

Geobiology 2013 Lecture 13

Evolution and Radiation of Photosynthetic Organisms

Cyanobacteria → Algae

Symbioses (algae, lichens, corals, some foraminifera,
radiolarians)

Vascular plants

Cyanobacteria in the Modern Ocean

Materials for this lecture are from the following websites where more detailed information can be obtained:

<http://tolweb.org>; <http://www.ucmp.berkeley.edu/>

<http://www.seaweed.ie/> <http://www.algaebase.org/>

Readings: Stanley Ch3 49-77 + later sections p. 222-228, p337-347 and 456-60.
Delwiche C.F. Am. Nat. 1999. Vol. 154, pp. S164–S177, 1999; Keeling Trends in
Eco & Evo 20, 2005; Heckman et al, Science 293, 1129, 2002.

Geobiology Lecture 12

Quiz April 8th

on the topic:

**Extreme climates in Earth's history including
'Snowball Earth'**

Geobiology Lecture 12

Reading:

Stanley Ch3 49-77 + later sections p. 221-228, p337-347 and 456-60.

Delwiche 1999 American Naturalist

Keeling et al, TRENDS in Ecology and Evolution Vol.20 No.12
December 2005

Need to Know:

The role of symbiosis in the Evolution Of Photosynthetic Eukaryotes

**Brief history of plant kingdom; basic characteristics of algae (incl. acritarchs) ; primitive vascular plants (mosses, ferns, lycopods), conifers and angiosperms.
An example of interrelationship between plant & animal divergences**

Who are the major groups of marine primary producers today?

Which groups dominated at different periods in the geologic past?

How is plankton growth recorded in rocks –and oil? (subsequent lecture)

What factors influence the completeness of the fossil record of marine plankton?

How has long-term ecological succession of marine plankton affected the evolution of other organisms and biogeochemical cycles?

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Marine Primary Producers

Today, 2 major groups:

Acquired photosynthesis by secondary endosymbiosis

Were preceded by red/green algae & prokaryotic phototrophs

Left a rich body & molecular fossil record

Rose to ecological prominence relatively recently

Picocyanobacteria
Prochlorococcus
Marine *Synechococcus*

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Chl a+c Phytoplankton
Diatoms
Dinoflagellates
Coccolithophorids

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CYANOBACTERIA

Two kinds cyanobacteria from the Bitter Springs Fm (850Ma), a chert from the Amadeus Basin central Australia. On the left is a colonial chroococcalean form, and on the right is the filamentous *Palaeolyngbya*.

Morphologies in the group have remained much the same for billions of years, and they may leave **chemical fossils** behind as well, in the form of breakdown products of lipids.

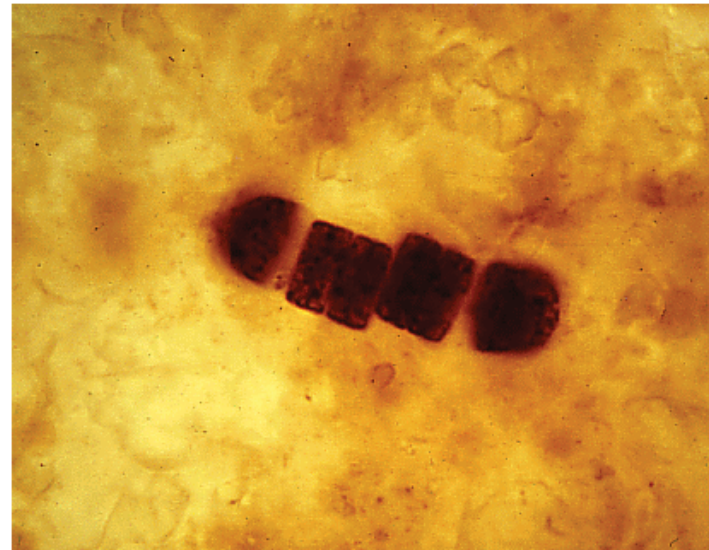
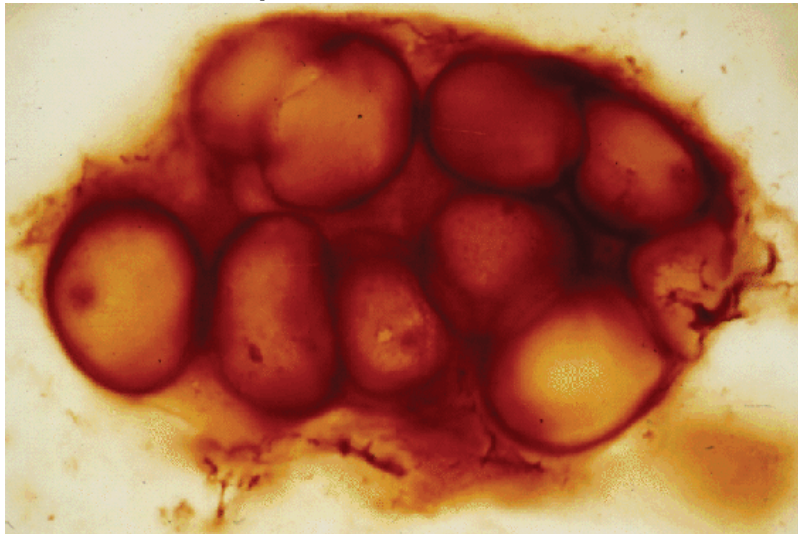


Image courtesy of ucmp.berkeley.edu. Used with permission.

Stromatolites & Cyanobacterial Mats



Precambrian stromatolites
Siyeh Formation, Glacier Nat'l Park
Courtesy NPS

Stromatolitic bioherm, 800Ma
Central Aust. R Summons



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Cyanobacterial photosynthesis in the oceans: the origins and significance of divergent light-harvesting strategies

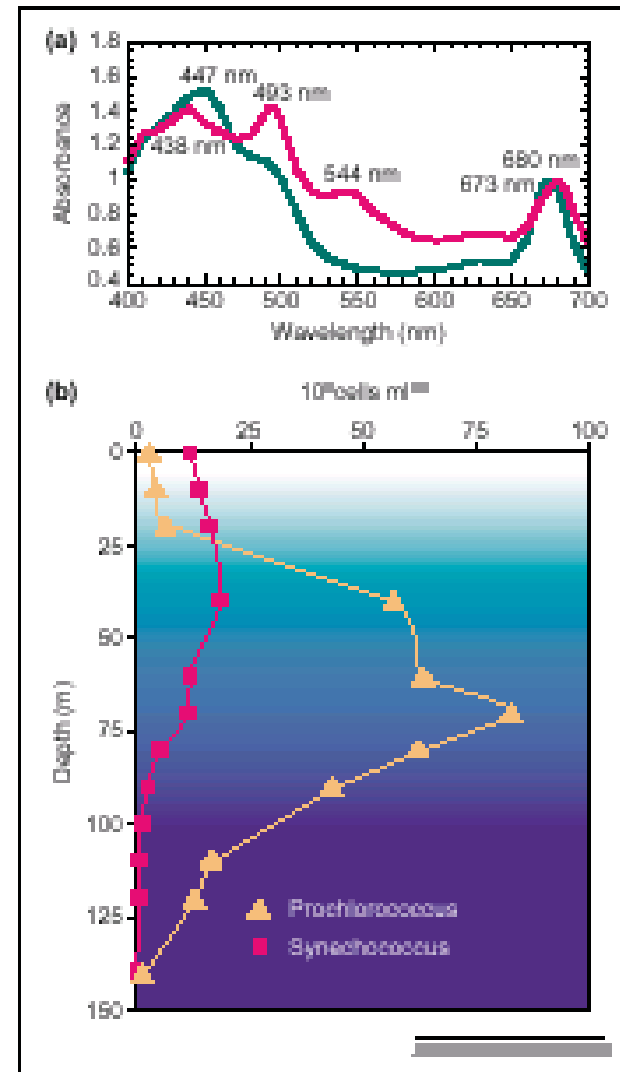
Claire S. Ting, Gabrielle Rocap, Jonathan King and Sallie W. Chisholm

