (operational taxonomic units – OTU's)





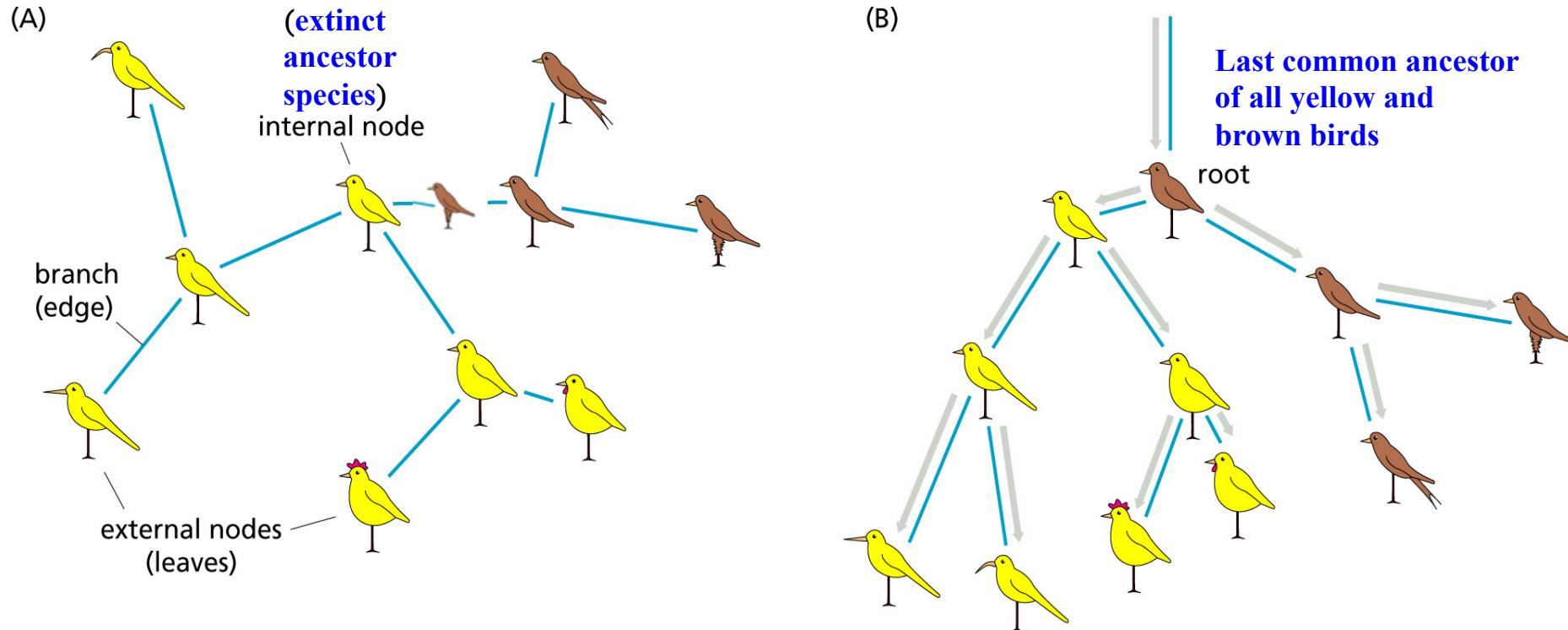
# Flipping nodes: these trees are the same



# Terminology

- OTUs or leaf nodes – the tree's input sequences
- Clade/taxon (plural = taxa) – an internal node, plus everything that descends from that node
- Outgroup – is a group used in phylogenetic analyses and falls outside the clade being studied. All members of the group being studied are more closely related to each other than to the outgroup.

# Unrooted and Rooted Trees

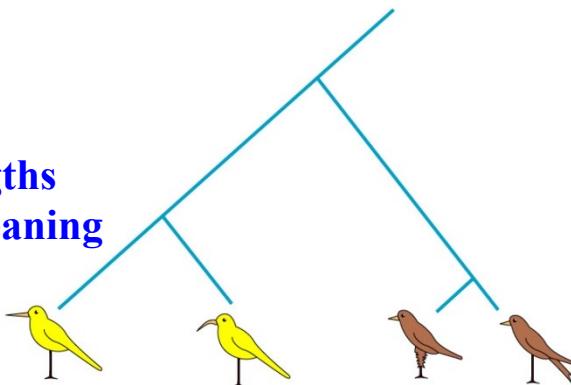


**Unrooted:  
cannot tell**

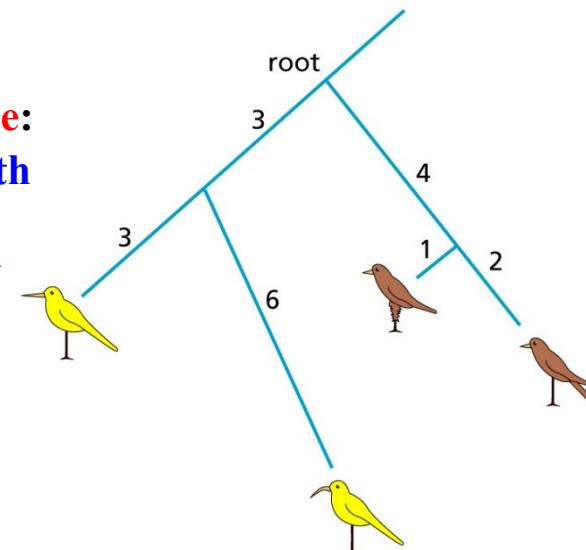
**Have yellow birds evolved from  
brown birds, or brown birds from  
yellow birds?**

**Rooted:  
can tell**

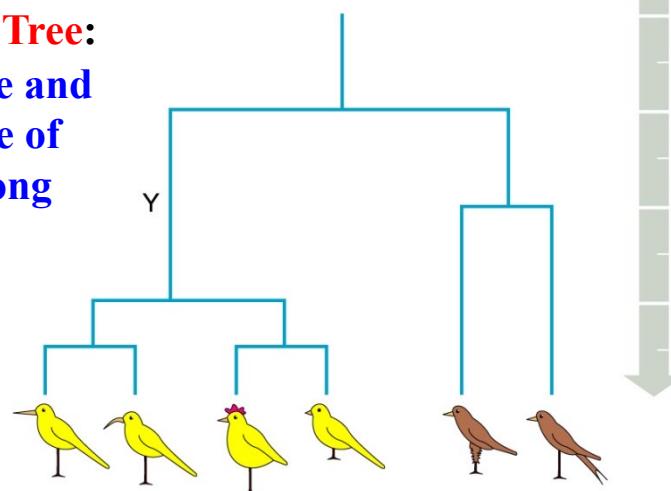
**Cladogram:**  
Branch lengths  
carry no meaning



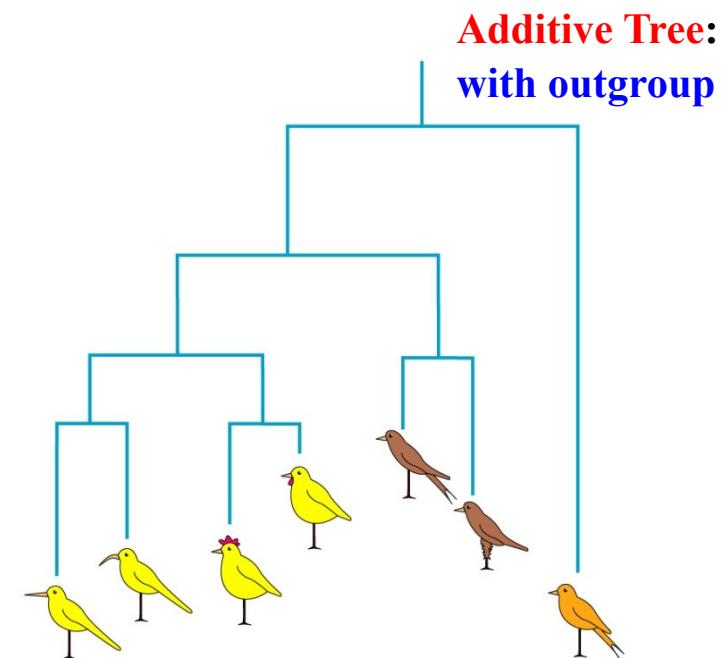
**Additive Tree:**  
Branch length  
measures  
evolutionary  
divergence



**Ultrametric Tree:**  
Additive tree and  
constant rate of  
mutation along  
branches

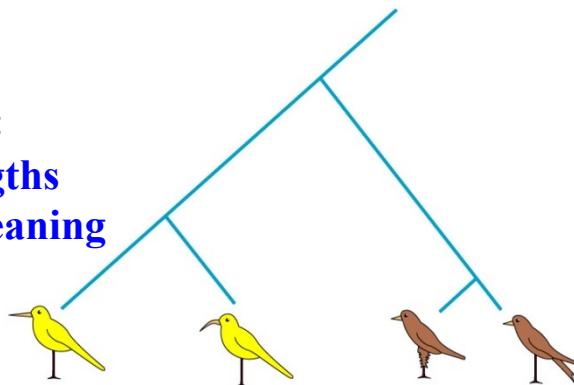


time  
4  
3  
2  
1

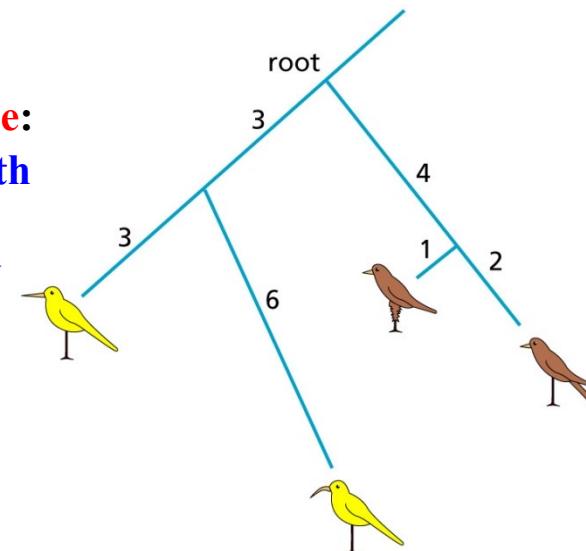


**Additive Tree:**  
with outgroup

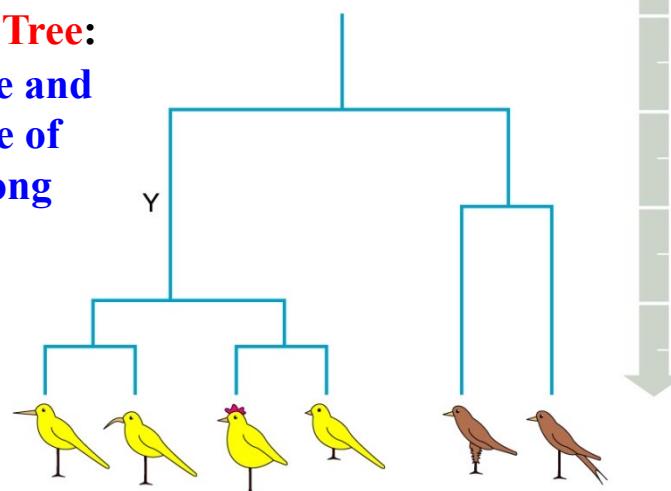
**Cladogram:**  
Branch lengths  
carry no meaning



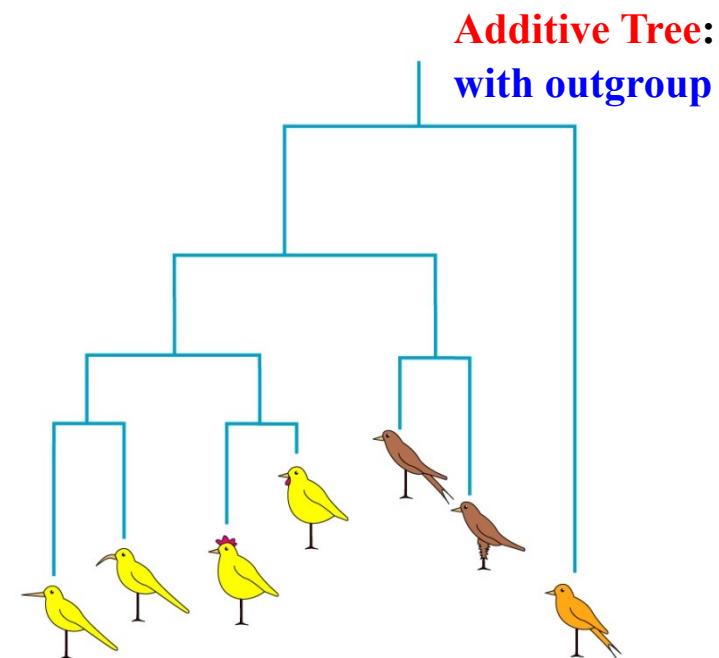
**Additive Tree:**  
Branch length  
measures  
evolutionary  
divergence