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Blue

Green

Red



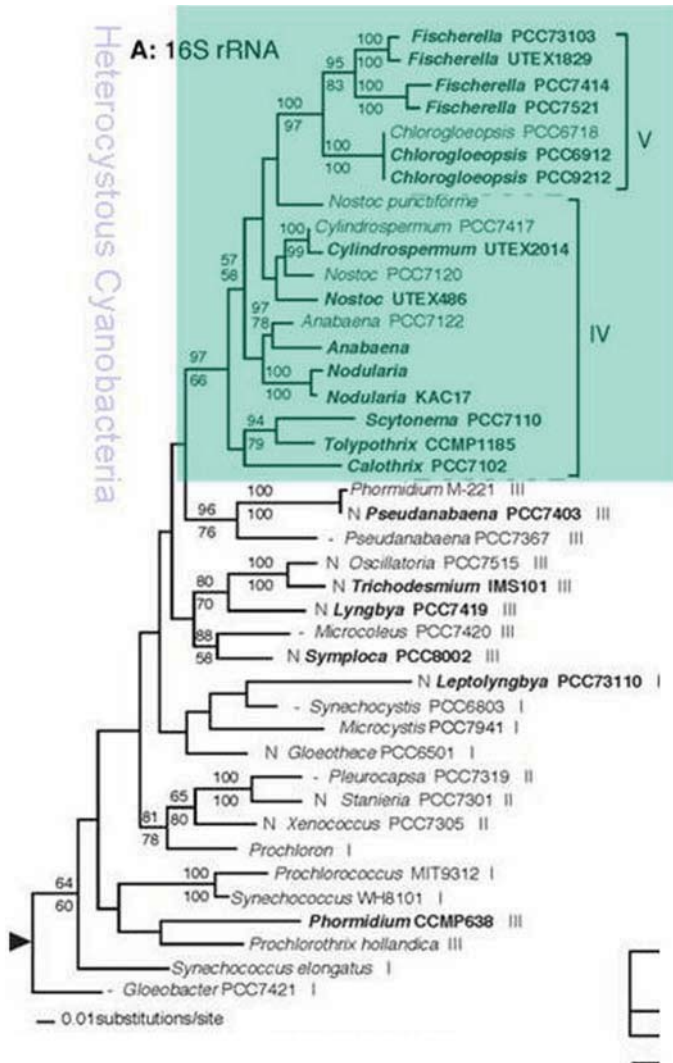
Red light
Blue-Gr. light

Blue light

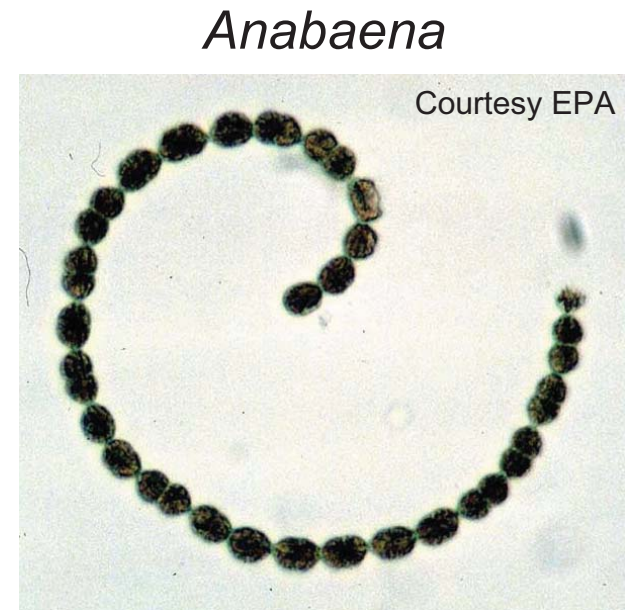
Cyanobacteria, Mesoproterozoic and Modern

Heterocysts/
Akinetes

Archaeoellipsoides

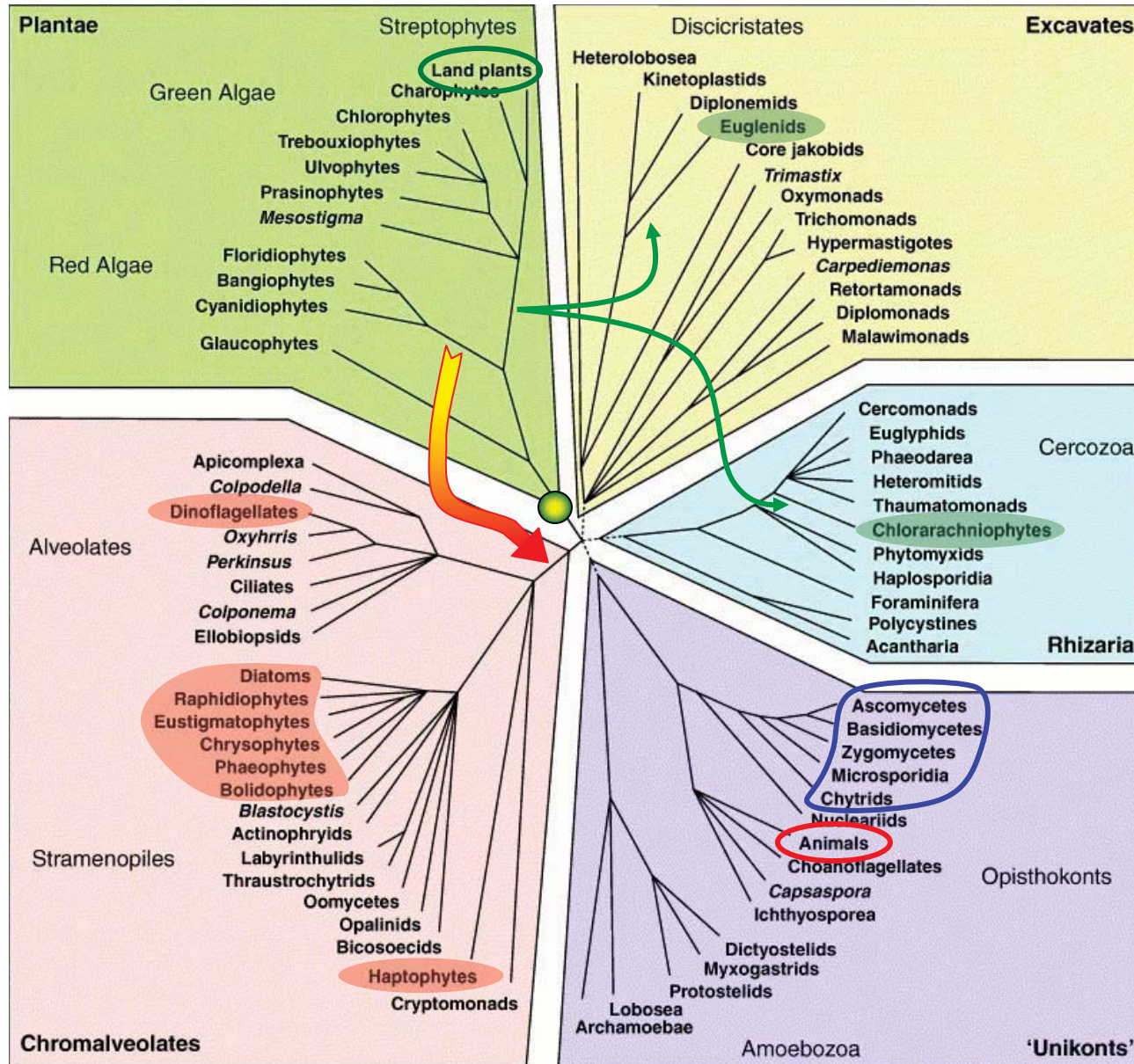


Courtesy of National Academy of Sciences, U. S. A. Used with permission. Source: Fig. 1a in Tomitani, Akiko, et al. "The Evolutionary Diversification of Cyanobacteria: Molecular-phylogenetic and paleontological perspectives." *PNAS* 103 (2006): 5442-5447. © 2006 National Academy



Eukaryote Diversity & Chloroplast Endosymbiosis

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<http://www.sciencedirect.com>.
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TRENDS in Ecology & Evolution

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Please see Fig. 3 in Heckman, Daniel S., et al.
“Early Colonization of Land by Fungi and Plants.”
Science 293 (August 10, 2001): 1129-1133.

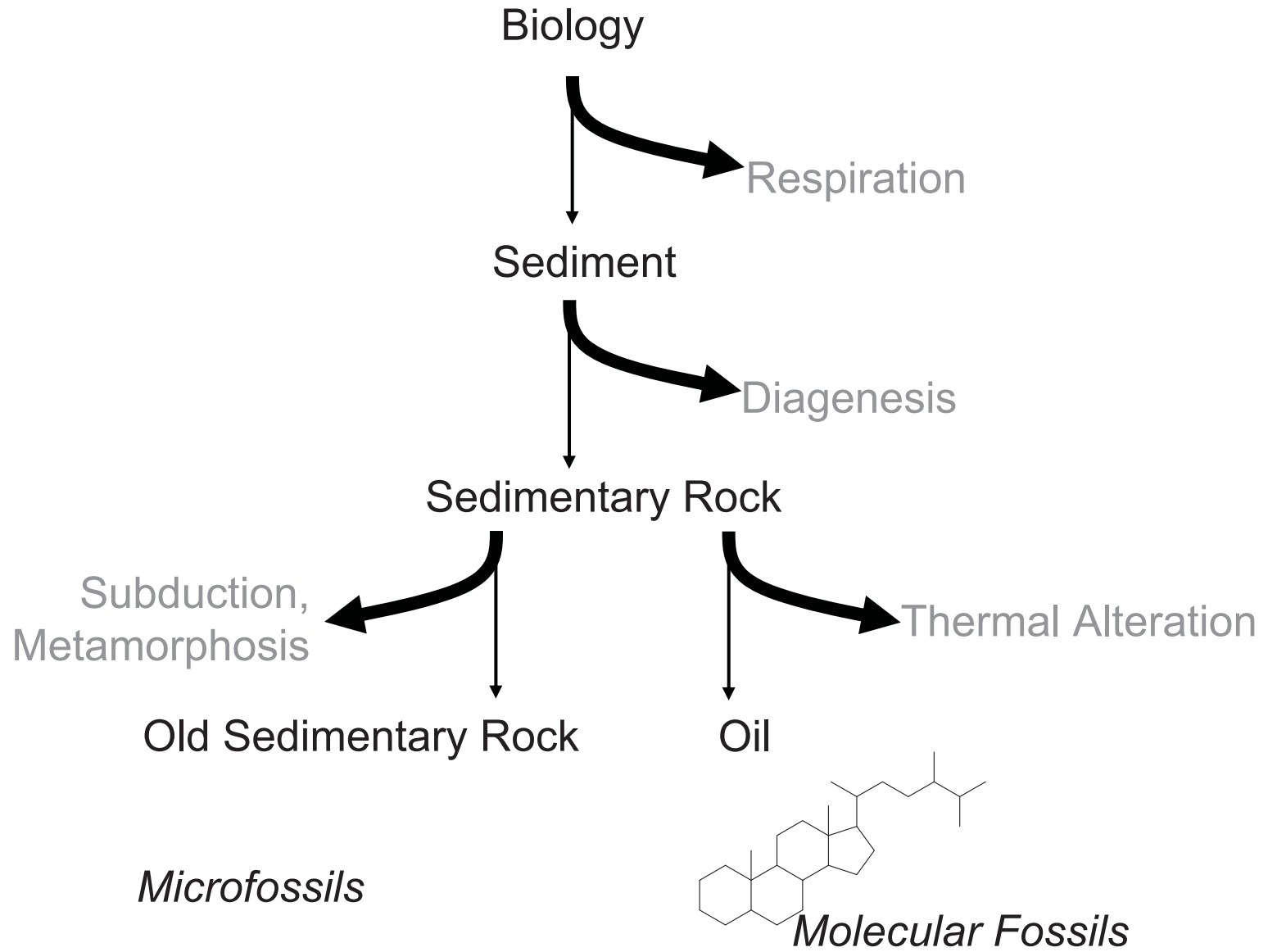
Plankton Biogeography

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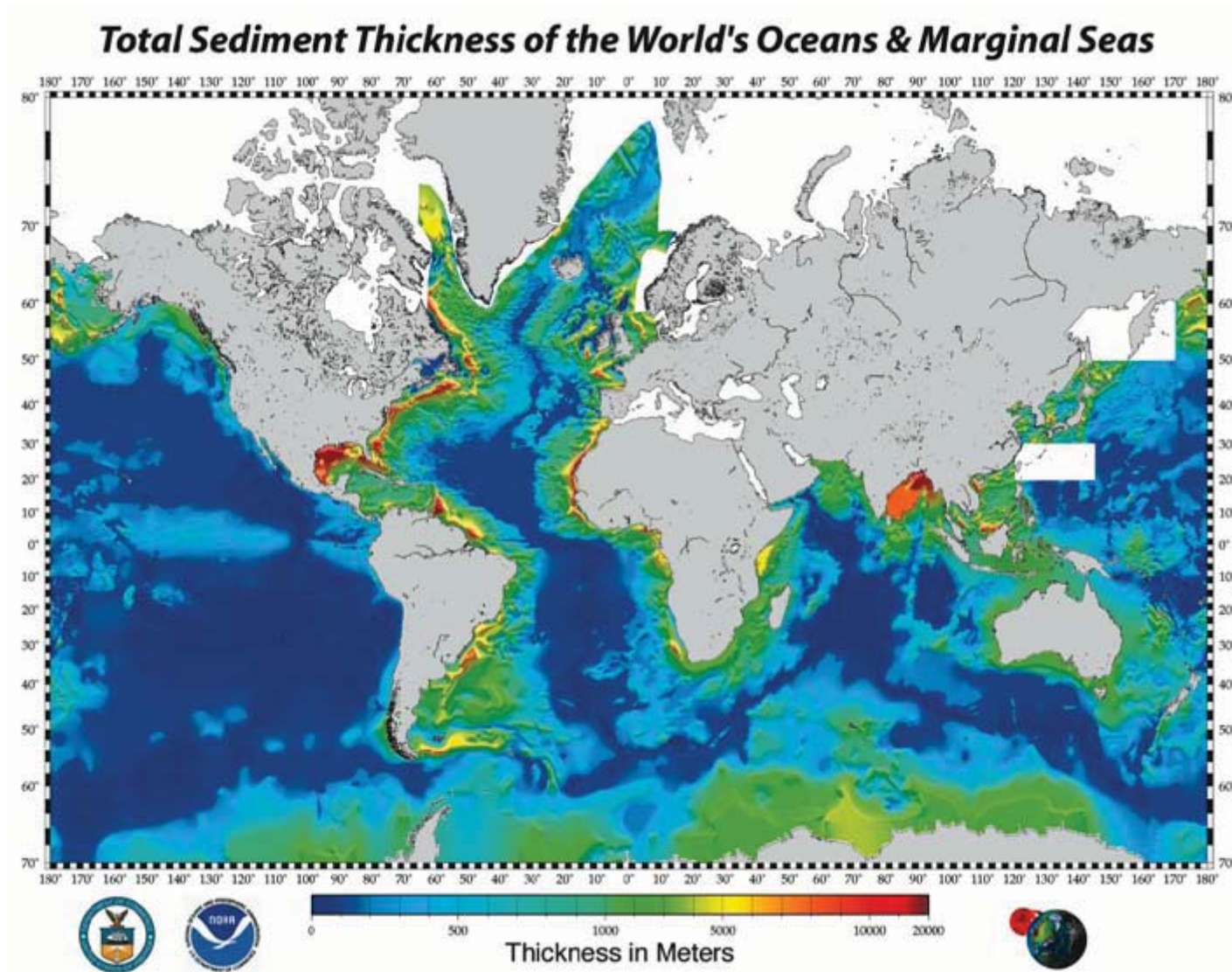
Please see Fig. 55, 58, 81, 92, and 112 in Beaugrand, G. “Continuous Plankton Records: Plankton Atlas of the North Atlantic Ocean (1958-1999).” *Marine Ecology Progress Series Supplement* (2004).

<http://www.int-res.com/articles/CPRatlas/CPRp011.pdf>

Building a Fossil Record



The Fossil Record of Phytoplankton



Courtesy NOAA

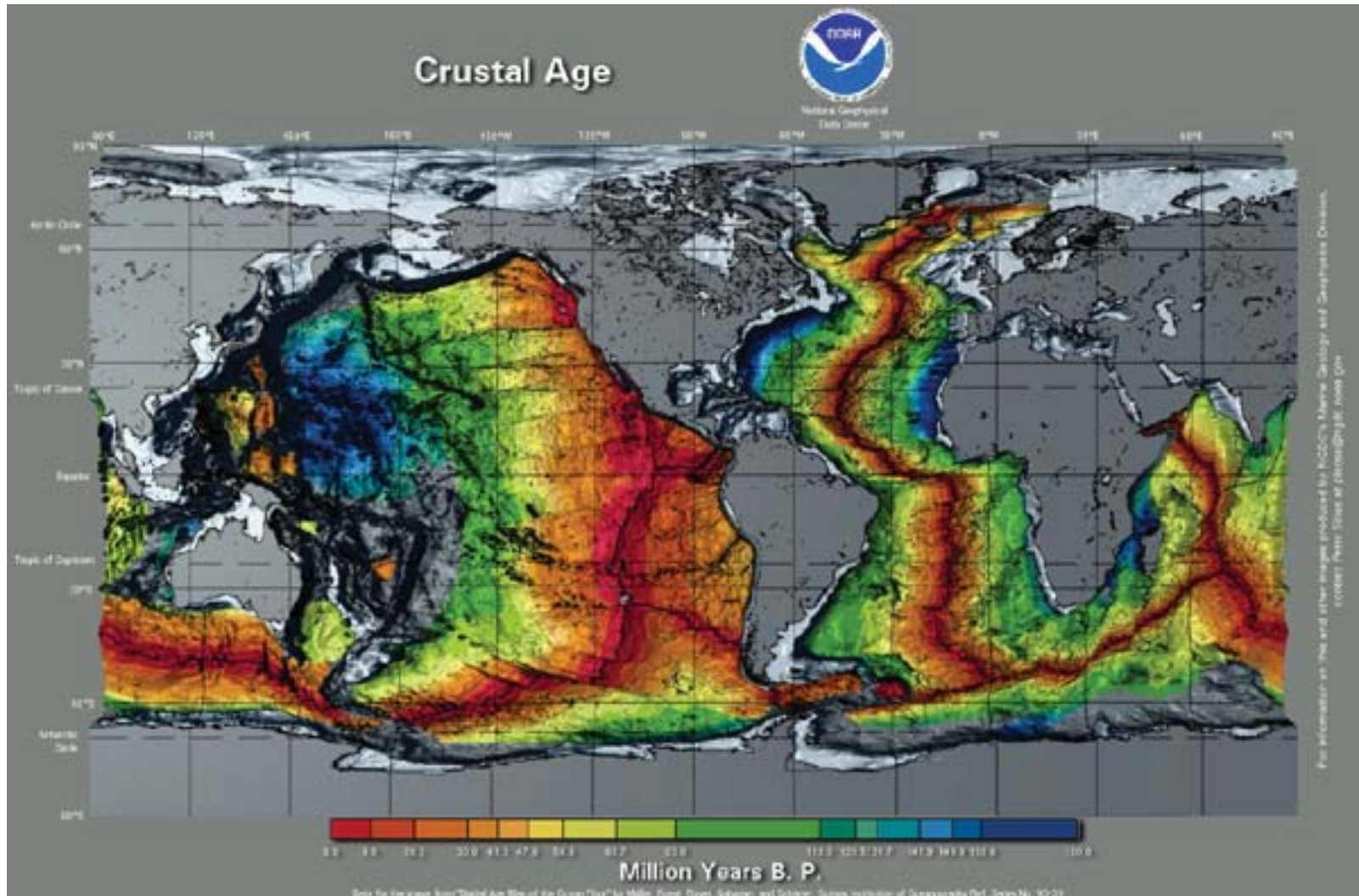
<http://www.ngdc.noaa.gov/mgg/image/sedthick9.jpg>

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Please see Fig. 2 and 3 in Rea, David K., et al.
“Broad Region of no Sediment in the Southwest
Pacific Basin.” *Geology* 34 (October 2006): 873-876.