**Ultrametric Tree:**  
Additive tree and  
constant rate of  
mutation along  
branches



time  
4  
3  
2  
1

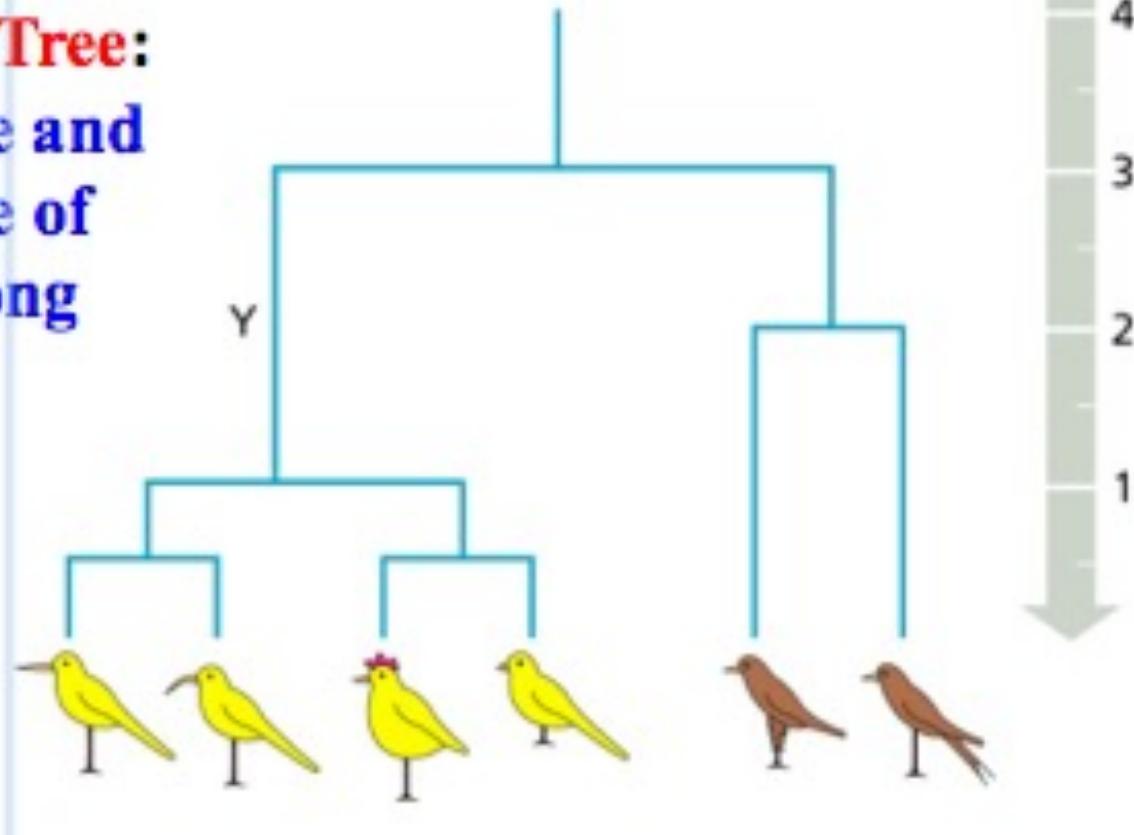


**Additive Tree:**  
with outgroup

□

□ C)

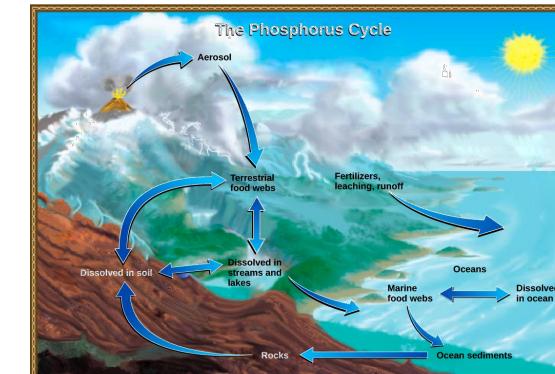
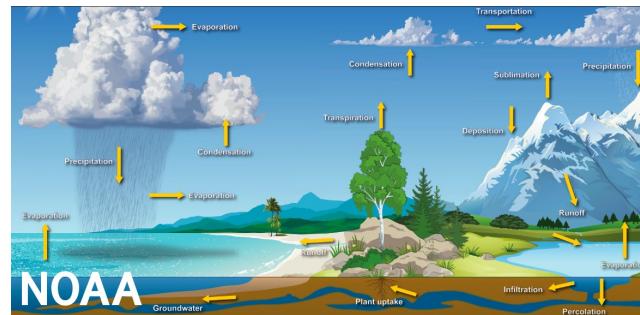
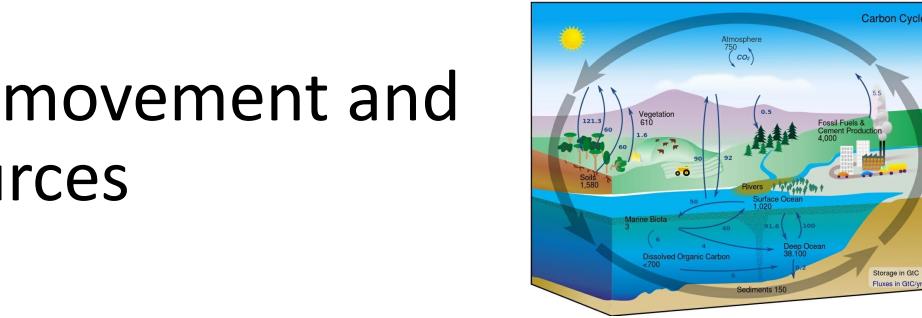
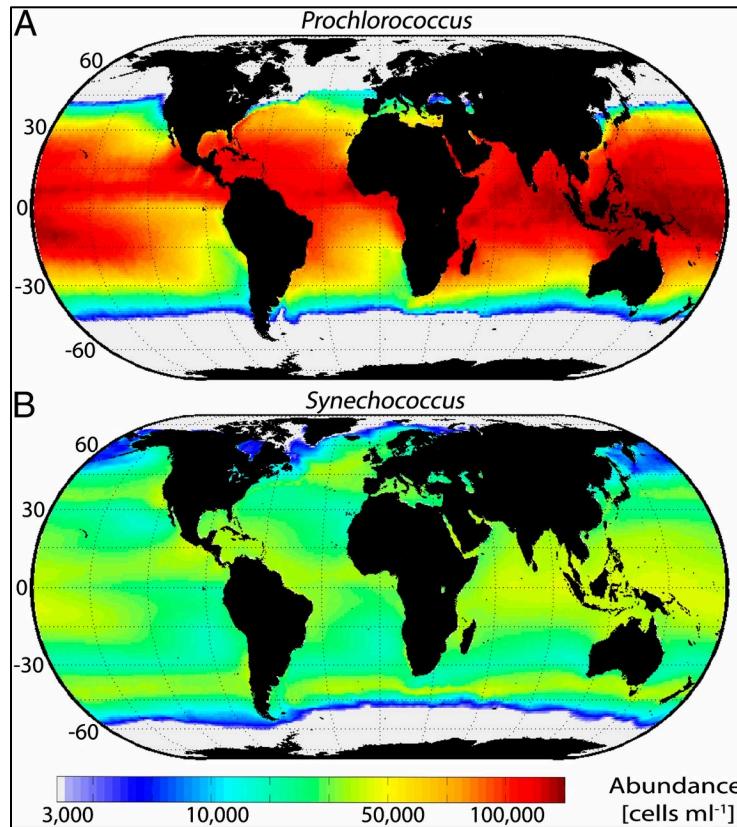
**Ultrametric Tree:  
Additive tree and  
constant rate of  
mutation along  
branches**



The *Ultrametric property*:  
Constant distance from any OTU to root

# Ecology studies abundance and distribution of organisms

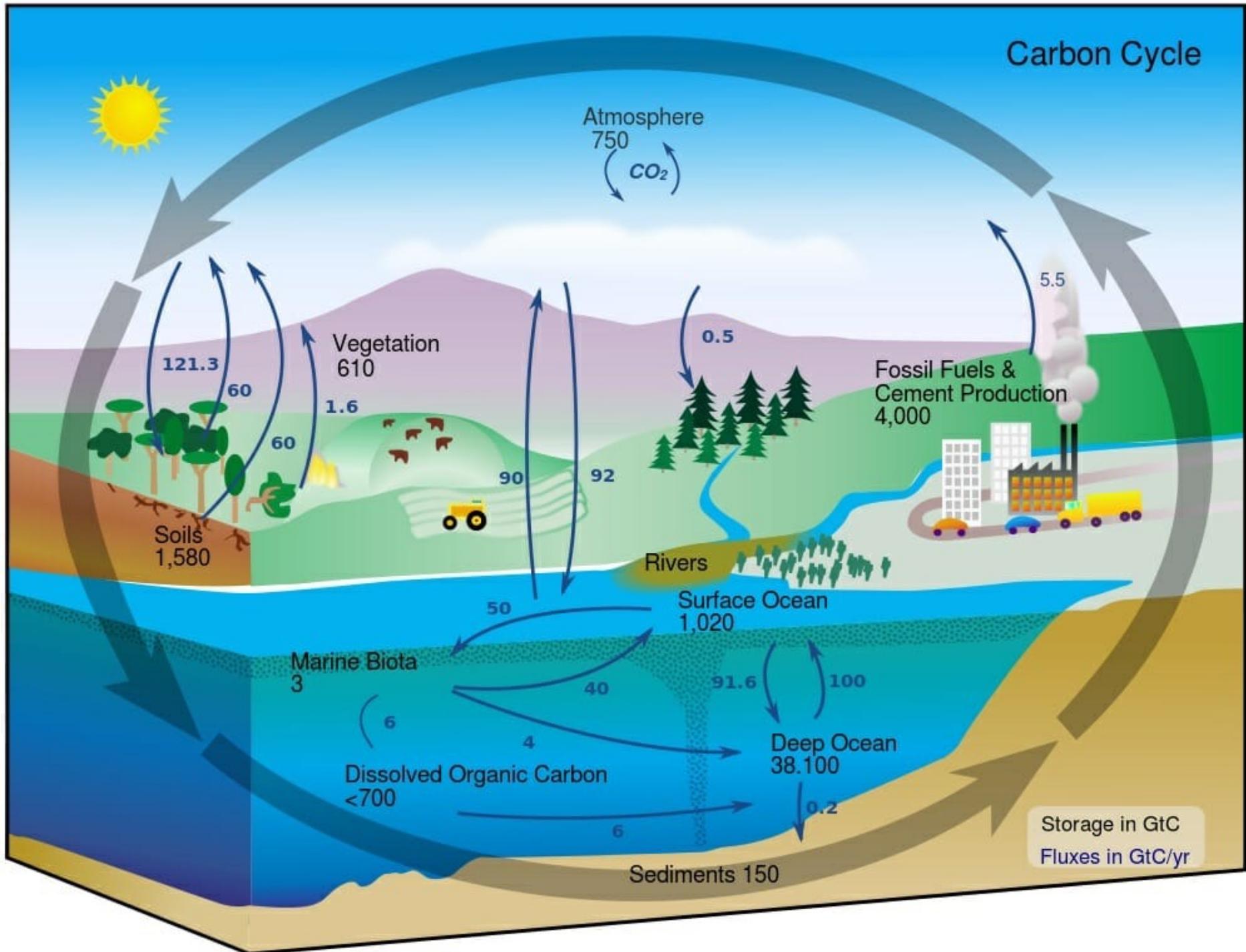
- It does this by studying movement and transformation of resources



# Ecology studies movement and transformation of resources

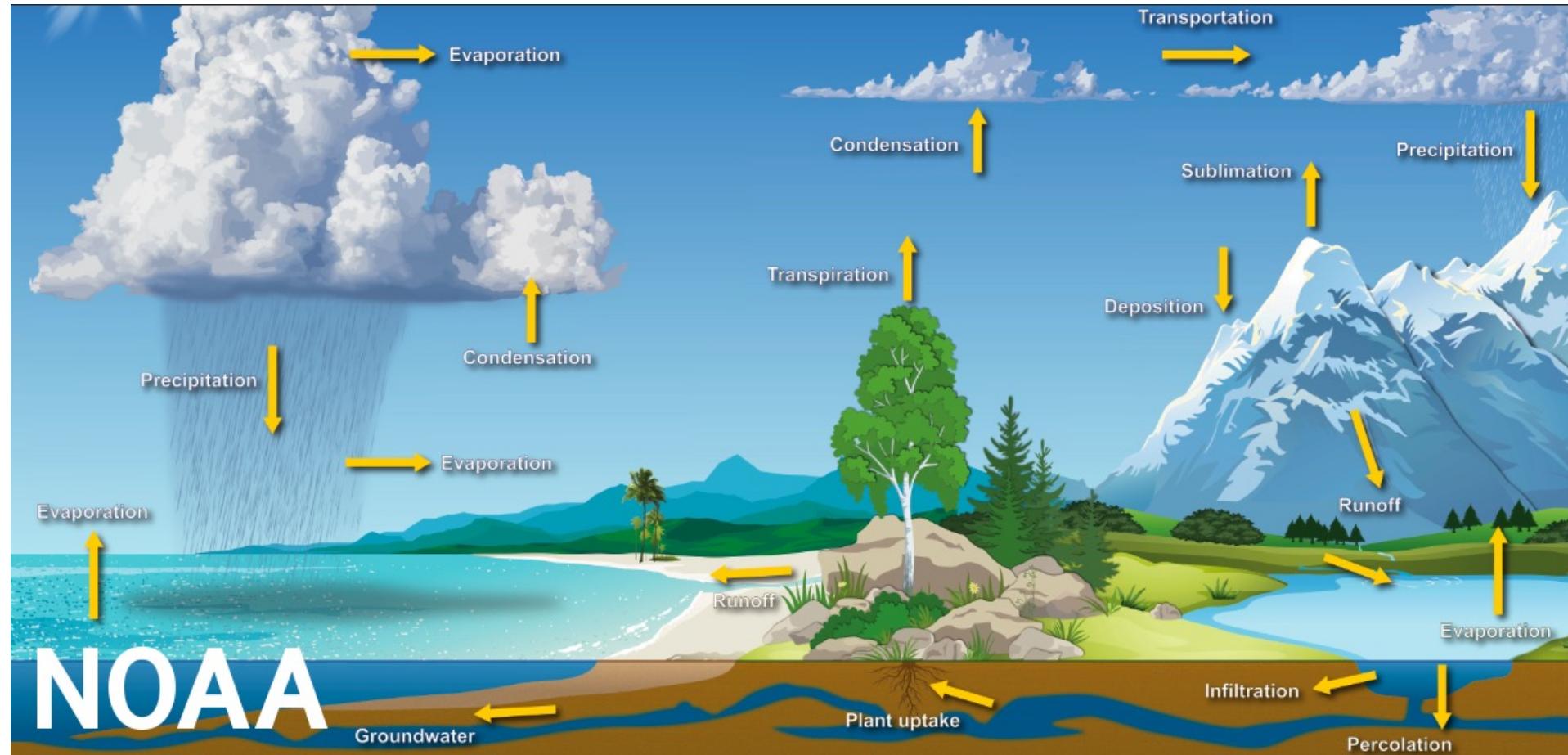
- E.g. Carbon
  - CO<sub>2</sub>, biomass, dissolved organic carbon (DOC), particulate organic carbon (POC) ...
- E.g. Water
  - Oceans, lakes, rivers, clouds, sea ice ...
- E.g. Phosphorus
  - Fertilizer, sediments, minerals, bones ...
- E.g. Nitrogen
  - N<sub>2</sub>(g), ammonia, nitrate, nitrate ...