Age of the Ocean Floor

Image courtesy Dr. Peter Sloss and NDGC/NOAA. Original data from:
R. Dietmar Müller, Department of Geology and Geophysics, University of Sydney, Australia;
Walter R. Roest, Geological Survey of Canada; Jean-Yves Royer, Lab. de Géodynamique, Villefranche Sur Mer, France; Lisa M. Gahagan, Institute for Geophysics, University of Texas, Austin, Texas; John G. Sclater, Scripps Institution of Oceanography, La Jolla, California.



Rocks Made Of Plankton

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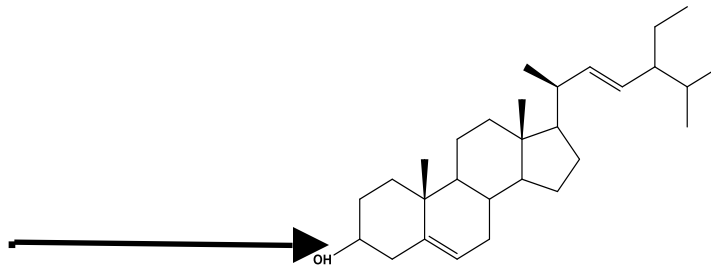
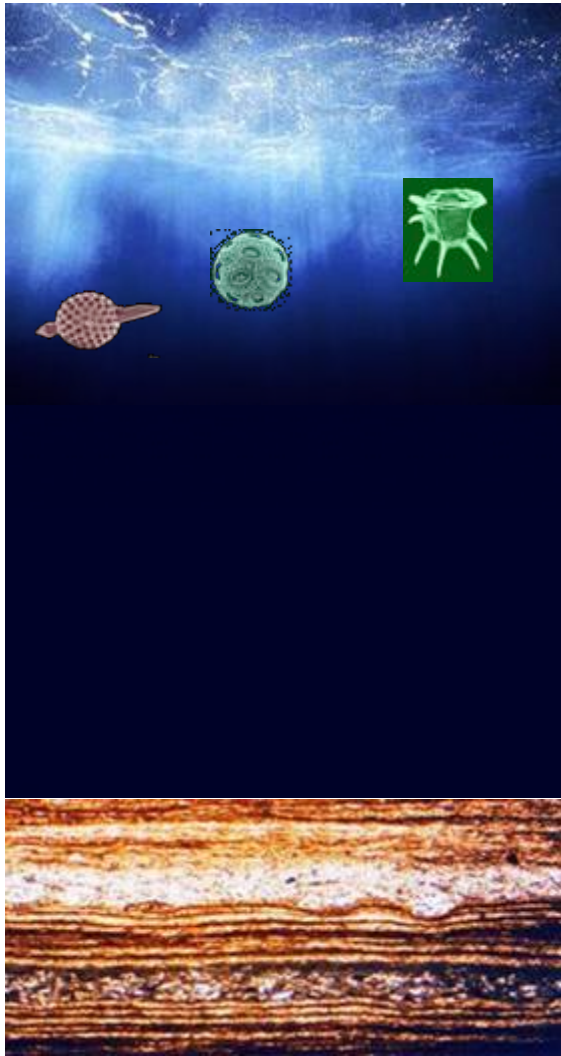
Please see the image on
http://www.paxgaea.com/images/White_Cliffs_Dover.jpg



Image Courtesy of Kansas Geological Survey. Used with permission.



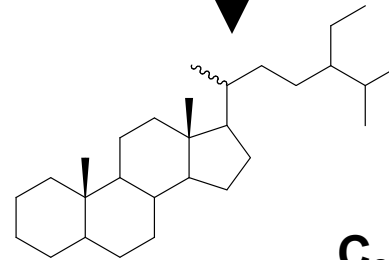
Biomarkers: Molecular Fossils



Stigmasterol
Biomolecule

**Destruction of
Labile Compounds
(Nucleic Acids, Proteins)**

**Burial,
Diagenesis,
Heating**



C₂₉ Sterane
Molecular Fossil

**Loss of functional groups, unsaturation;
Alteration of stereochemistry**

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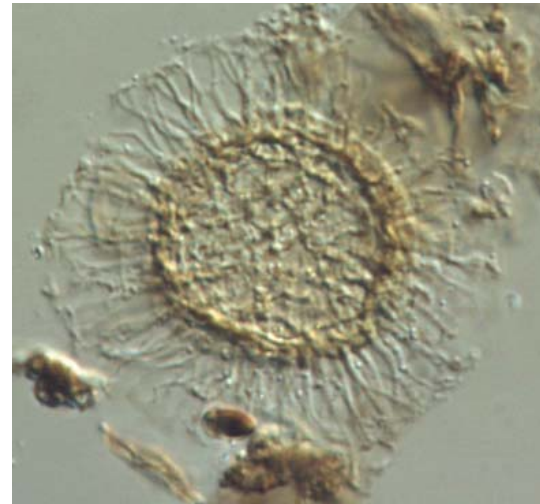
The image is from the book
Echoes of Life: What Fossil Molecules Reveal about Earth History
by Susan M. Gaines, Geoffrey Eglinton, Jurgen Rullkotter

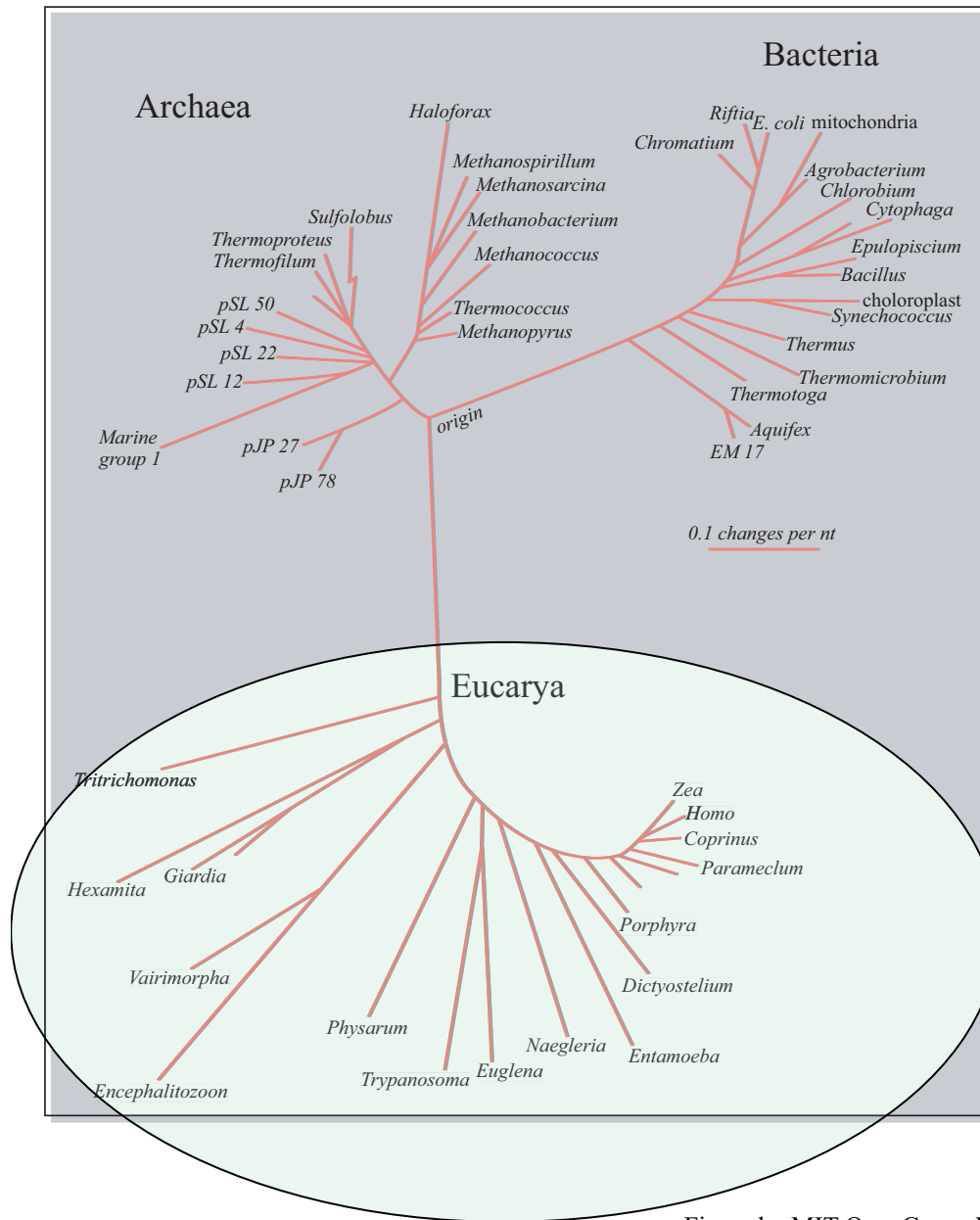
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The image is also from the book
Echoes of Life: What Fossil Molecules Reveal about Earth History
by Susan M. Gaines, Geoffrey Eglinton, Jurgen Rullkotter

Microfossils

- Advantages:
 - Large populations, widely deposited
 - Can provide fine-scale systematic information
- Disadvantages
 - Not all groups make preservable walls
 - Preserved fossils may not be diagnostic
 - Diagenesis can obliterate mineralized or unmineralized walls





Fossils of Protists (single-celled eukaryotes)

Cell walls contain resistant biopolymers e.g. algaenans, spropollinen

Minerals: silica, calcite

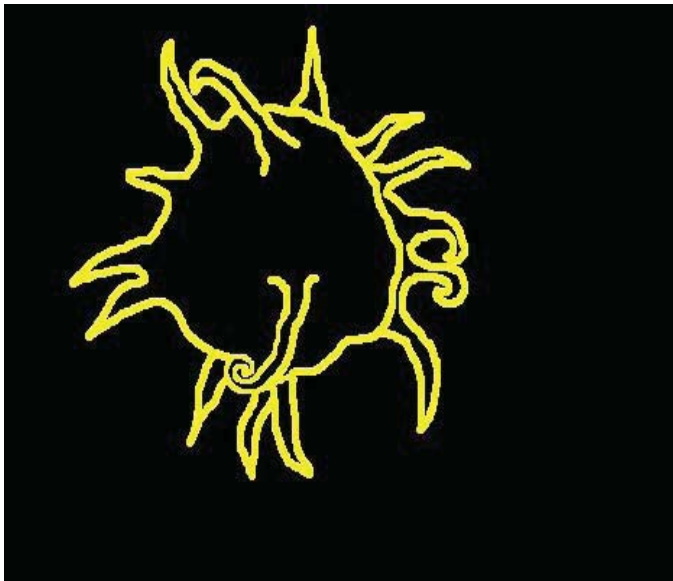
Preservation superior to prokaryotes

Record of acritarchs since 1.8-2 Ga

Figure by MIT OpenCourseWare.

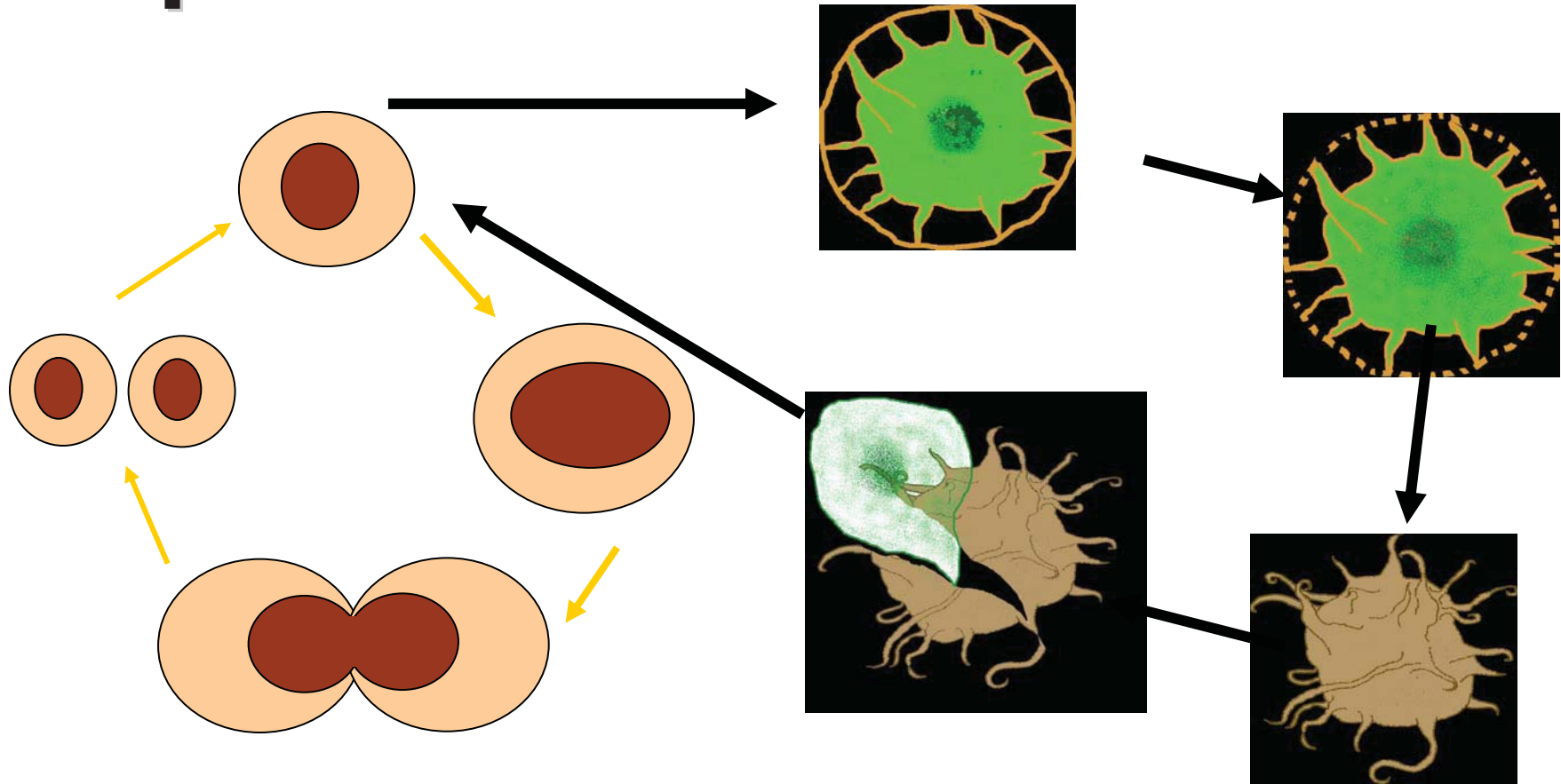
What are acritarchs?

- **acid-insoluble microfossils**
 - **single-celled**
 - **algae**
 - **planktonic**
 - **photosynthetic**



Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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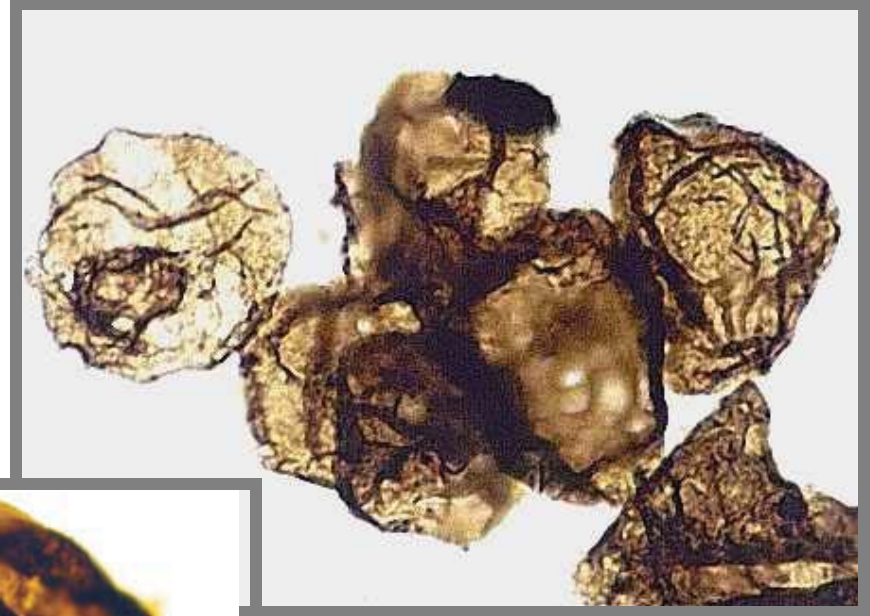
Leiosphere cycle simple cell division



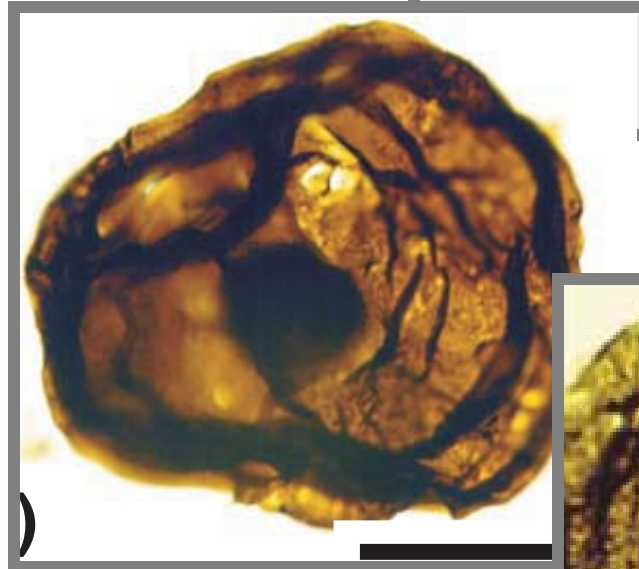
Acanthomorph resting cyst cycle

Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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- **Benthic mat fragments and filaments are common but declined c. 580 Ma**
- **Spherical acritarchs (leiospheres) dominate from c. 1200 Ma onward**