## Carbon Cycle



# Ecology studies movement and transformation of resources

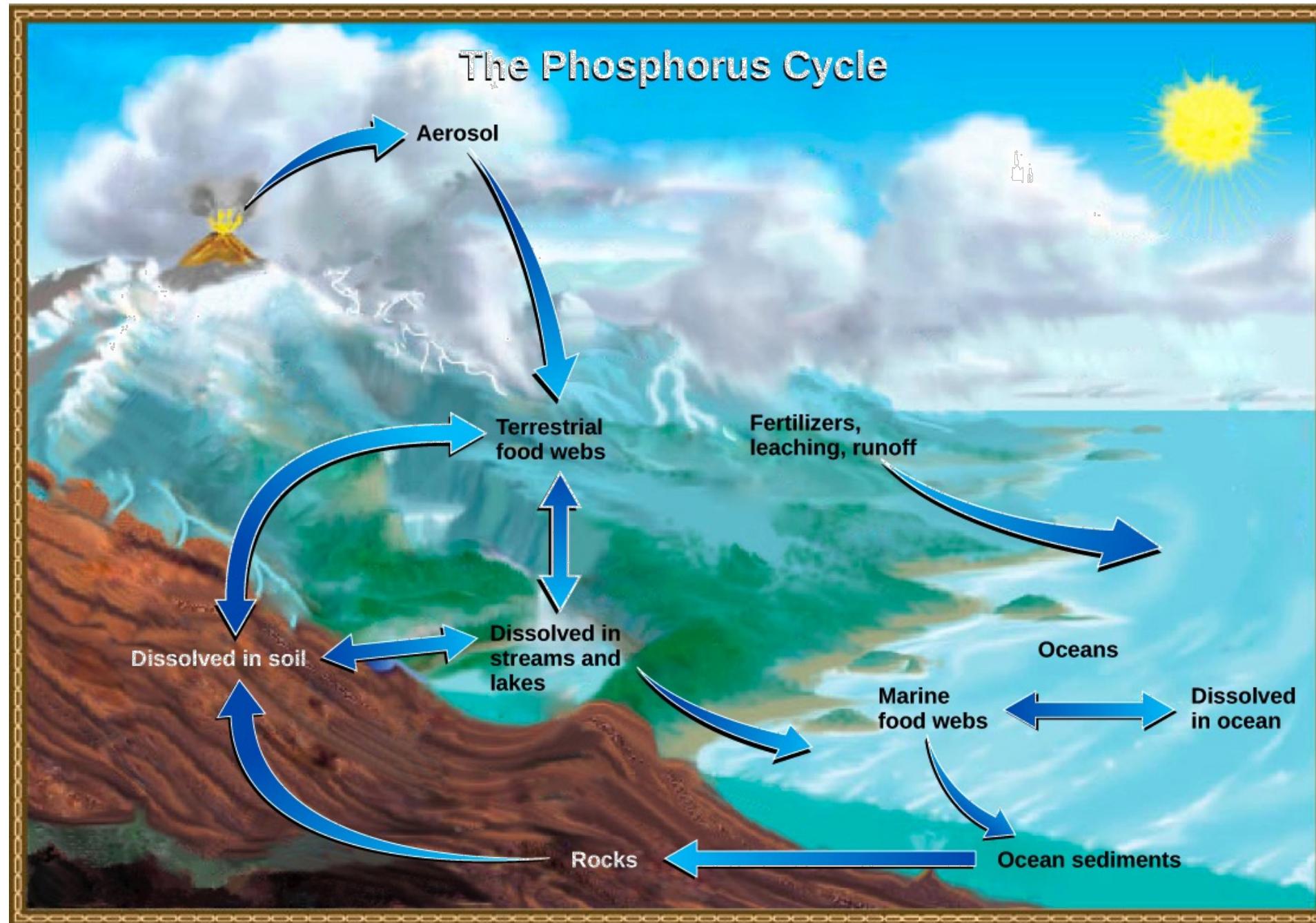
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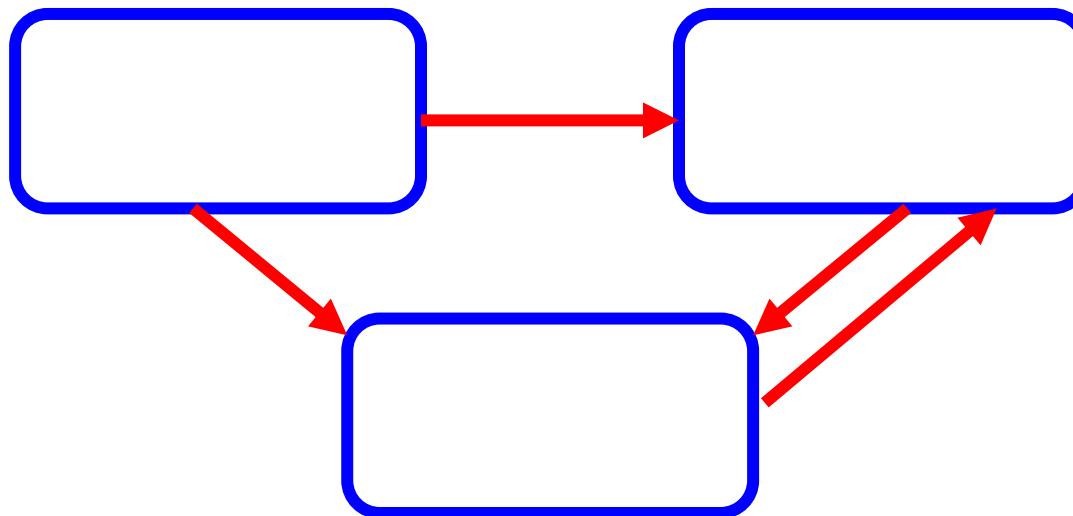
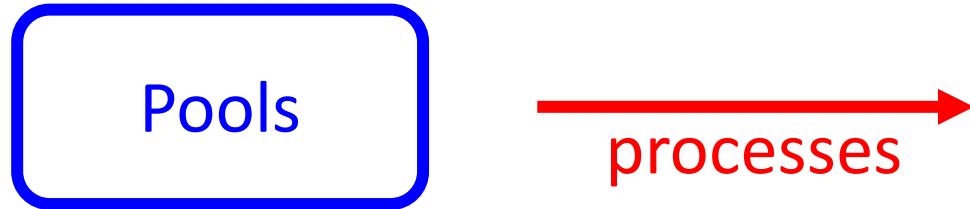
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- E.g. Carbon
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- E.g. Phosphorus
  - Fertilizer, sediments, minerals, bones ...
- E.g. Nitrogen
  - N<sub>2</sub>(g), ammonia, nitrate, nitrate ...

# The Phosphorus Cycle



Generally...

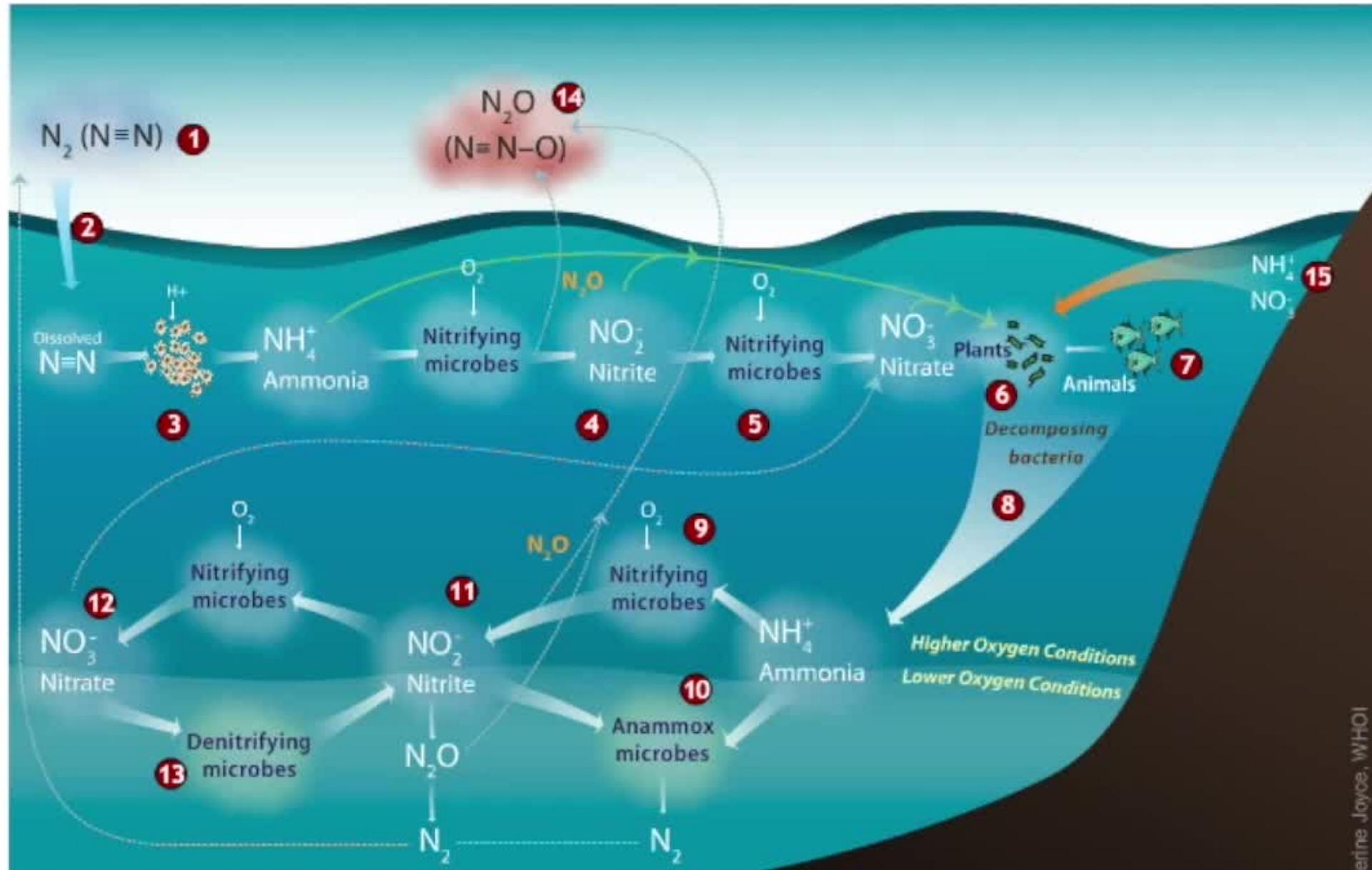


- Process rates are complicated functions of many variables
  - Which vary over time
  - Partial differential equations

# Ecology studies movement and transformation of resources

- E.g. Carbon
  - CO<sub>2</sub>, biomass, dissolved organic carbon (DOC), particulate organic carbon (POC) ...
- E.g. Water
  - Oceans, lakes, rivers, clouds, sea ice ...
- E.g. Phosphorus
  - Fertilizer, sediments, minerals, bones ...
- E.g. Nitrogen
  - N<sub>2</sub>(g), ammonia, nitrate, nitrate ...

# The Marine Nitrogen Cycle



If you understand the arrows, you can derive differential equations

$$\begin{aligned}\sigma_{N^*}^2 &= \left( \frac{\partial N^*}{\partial N} \sigma_N \right)^2 + \left( \frac{\partial N^*}{\partial P} \sigma_P \right)^2 \\ &\quad + \left( \frac{\partial N^*}{\partial r_{\text{nitr}}^{N:P}} \sigma_{r_{\text{nitr}}^{N:P}} \right)^2 + \left( \frac{\partial N^*}{\partial r_{\text{denitr}}^{N:P}} \sigma_{r_{\text{denitr}}^{N:P}} \right)^2 \\ &= \left( \frac{r_{\text{denitr}}^{N:P}}{r_{\text{denitr}}^{N:P} - r_{\text{nitr}}^{N:P}} \sigma_N \right)^2 \\ &\quad + \left( \frac{r_{\text{denitr}}^{N:P}}{r_{\text{denitr}}^{N:P} - r_{\text{nitr}}^{N:P}} r_{\text{nitr}}^{N:P} \sigma_P \right)^2 \\ &\quad + \left( \frac{r_{\text{denitr}}^{N:P}}{r_{\text{denitr}}^{N:P} - r_{\text{nitr}}^{N:P}} \right. \\ &\quad \left. \left( -P + \frac{N - r_{\text{nitr}}^{N:P} P + \text{const}}{r_{\text{denitr}}^{N:P} - r_{\text{nitr}}^{N:P}} \right) \sigma_{r_{\text{nitr}}^{N:P}} \right)^2 \\ &\quad + \left( (N - r_{\text{nitr}}^{N:P} P + \text{const}) \right. \\ &\quad \left. \frac{-r_{\text{nitr}}^{N:P}}{(r_{\text{denitr}}^{N:P} - r_{\text{nitr}}^{N:P})^2} \sigma_{r_{\text{denitr}}^{N:P}} \right)^2.\end{aligned}$$

GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 11, NO. 2, PAGES 235–266, JUNE 1997

Global patterns of marine nitrogen fixation  
and denitrification

Nicolas Gruber

Climate and Environmental Physics, Physics Institute, University of Bern, Bern, Switzerland

Jorge L. Sarmiento

Program in Atmospheric and Oceanic Sciences, Princeton University, Princeton, New Jersey



Means partial derivative, i.e.  
life just got very hard

If you understand the arrows, you can derive differential equations

$$\Theta(x; x_c, \lambda) \equiv \frac{1}{2}(1 - \tanh(\frac{x - x_c}{\lambda}))$$

[nature](#) > [articles](#) > [article](#)

Article | [Published: 13 February 2019](#)

## Convergent estimates of marine nitrogen fixation

[Wei-Lei Wang](#), [J. Keith Moore](#), [Adam C. Martiny](#) & [François W. Primeau](#) 

[Nature](#) **566**, 205–211 (2019) | [Cite this article](#)

12k Accesses | 109 Citations | 65 Altmetric | [Metrics](#)

Trig???  
Seriously???

*Change over time = a rate, we do those with derivatives → PDEs*

# So here's the thing about PDEs

- Best case: very very hard
- Worst case: impossible
- Or run computer models

# So here's the thing about PDEs

- Best case: very very hard
- Worst case: impossible
- Or run computer models
  - The only practical way
  - Estimate initial quantity in each pool at some starting time
  - Compute transfer in/out of each pool during next simulated day/hour/minute/??? using the PDEs
    - Repeat as long as you like
    - Always some error, which increases over time
    - But good computer models are very good

A photograph of a night sky filled with stars, with a body of water in the foreground showing bioluminescent blue-green waves under moonlight.

$10^{24}$  stars

$10^{29}$  bacteria

# Bacteria in the ocean



# Bacteria in the ocean

- Average concentration:  $10^6$  cells / ml (Whitman et al. 1998)
- Higher near land (nutrient runoff), near surface (photosynthesis)
- Lower at depth (no sunlight), in oligotrophic open ocean

# Bacteria in the ocean

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- Lower at depth (no sunlight), in oligotrophic open ocean

“The moment you sample ocean water,  
you have a big-data problem”

- PH

# But this is relatively new knowledge

- The old belief:
  - Green / turquoise / light blue = chlorophyll = life
    - Only in shallow water, near land
    - Cyanobacteria = phylum of photosynthesizing bacteria
    - Cyan: R=0, G=255, B=255
  - Dark blue = desert
    - The open ocean
    - Indigo: R=0, G=65, B=106

# But this is relatively new knowledge

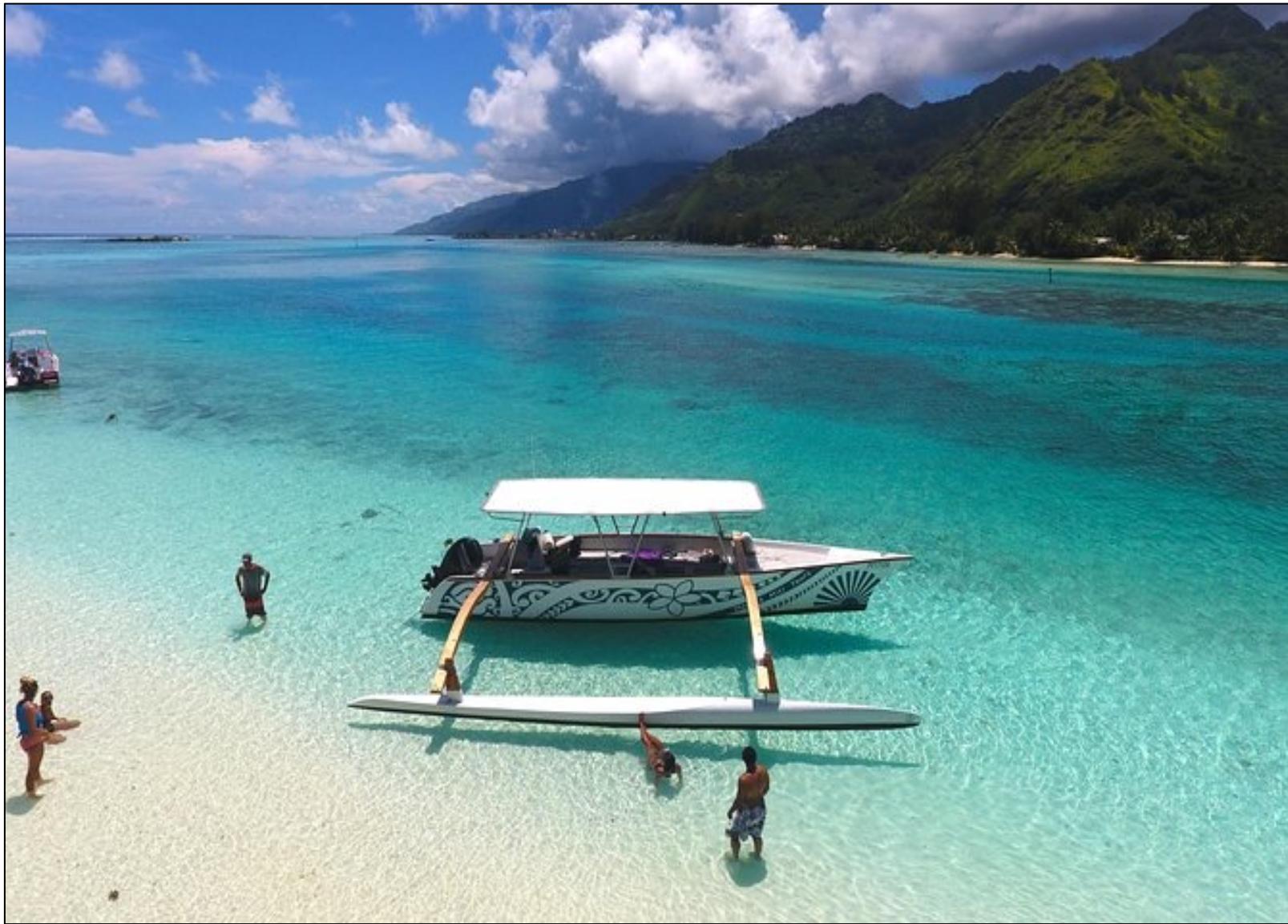
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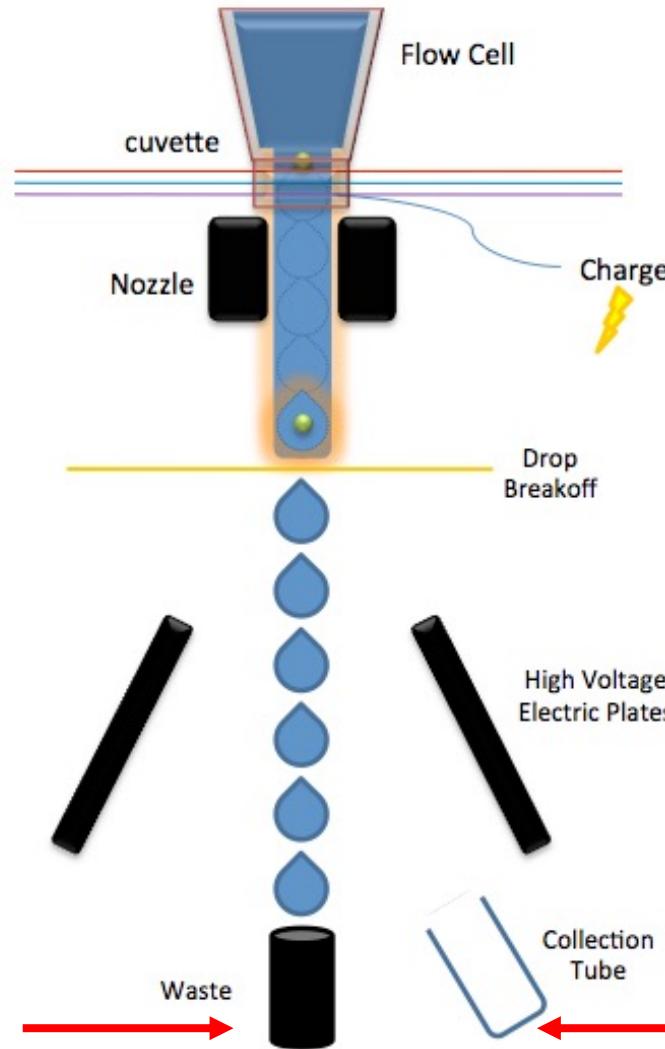


# Sallie (Penny) Chisholm



[https://www.ted.com/talks/penny\\_chisholm\\_the\\_tiny\\_creature\\_that\\_secretly\\_powers\\_the\\_planet#t-985653](https://www.ted.com/talks/penny_chisholm_the_tiny_creature_that_secretly_powers_the_planet#t-985653)

Flow Cytometers can separate cells based on size/shape/color

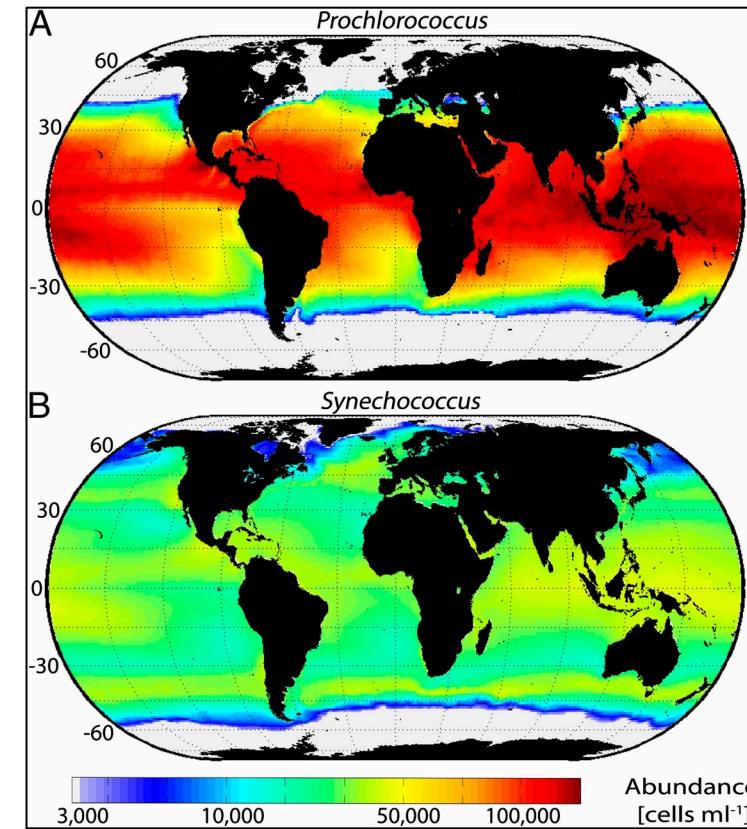


What you  
don't want

What you  
want

# Prof. Chisholm's great discovery

- Flow cytometers work on ships
- Genus *Prochlorococcus*
- A tiny cyanobacterium (photosynthesizer)
- Found in much of the open ocean except high northern and southern latitudes
- (*Synechococcus*: the previously known open-ocean tiny cyano ... note much lower abundance)