- **Dark centre may be cell contents**



- **Some show cell division**
- **May be original cells rather than cysts**



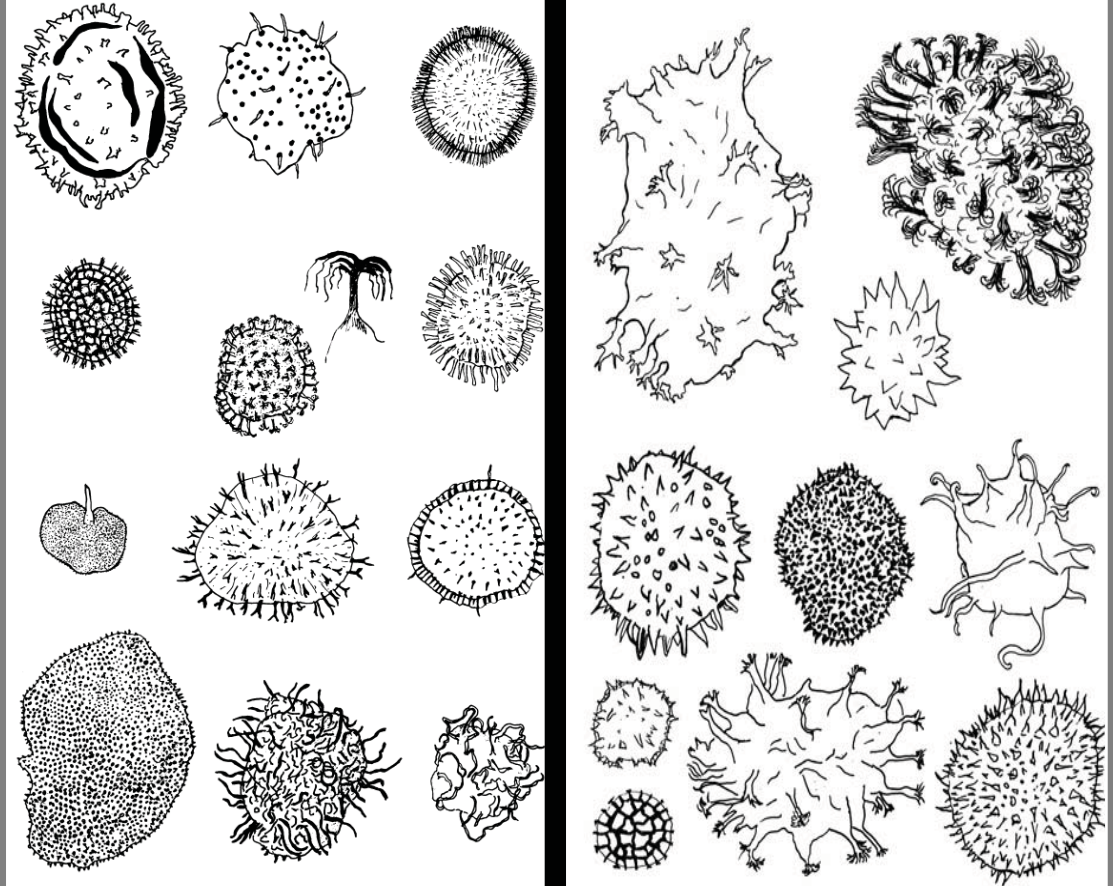
Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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580–565 Ma

- **acanthomorphs (spiny acritarchs) radiated rapidly**

• complex morphology

- **subtly different from earlier spiny forms**



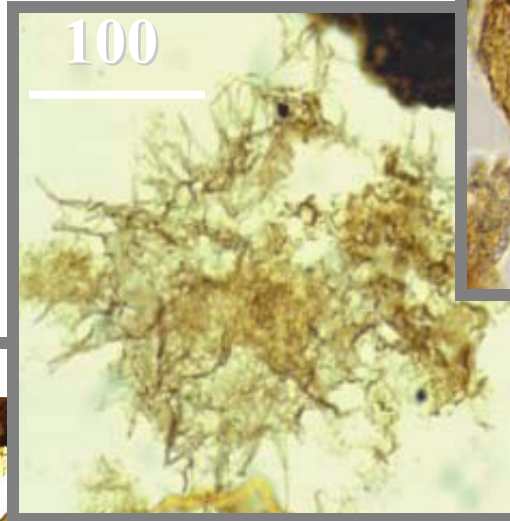
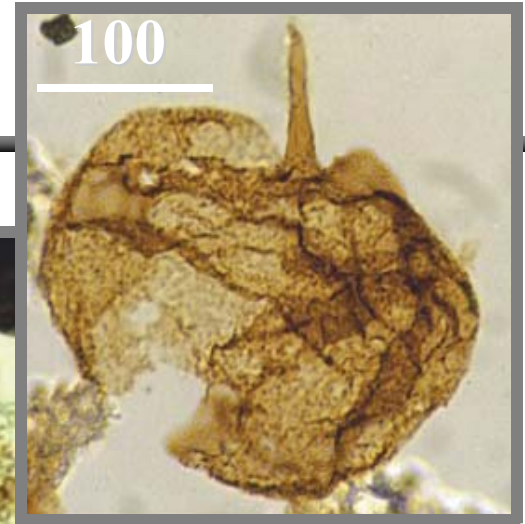
- **diversification unrelated to lithology, facies, or stratigraphic sequences**

Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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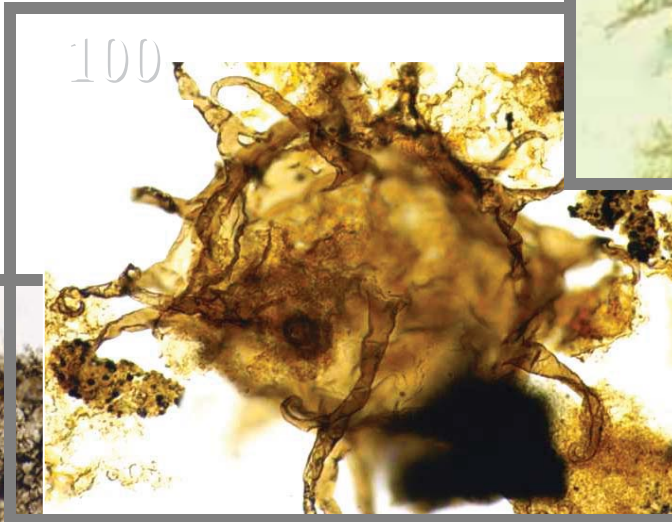
Zones

new genus

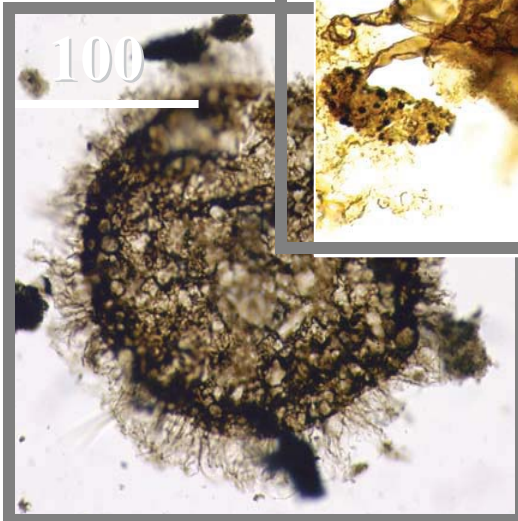
Range-chart plots show
four acanthomorph
zones



Tanarium irregulare



Tanarium conoideum



Appendisphaera

Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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Plastids

- Endosymbiotic organelles derived from previously free-living cyanobacteria
- Genetically dependent on the host for proteins coded for by the nuclear genome
- Reduced genome due to loss or transfer to host nuclear genome
- Greens, reds and Glaucocystophyta have primary plastids; all other lineages involve secondary symbioses

Delwiche C.F. Am. Nat. 1999. Vol. 154, pp. S164–S177, 1999

Symbiogenesis: the phylogenetic tapestry of eukaryotes

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Please see Fig. 1 in Delwiche, Charles F. "Tracing the Thread of Plastid Diversity through the Tapestry of Life." *The American Naturalist* 154 Supplement (October 1999): S164-S177.