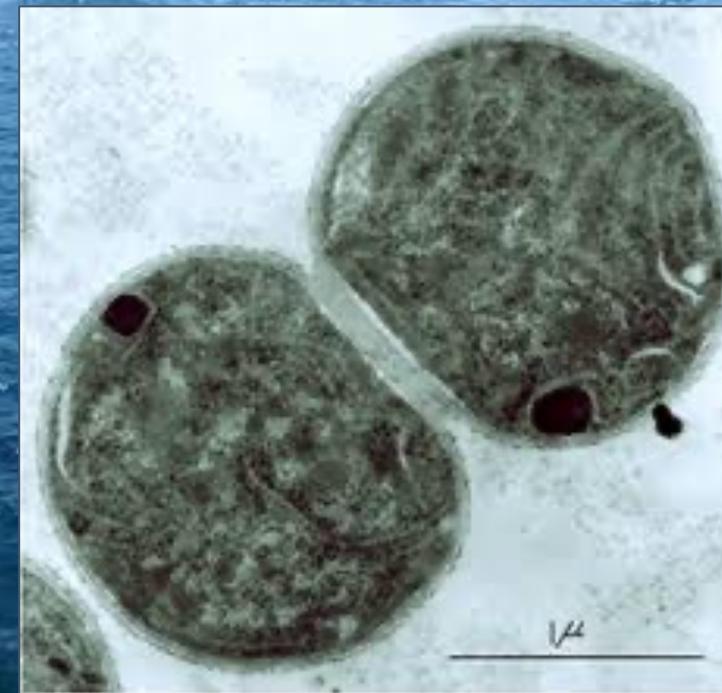
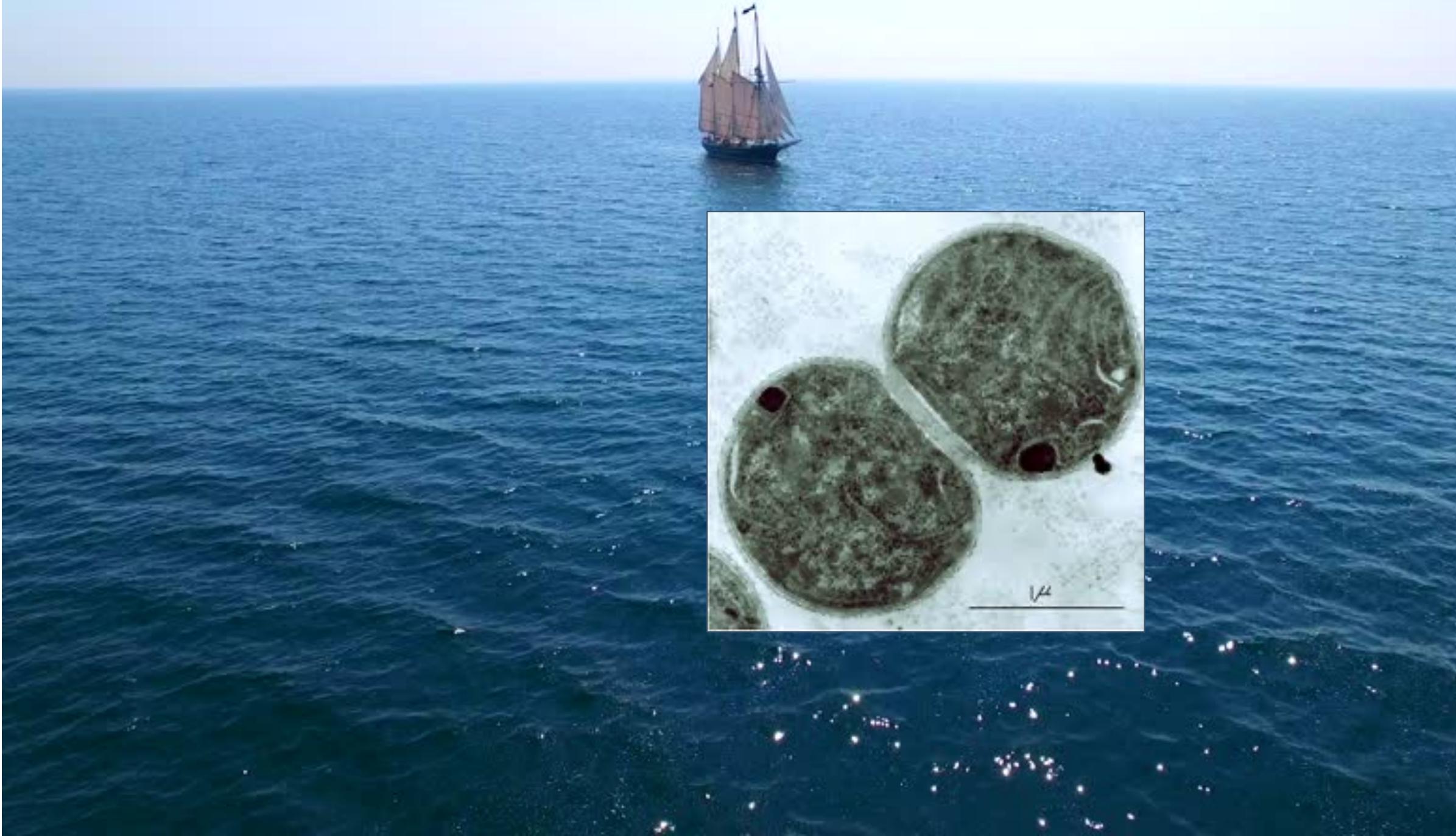
Flombaum et al. PNAS 2013

Link to article in note for this slide

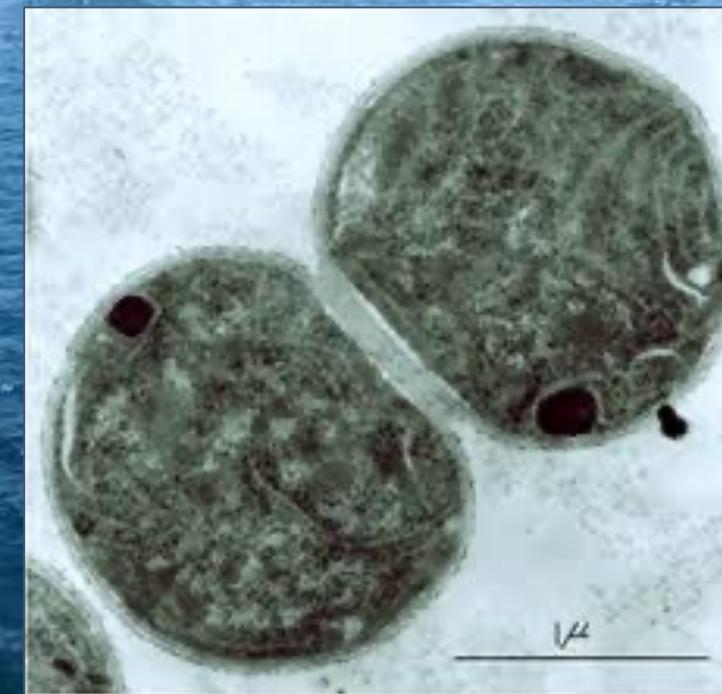
# So for a long time

- *Prochlorococcus* and *Synechococcus* were believed to be the main open-ocean bacteria.
- But the ecological budget didn't balance.
- We need metagenomic studies to figure it out





500,000,000 km<sup>2</sup>

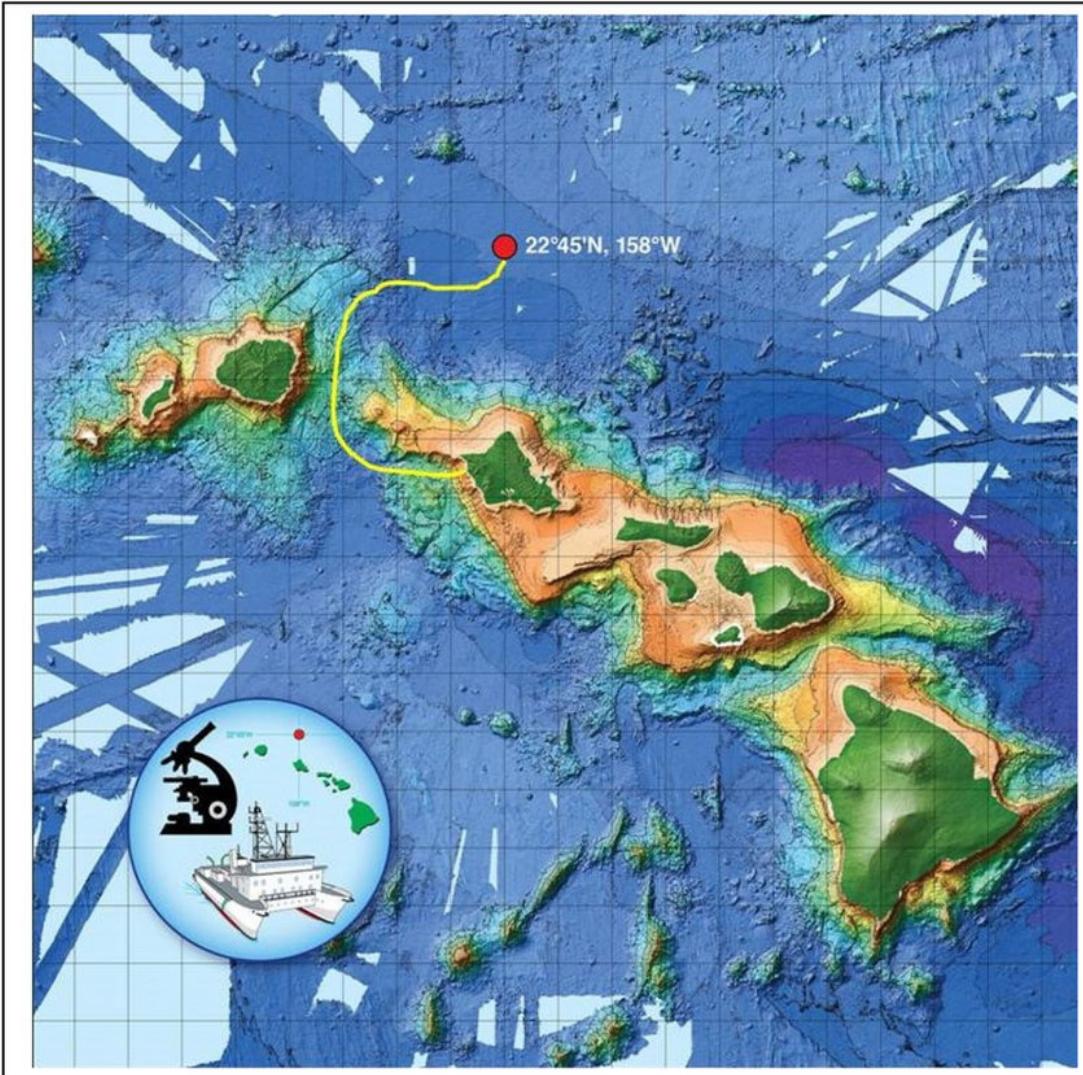


500,000,000 km<sup>2</sup>



.000000000004 m<sup>2</sup>

# A metagenomic search for marine nitrogen fixers at Station Aloha



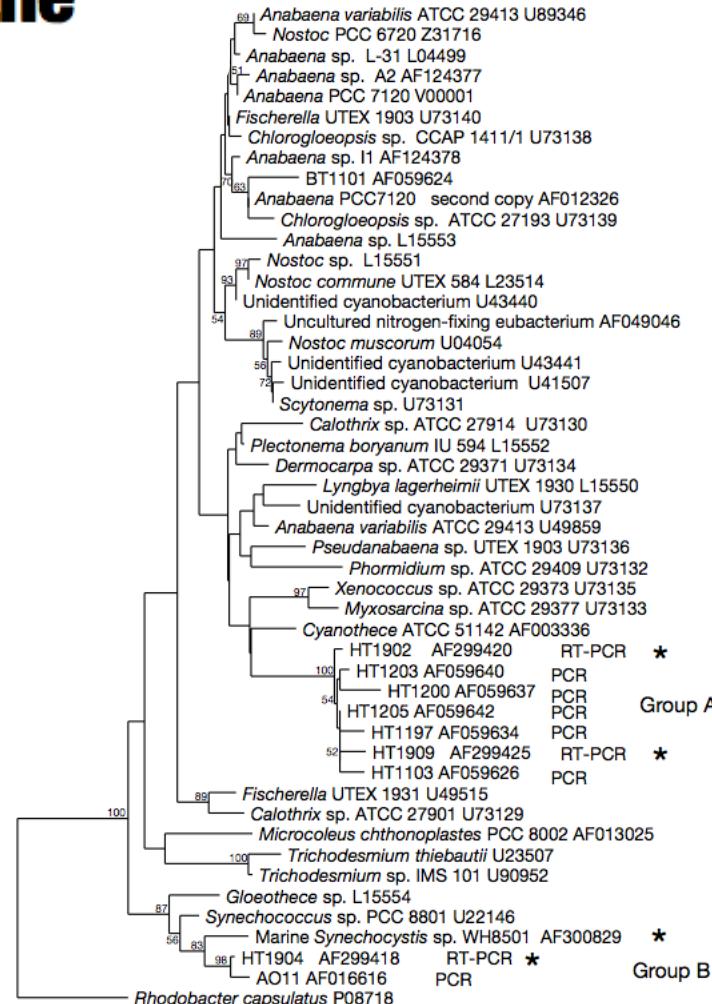
- Sample oligotrophic ocean water
- PCR with *nifH* primers

# Discovery of unicellular marine nitrogen fixers

## Unicellular cyanobacteria fix N<sub>2</sub> in the subtropical North Pacific Ocean

Jonathan P. Zehr\*, John B. Waterbury†, Patricia J. Turner\*,  
Joseph P. Montoya‡, Enoma Omoregie\*, Grieg F. Steward\*,  
Andrew Hansen§ & David M. Karl§