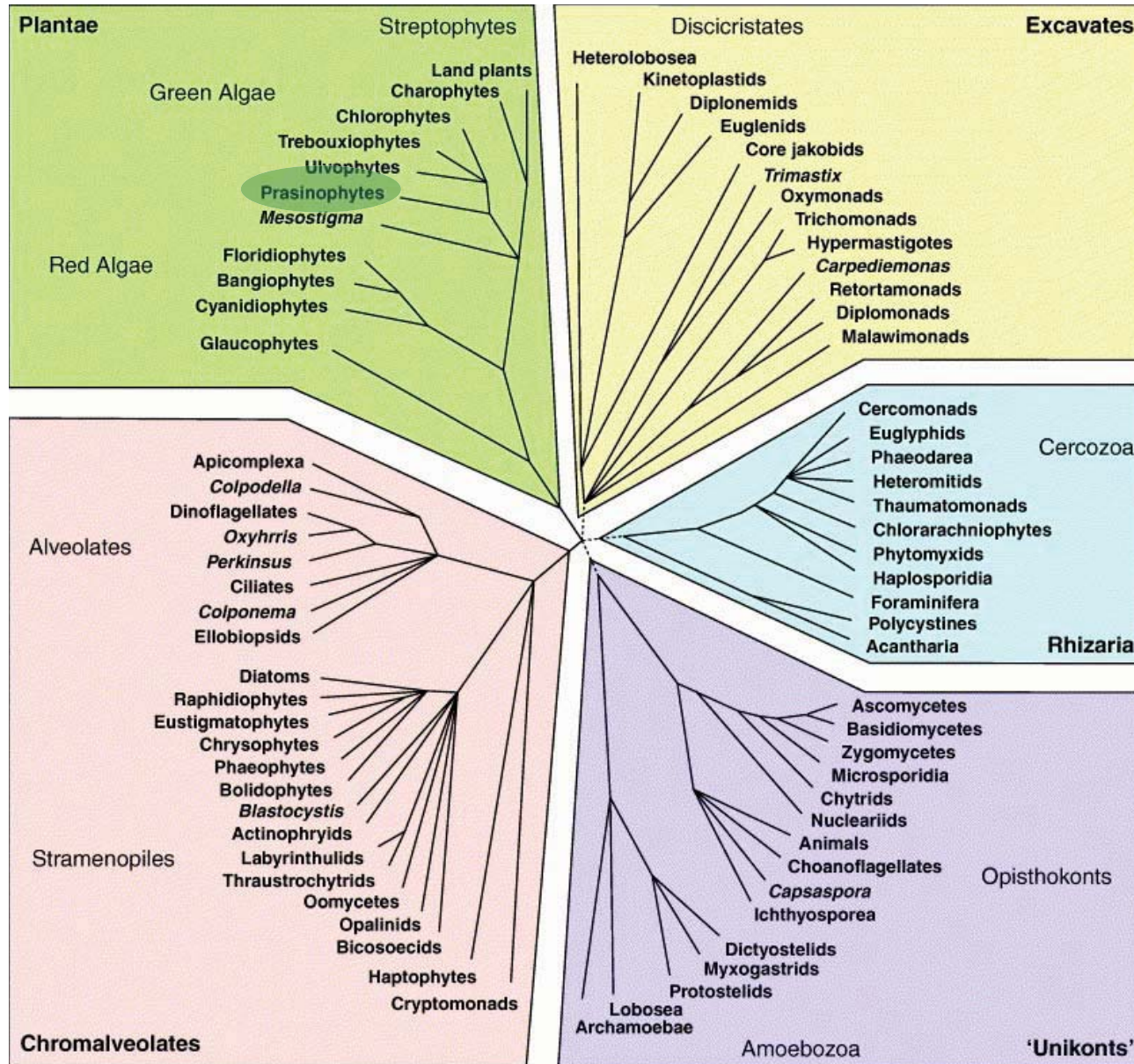
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Please see Fig. 1 in Baldauf, S. L. “The Deep Roots of Eukaryotes.” *Science* 300 (June 13, 2003): 1703-1706.

Fig. 1. A consensus phylogeny of eukaryotes. The vast majority of characterized eukaryotes, with the notable exception of major subgroups of amoebae, can now be assigned to one of eight major groups. Opisthokonts (basal flagellum) have a single basal flagellum on reproductive cells and flat mitochondrial cristae (most eukaryotes have tubular ones). Eukaryotic photosynthesis originated in Plants; theirs are the only plastids with just two outer membranes. Heterokonts (different flagellae) have a unique flagellum decorated with hollow tripartite hairs (stramenopiles) and, usually, a second plain one. Cercozoans are amoebae with filose pseudopodia, often living with in tests (hard outer shells), some very elaborate (foraminiferans). Amoebozoa are mostly naked amoebae (lacking tests), often with lobose pseudopodia for at least part of their life cycle. Alveolates have systems of cortical alveoli directly beneath their plasma membranes. Discicristates have discoid mitochondrial cristae and, in some cases, a deep (excavated) ventral feeding groove. Amitochondrial excavates lack substantial molecular phylogenetic support, but most have an excavated ventral feeding groove, and all lack mitochondria. The tree shown is based on a consensus of molecular (1–4) and ultrastructural (16, 17) data and includes a rough indication of new ciPCR "taxa" (broken black lines) (7–11). An asterisk preceding the taxon name indicates probable paraphyletic group

Baldauf, Science, Vol 300, Issue 5626, 1703-1706 , 13 June 2003

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TRENDS in Ecology & Evolution

Algae

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Please see *Dicrionium crissatulum* and *Euglena oxyuris* on
http://tolweb.org/accessory/Algae%3A_Protists_with_Chloroplasts?acc_id=52

Algae: Comprise several subdivisions of the Eukarya

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Please see: <http://tolweb.org/tree?group=Eukaryotes&contgroup=Life>

Algae

Ecology

- **Basis (with cyanobacteria) of oceanic and aquatic ecosystems**
- **'Out of balance' ecosystems may lead algal populations to grow large**
- **Algae blooms caused by high nutrients (natural or anthropogenic) → C_{org} decomposition depletes O_2 in the water eg. Red Tides (Dinoflagellates, Brown tides (Diatoms))**
- **Important in global carbon cycle because algal blooms may lead to enhanced organic matter accumulation & burial**
- **Many groups of algae capable of calcification (or silicification) → limestone → reefs**
- **Sink for natural and anthropogenic CO_2**

Algae: 'Protists with Chloroplasts'

Polyphyletic (several phyla) and paraphyletic (not all close relatives included) group of organisms:

The subset of photosynthetic eukaryotes that excludes the higher plants, the sister group of the green algae

Much controversy on how to classify

Multiple origins for both plastids and protistan hosts makes phylogenetic analysis complex

Characteristics used:

Photosynthetic pigments

Cell wall components

Carbohydrate storage

Flagella

Habitat

DNA sequences [http://tolweb.org/bchYg#3bchYS\]X1](http://tolweb.org/bchYg#3bchYS]X1)) &

Algae: 'Protists with Chloroplasts'

http://tolweb.org/accessory/Algae%3A_Protists_with_Chloroplasts?acc_id=52

GROUP	COMPOSITION	ORGANIZATION	MAJOR PIGMENTS
ALVEOLATES*	Contains some algae, autotrophic dinoflagellates, diverse, Peridinium, Symbiodinium, Ceratium	unicellular, colonial, syncytial; free-living, symbiotic and parasitic	chlorophylls a and c, some symbionts
CHLORARACHNIOPHYTES	A few genera of amoeboid organisms all with symbiotic algae, Chlorarachnion	syncytial, free-living	Chlorophyll b,
CRYPTOMONADS	About 12 genera of flagellates, Cryptomonas	single cells, rarely forming colonies, some are endobiotic	Chlorophylls a and c, phycobilins
EUGLENIDS	about half of the genera (35) contain members with green chloroplasts, flagellates, Euglena, Trachelomonas	single cells	Chlorophyll b
GLAUCOPHYTES	Several genera of flagellated and non-flagellated protists with similar phycobilin-rich symbionts, e.g. Glaucocystis, Cyanophora	flagellated and non-flagellated cells	Phycobilin
HAPTOPHYTES*	Diverse, with many genera, all or all bar one genera with plastids, with naked species and those with scales (coccolithophores)	single cells, some are endosymbionts	Chlorophylls a and c
RED ALGAE (Rhodophyta)*	All species are regarded as algal	free-living and parasitic, single celled and multicellular	Phycobilins
STRAMENOPILES*	Most but not all stramenopiles are algae, the group includes diatoms, brown algae, synurophytes and other 'chrysophytes'	single celled, colonial and multicellular, free-living and parasitic	Chlorophylls a and c
VIRIDAEPLANTAE* *Geologically Important	The green algae, all but a few genera are algal, prasinophytes, chlorophyta (e.g. volvocalean algae, conjugatophytes, Ulvales, Charales)	single celled, colonial and multicellular, free-living	Chlorophyll b

Algae: 'Protists with Chloroplasts'

http://tolweb.org/accessory/Algae%3A_Protists_with_Chloroplasts?acc_id=52

GROUP	FOSSIL RECORD AND SIGNIFICANCE
ALVEOLATES*	<p>Dinoflagellates, diverse and important plankton group Cysts make exceptional index fossils from their Early Triassic radiation Symbiodinium (Gymnodinium) the most important symbiont in marine invertebrates especially corals, tridacnid clams and some foraminifera Diagnostic lipids (dinosterol) and pigments Many toxic species contribute to fish kills and shellfish toxicity</p>
HAPTOPHYTES*	<p>Diverse, with many genera. Important plankton, index fossils in Mesozoic and Cenozoic; scales (coccolithophores) of calcium carbonate carry C and O isotopic signature of seawater Diagnostic lipids (Alkeneones) carry the signature of sea surface temperature and the vital effects of C-fixation by <i>Emiliana huxleyi</i></p>
RED ALGAE (Rhodophyta)*	<p>All species are regarded as algal Some are calcareous Corallines since Jur and ancestors since Pre-Camb.; Fossil record to ~ 1200M ; oldest algal fossil of specific clade?</p>
STRAMENOPILES*	<p>Most but not all stramenopiles are algae, the group includes diatoms, brown algae, synurophytes and other 'chrysophytes'</p>
VIRIDAEPLANTAE*	<p>The green algae, all but a few genera are algal, prasinophytes, chlorophyta (e.g. volvocalean algae, conjugatophytes, Ulvales, Charales)</p>

ALVEOLATES-Dinoflagellates

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Please see <http://tolweb.org/Myzozoa>

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Please see Spiniferites, Ceratium sp., and Dinophysis sp. from
and
Balmula pentaradiata from

ALVEOLATES-Dinoflagellates

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ALVEOLATES-Dinoflagellates

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ALVEOLATES-Dinoflagellates

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Please see

<http://www.geo.ucalgary.ca/~macrae/palynology/dinoflagellates/Florentinia.gif>

and

<http://www.geus.dk/departments/quaternary-marine-geol/research-themes/env-cli-dino-uk-dino-cycle.jpg>

Geological Record of Dinoflagellate Cysts

Cysts are Organofossils: Constructed of
recalcitrant, non-hydrolysable
polymeric organic matter =
sporopollenin.