-- Nature, 2001



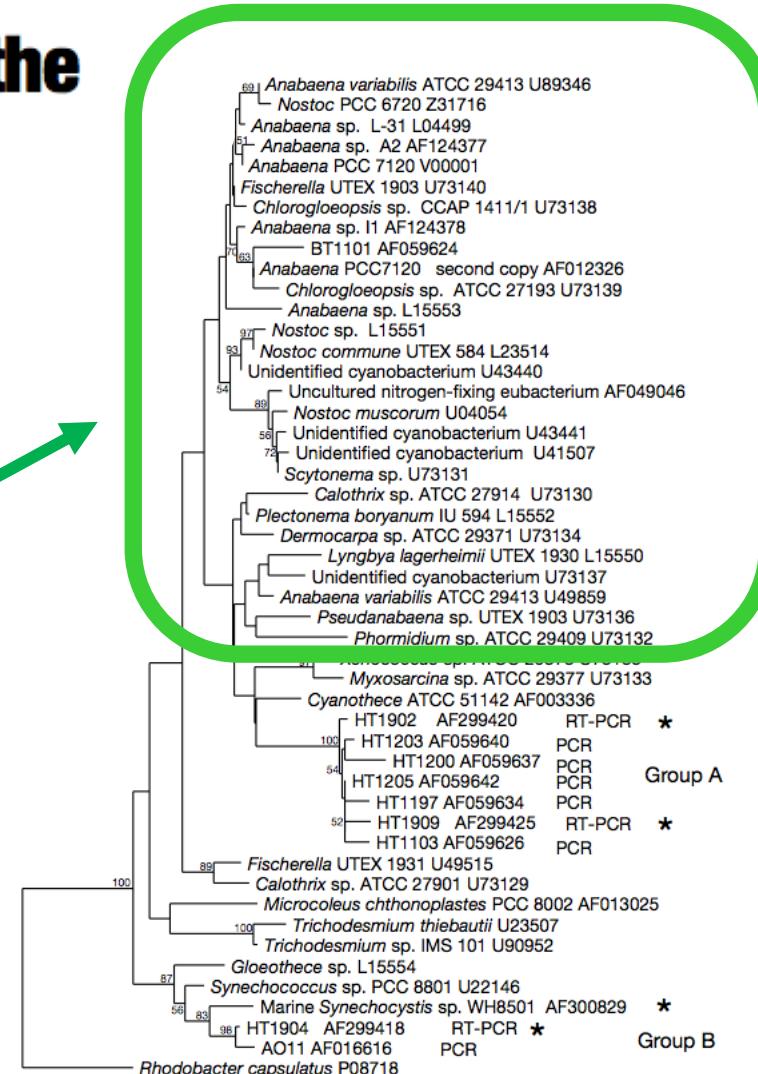
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-- Nature, 2001

Already known to science  
(note the scientific names)



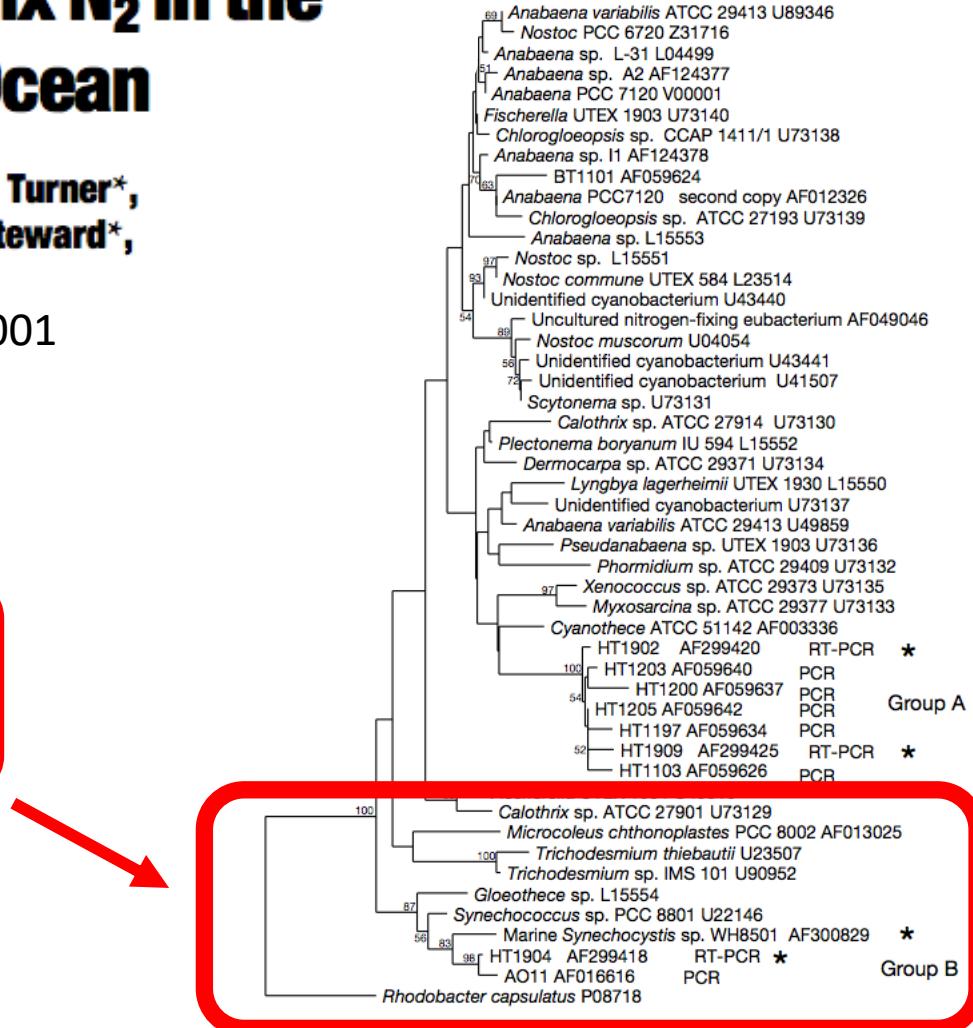
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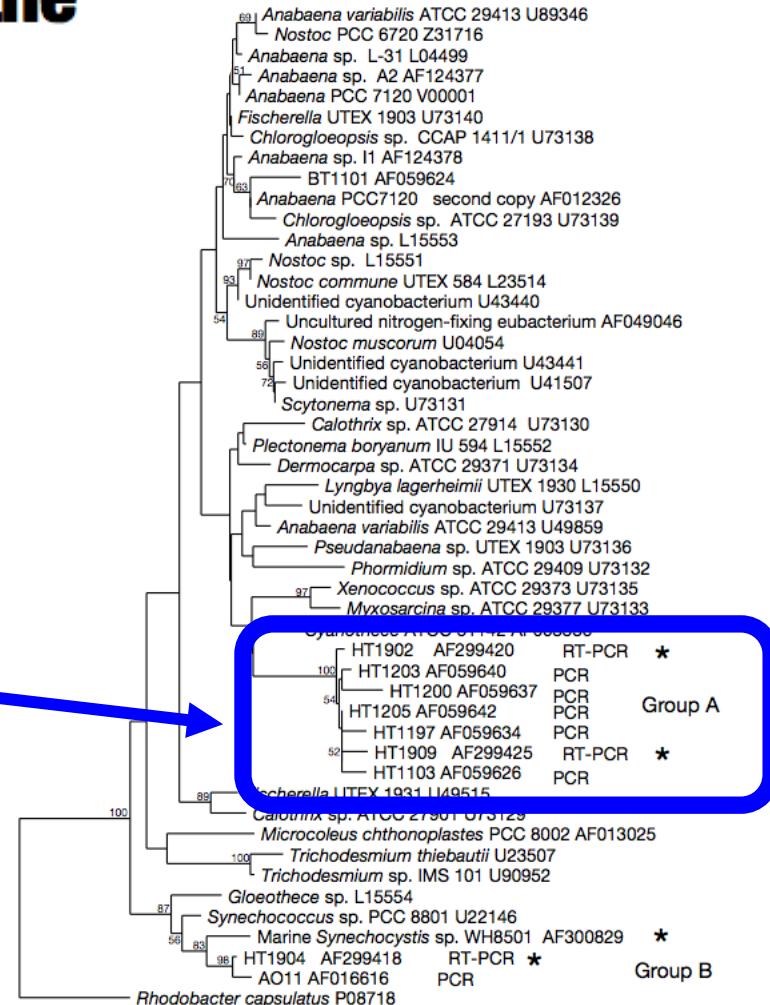
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-- Nature, 2001

Unknown to science  
(no exact BLAST hits)

“Group A”



# Discovery of unicellular marine nitrogen fixers

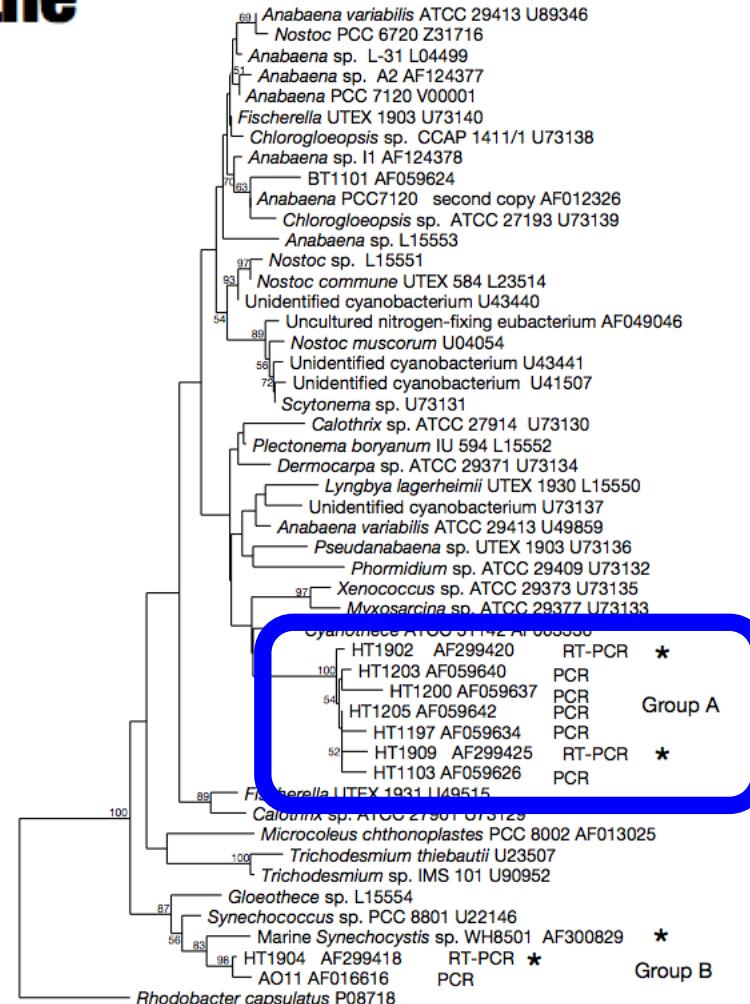
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-- Nature, 2001

# UCYN-A

Unicellular Cyanobacteria, Group A



# Ok, now what?

## Questions

- What's the genetic potential of UCYN-A?
- Is UCYN-A widespread?
- If it's widespread, why was it unknown for so long?

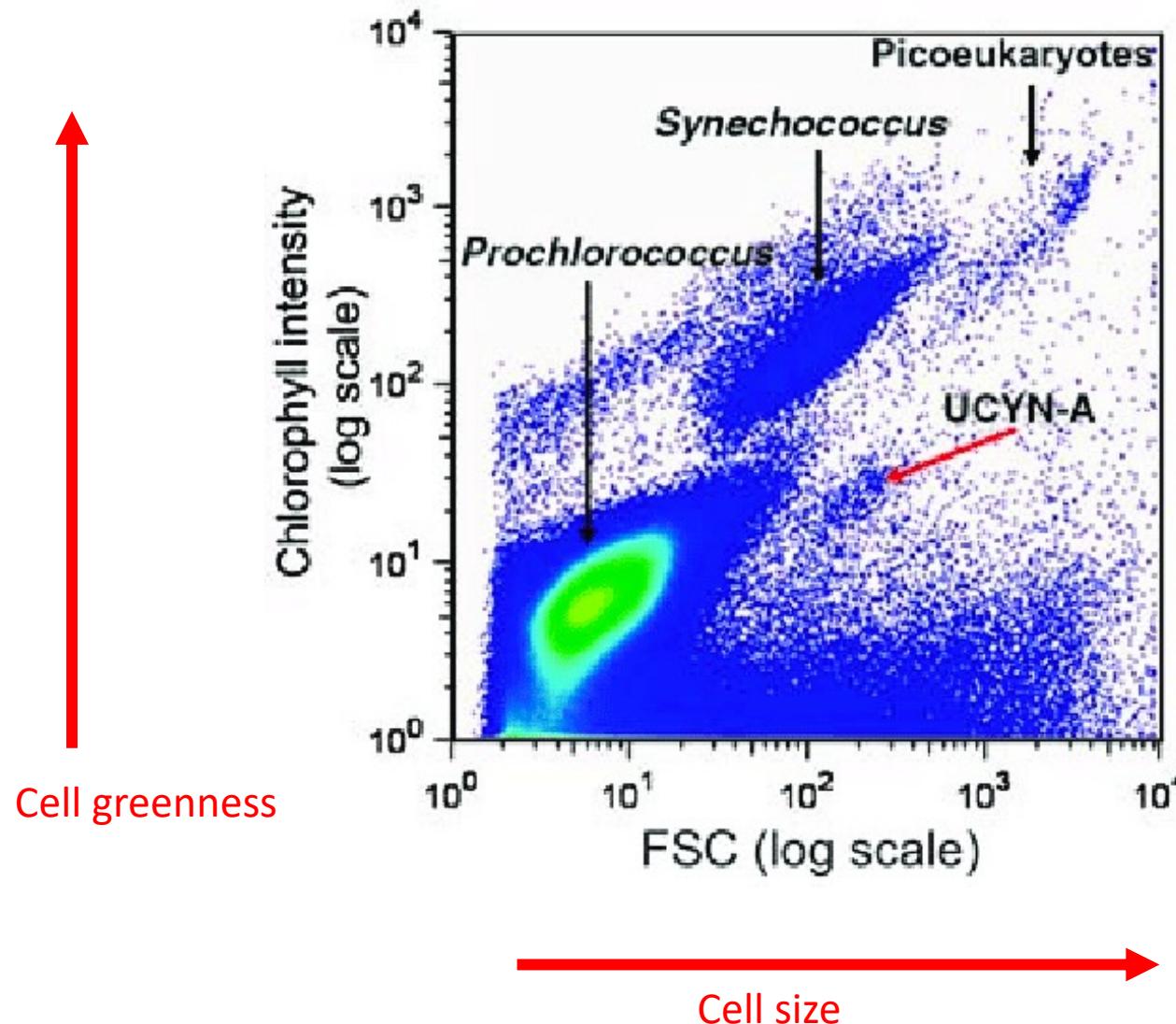
## Techniques

- Assembly and annotation.
- Look in different environments (e.g. coastal)
- ???????????

# The genetic potential of UCYN-A

1. Get some cells (so far only had *nifH* molecules)
2. Extract and amplify all the DNA
3. Assemble
4. Annotate

# Step 1: Get some cells

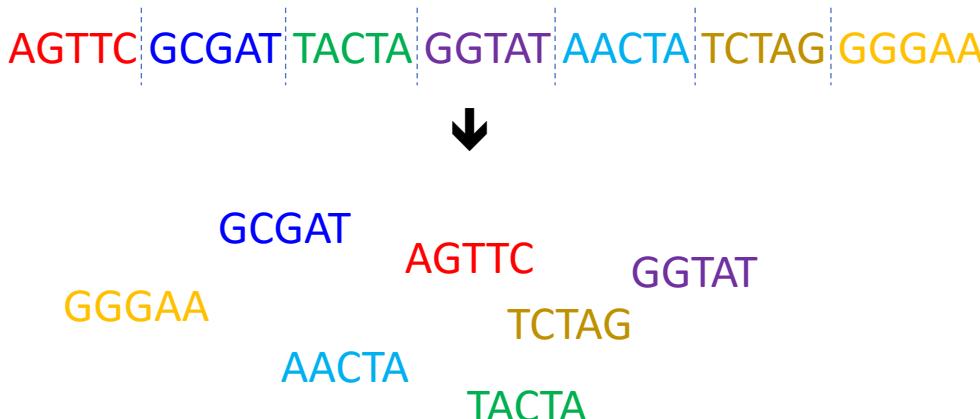


This is a *cytogram*

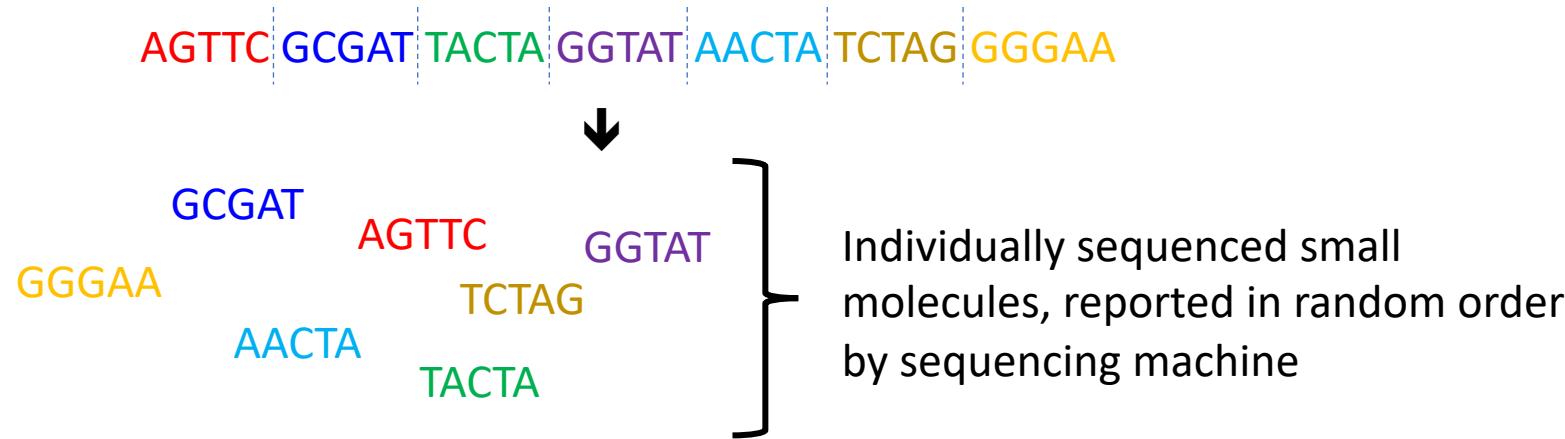
- 1.A Generate cytogram
- 1.B Exhaustive PCR search for UCYN-A *nifH*
- 1.C Isolate UCYN-A cells

# Step 2: Extract and amplify all the DNA

- Sequence tech, especially at that time, couldn't determine nucleotide sequences longer than a few hundred base pairs (bp).
- Microbial chromosomes are at least 1M bp.
- There are “restriction” enzymes that cut DNA into right-sized chunks.
- What if you use them, and sequence every chunk? (pretend chunk size = 5).



## Step 2: Extract and amplify all the DNA



- What's the right order?
- The data gives no clues.
- There are 5,039 wrong orders *just in this tiny example!*
- What if you use them, and sequence every chunk?  
(pretend chunk size = 5)
- There has to be a better way

# Step 2, the better way: Shotgun Sequencing

Shotgun pellets fragment targets in random patterns and sizes



## Step 2, better way: Shotgun Sequencing (tiny example)

Original

ACGGTACTCGATCGATCGGC

Copies

ACGGTACTCGATCGATCGGC  
ACGGTACTCGATCGATCGGC  
ACGGTACTCGATCGATCGGC  
ACGGTACTCGATCGATCGGC

After  
Shotgun  
Fragmentation

ACG     GTACTCGATC     GATCGGC  
ACGGTACTC     GATCGATCGGC  
ACGGT     ACTCGATCGAT     CGGC  
ACGGTACTCG     ATCGATCGGC

*Now we have overlapping fragments: a 1-dimensional jigsaw puzzle*

*Wait, where were we?*

## The genetic potential of UCYN-A

1. Get some cells (so far only had *nifH* molecules) **ok**
  2. Extract and amplify all the DNA
  3. Assemble
  4. Annotate
- 
- Shotgun sequencing  
plus assembly of the  
jigsaw puzzle

# The genetic potential of UCYN-A

1. Get some cells (so far only had *nifH* molecules)
2. Extract and amplify all the DNA
3. Assemble
4. Annotate 
  - Use software tools to find gene boundaries in assembled chromosome
  - For each of those genes...
    - Use BLAST to find highly similar sequences
    - of known function
    - in closely related organisms

So they did that ...

REPORTS

# Globally Distributed Uncultivated Oceanic N<sub>2</sub>-Fixing Cyanobacteria Lack Oxygenic Photosystem II

Jonathan P. Zehr,<sup>1\*</sup> Shellie R. Bench,<sup>1</sup> Brandon J. Carter,<sup>1</sup> Ian Hewson,<sup>1</sup> Faheem Niazi,<sup>2</sup> Tuo Shi,<sup>1</sup> H. James Tripp,<sup>1</sup> Jason P. Affourtit<sup>2</sup>

Biological nitrogen (N<sub>2</sub>) fixation is important in controlling biological productivity and carbon flux in the oceans. Unicellular N<sub>2</sub>-fixing cyanobacteria have only recently been discovered and are widely distributed in tropical and subtropical seas. Metagenomic analysis of flow cytometry–sorted cells shows that unicellular N<sub>2</sub>-fixing cyanobacteria in “group A” (UCYN-A) lack genes for the oxygen-evolving photosystem II and for carbon fixation, which has implications for oceanic carbon and nitrogen cycling and raises questions regarding the evolution of photosynthesis and N<sub>2</sub> fixation on Earth.

# Ok, now what?

## Questions

- What's the genetic potential of UCYN-A?
- Is UCYN-A widespread?
- If it's widespread, why was it unknown for so long?

## Techniques

- Assembly and annotation.
- Look in different environments (e.g. coastal)
- ???????????

So they did that ...

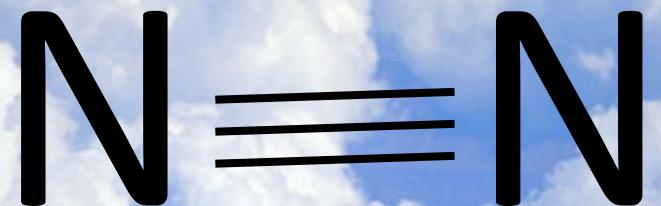
REPORTS

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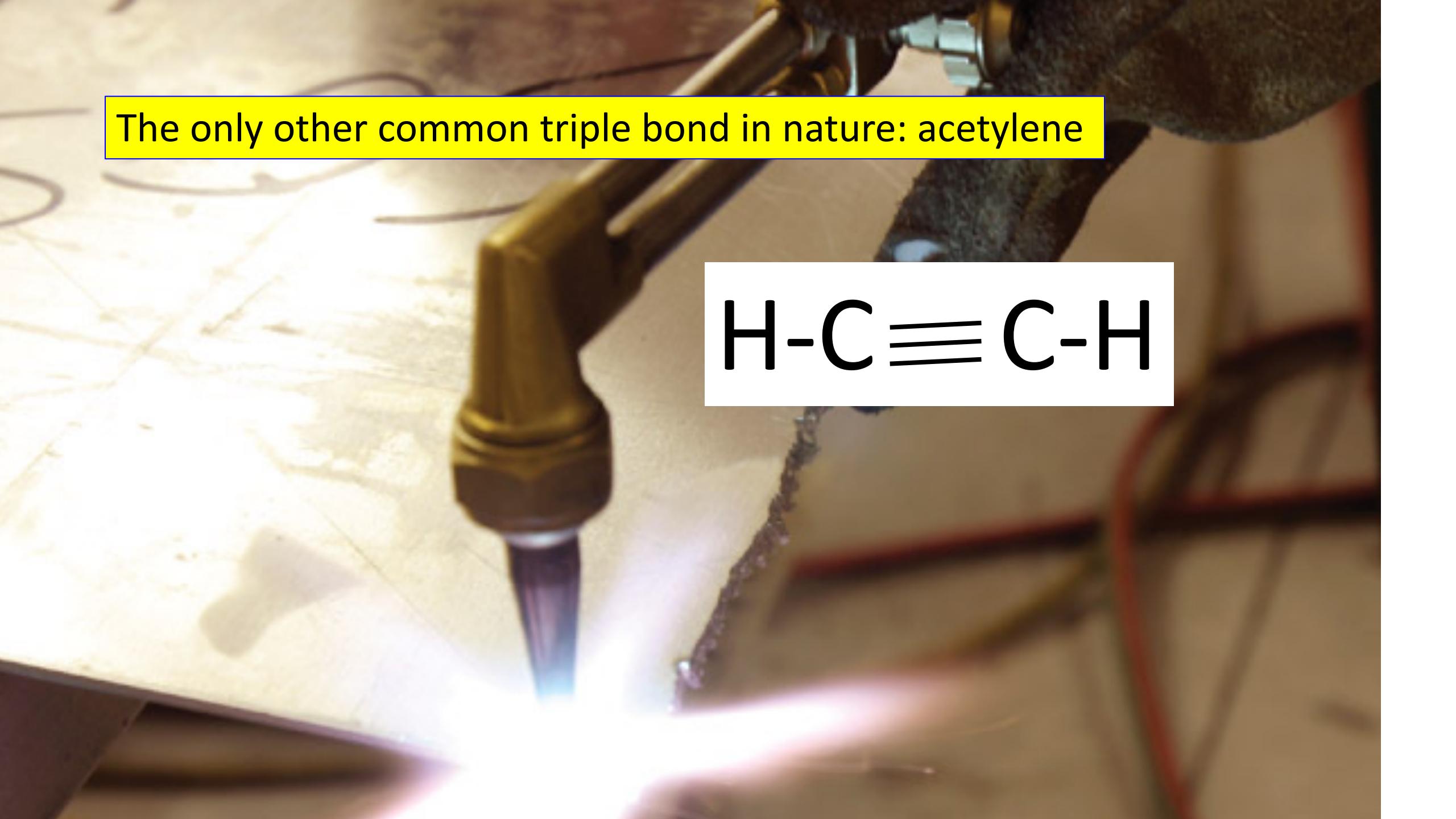
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# But that's just weird!



Nitrogen fixation needs a *lot* of energy to break that triple bond

A close-up photograph of a person's hands using a welding torch on a piece of metal. Sparks are visible as they strike the metal. The background is blurred.

The only other common triple bond in nature: acetylene



# Nitrogenase enzyme



High energy cost → most (?all?) nitrogen fixers are cyanobacteria  
(make their own energy)

How can the world's most common nitrogen fixer not harvest its own energy? All other ways to get energy are much less efficient.

REPORTS

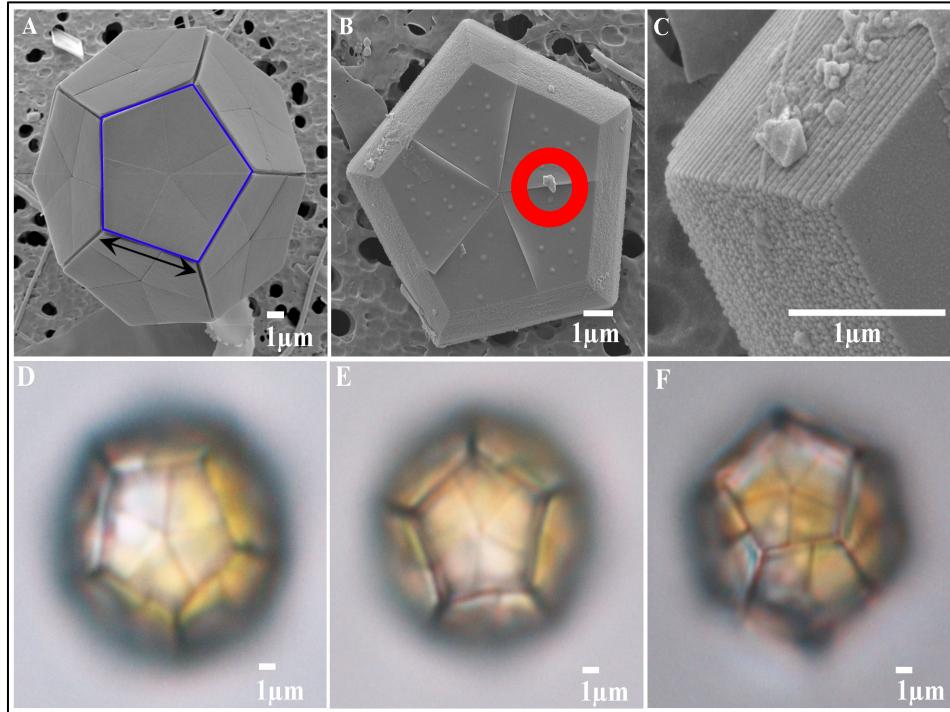
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# Jon Zehr's big insight

- It's a symbiont!
- Partner harvests light (photosystem II), provides energy to UCYN-A.
- UCYN-A provides reduced nitrogen to partner.
- If it's nestled inside its partner, no wonder it's so hard to find.



Source: Hagino et al., PLoS ONE 2013

# Ok, now what?

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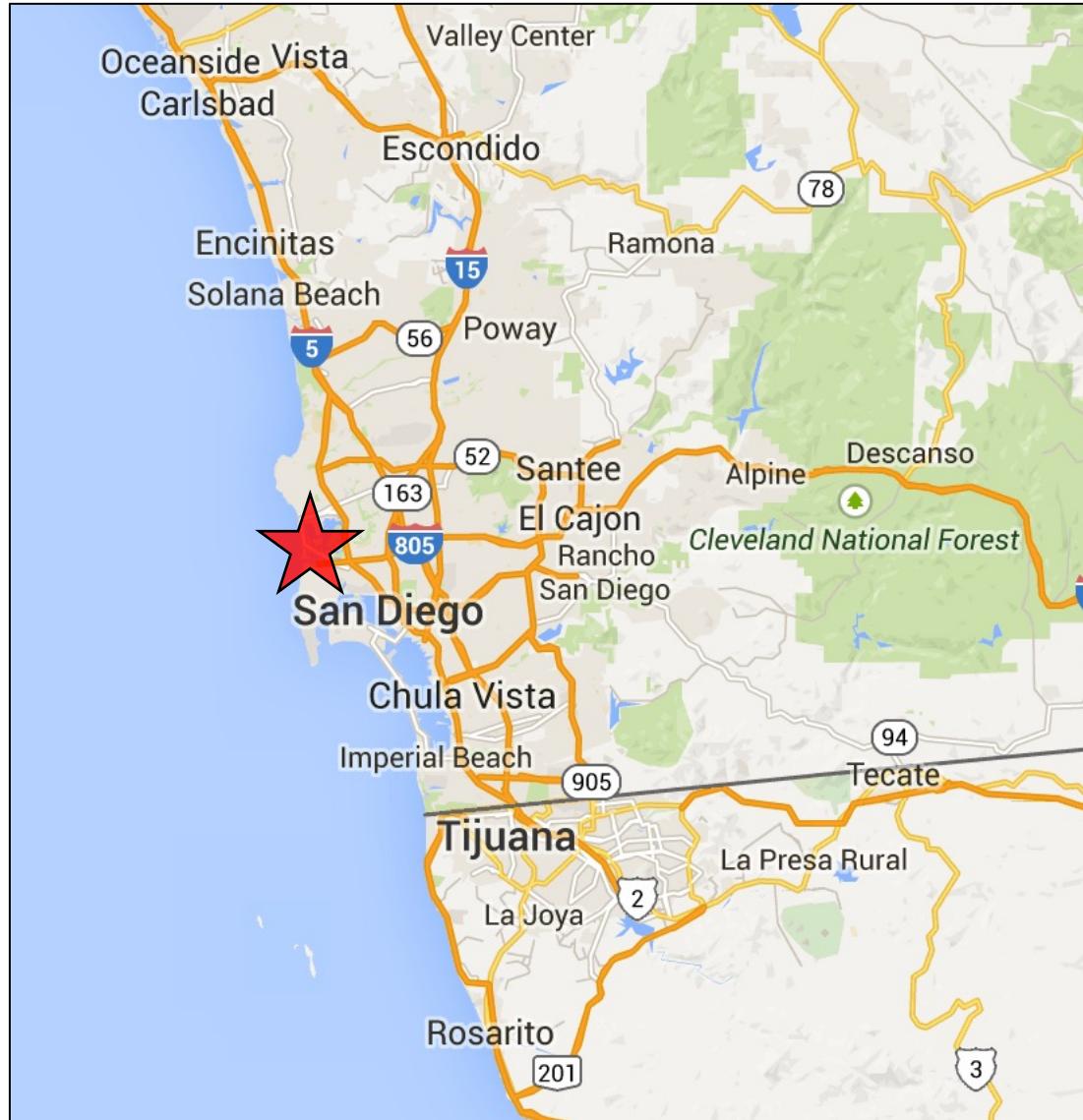
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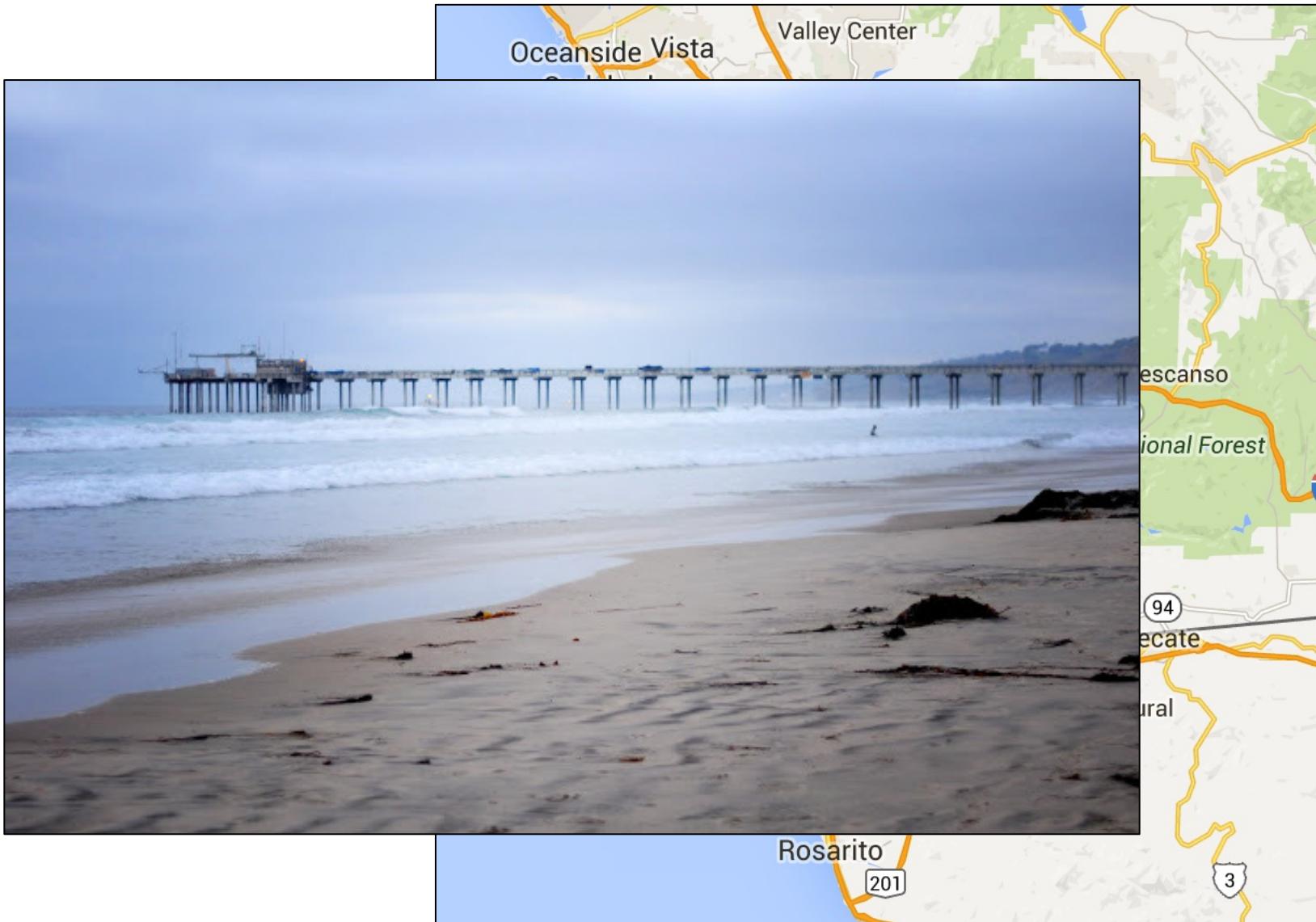
# Is UCYN-A really widespread?

- If UCYN-A is globally distributed, it must be present in other kinds of environment.
- Station Aloha is oligotrophic open ocean.
- Coastal environments are very different:
  - Shallower water.
  - Richer diversity.
  - Land runoff provides nutrients, other organics, human products.
  - Expect a differently adapted strain of UCYN-A.
- Scripps Pier (La Jolla, CA) is an easy coastal sampling point.

# Coastal Sampling Site: Scripps Pier, La Jolla, CA



# Coastal Sampling Site: Scripps Pier, La Jolla, CA



## ORIGINAL ARTICLE

# Comparative genomics reveals surprising divergence of two closely related strains of uncultivated UCYN-A cyanobacteria

Deniz Bombar<sup>1,4,5</sup>, Philip Heller<sup>2,4</sup>, Patricia Sanchez-Baracaldo<sup>3</sup>, Brandon J Carter<sup>1</sup> and Jonathan P Zehr<sup>1</sup>

<sup>1</sup>*Ocean Sciences Department, University of California, Santa Cruz, CA, USA;* <sup>2</sup>*Biomolecular Engineering Department, University of California, Santa Cruz, CA, USA* and <sup>3</sup>*Schools of Biological and Geographical Sciences, University of Bristol, Bristol, UK*

“UCYN-A2”

# Today: Many successful searches for known and new UCYN-A strains



ORIGINAL RESEARCH  
published: 05 April 2018  
doi: 10.3389/fmicb.2018.00554



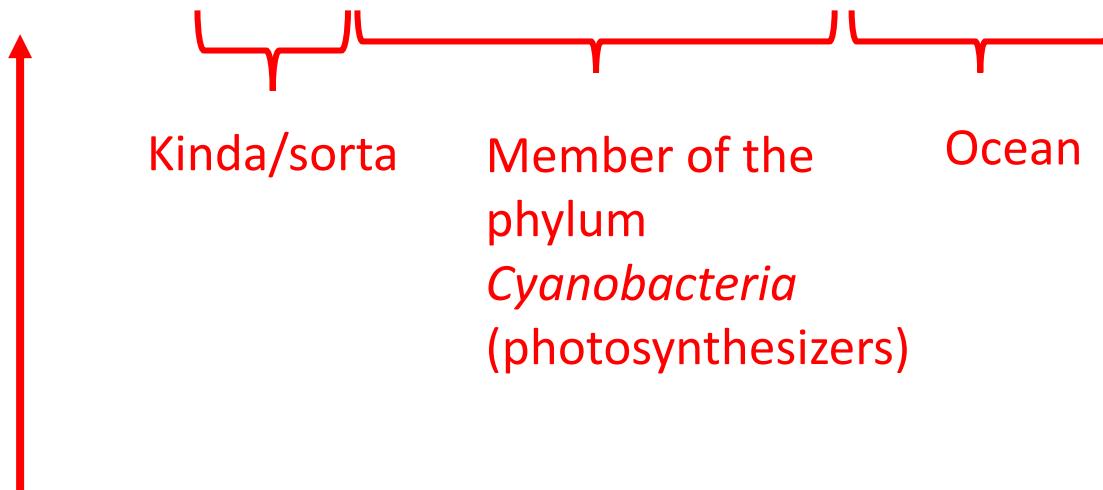
## Distributions and Abundances of Sublineages of the N<sub>2</sub>-Fixing Cyanobacterium *Candidatus Atelocyanobacterium thalassa* (UCYN-A) in the New Caledonian Coral Lagoon

Britt A. Henke<sup>1\*</sup>, Kendra A. Turk-Kubo<sup>1</sup>, Sophie Bonnet<sup>2</sup> and Jonathan P. Zehr<sup>1</sup>

<sup>1</sup> Department of Ocean Sciences, University of California, Santa Cruz, Santa Cruz, CA, United States, <sup>2</sup> IRD, MIO, UM 110 – IRD Centre of Noumea, Aix-Marseille University, University of South Toulon Var, CNRS/INSU, Noumea, France

# Today: A scientific name has been assigned

- *Candidatus Atelocyanobacterium Thalassa*



Prokaryote,  
Well characterized,  
Not cultured

- Nobody likes it, we still call it UCYN-A

# The UCYN-A Team (Zehr Lab, UCSC, 2011)



# The UCYN-A Team (Zehr Lab, UCSC, 2011)

Jon Zehr  
(PI)

Jim Tripp  
(assembly,  
1<sup>st</sup> strain)



# The UCYN-A Team (Zehr Lab, UCSC, 2011)

Deniz  
Bombar  
and some  
other guy  
(assembly,  
2<sup>nd</sup> strain)



# The UCYN-A Team (Zehr Lab, UCSC, 2011)



Shellie  
Bench  
(anno-  
tation,  
1<sup>st</sup> strain)

Anne  
Thomp-  
son  
(iden-  
tified the  
symbi-  
ont)

Brandon  
Carter  
(flow  
cytome-  
try)