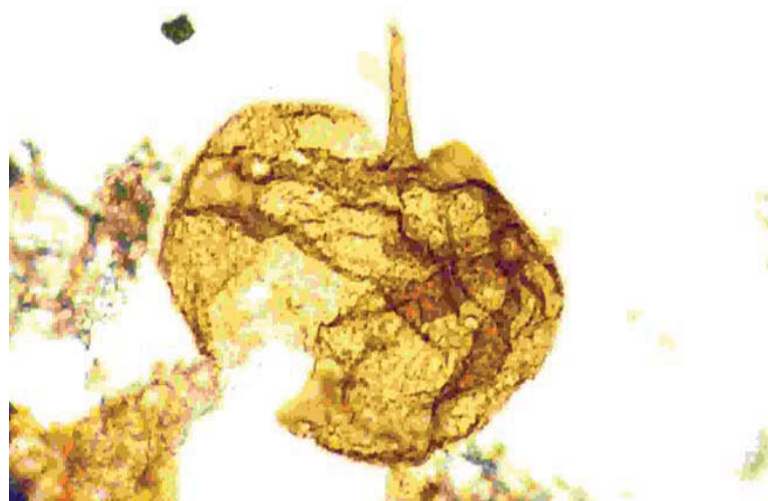
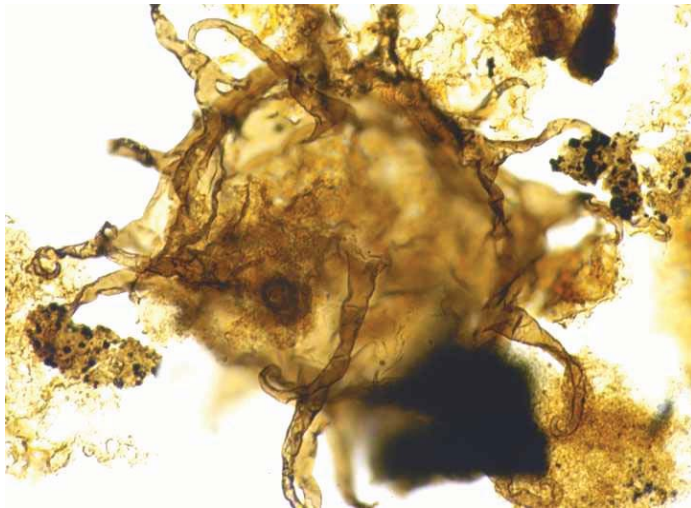
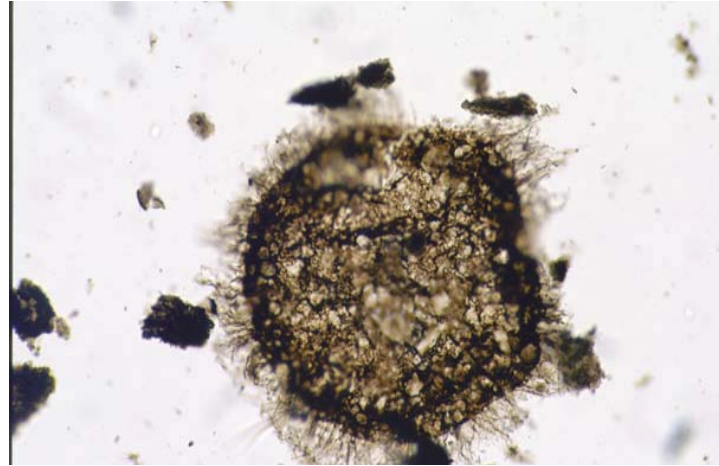
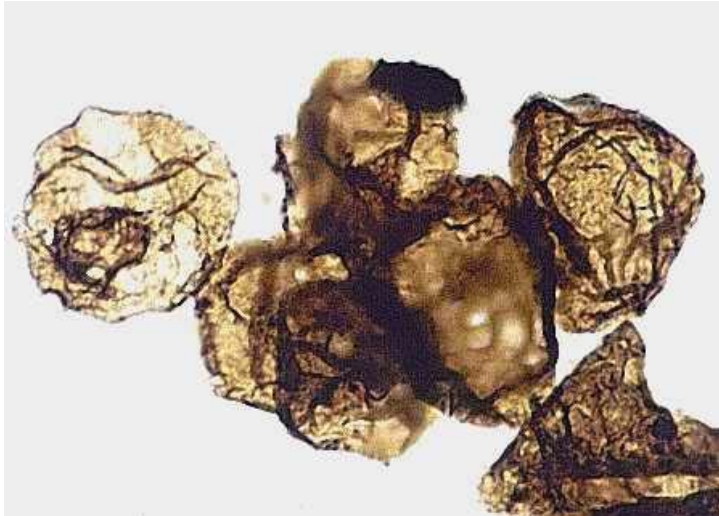
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Please see

<http://www.geus.dk/departments/quaternary-marine-geol/research-themes/env-cli-dino-uk-diversity.gif>

Important as biostratigraphic markers
throughout the Mesozoic and Cenozoic

Neoproterozoic Acritarchs = Algal Fossils Dinoflagellates???



Courtesy of Dr. Kathleen Grey, Geological Survey of Western Australia.
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Dinoflagellates as Symbionts

coral.aoml.noaa.gov



www.odysseyexpeditions.org

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Radiolaria (not algae)

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Please see

<http://www.ucmp.berkeley.edu/protista/radiolaria/rads.html>

and

<http://www.ucmp.berkeley.edu/protista/radiolaria/radmm.html>

HAPTOPHYTES

- <http://www.soes.soton.ac.uk/staff/tt/eh/coccoliths.html>

This page describes *Ehux* coccoliths, i.e. the characteristic calcareous plates the cell produces. People often loosely refer to *Ehux* as a coccolith, which is strictly speaking incorrect. This is not drastically important but the correct terminology is:

Coccolithophore - the organism, including the cell and external coccoliths.

Coccosphere - the more or less spherical layer of coccoliths surrounding the cell.

Coccolith - the individual calcareous plates.

Ehux produces coccoliths that are approx. 2.5×10^{-6} metres in diameter, and which weigh approx. 1.8×10^{-12} g each. Of this weight, the average contents of carbon, oxygen and calcium atoms in the coccolith CaCO_3 have been measured to be 0.28, 0.87 and 0.67×10^{-12} g per coccolith respectively (Fagerbakke et al, 1994).

For comparison, the wavelength of visible light is in the range $0.4\text{-}0.7 \times 10^{-6}$ metres, and a pinhead is about 2000×10^{-6} metres in diameter.

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Please see: the image on <http://www.soes.soton.ac.uk/staff/tt/eh/coccoliths.html>.

HAPTOPHYTES

- Diagnostic lipids (Alkenones) carry the signature of sea surface temperature and the vital effects of C-fixation by *Emiliana huxleyi*

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Please see Fig. 7 in Laws, Edward A., et al. "Controls on the Molecular Distribution and Carbon Isotopic Composition of Alkenones in Certain Haptophyte Algae." *Geochemistry Geophysics Geosystems* 2 (January 25, 2001): 31.

And

Fig. 3 in Prahl, F., et al. "Status of Alkenone Paleothermometer Calibration: Report from Working Group 3." *Geochemistry Geophysics Geosystems* 1 (November 7, 2000): 13.

RED ALGAE - Rhodophyta

D. Wilson Freshwater

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Please see

<http://tolweb.org/tree?group=Rhodophyta&contgroup=Eukaryotes>

RED ALGAE - Rhodophyta

Traditionally the red algae were divided into two Classes the Bangiophyceae and Florideophyceae. Alternatively a single Class, the Rhodophyceae and two Subclasses, Bangiophycidae and Florideophycidae are used. Based on ultrastructure and molecular evidence the Bangiophyceae is now accepted as a paraphyletic group, while the Florideophyceae is considered to be monophyletic based on two synapomorphic characters - presence of a filamentous gonimoblast and tetrasporangia

Bangia fossils recognized on the basis of detailed morphology in the ca 1200 Ma Hunting Fm., Arctic of Canada

Butterfield, Knoll and Swett, Science 250, 104-107

Grow attached to substrate – ie not plankton

Coralline reds calcify – ie reef forming

This image has been removed due to copyright restrictions.

Cell walls = Cellulose fibrils embedded in an extensive gelatinous matrix = Agar

Chlorophyll a Phycobilins arranged in phycobilisomes; thylakoids are not stacked

STRAMENOPILES –Include Diatoms and Brown Algae

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STRAMENOPILES –Include Diatoms and Brown Algae

Mitchell L. Sogin and David J. Patterson

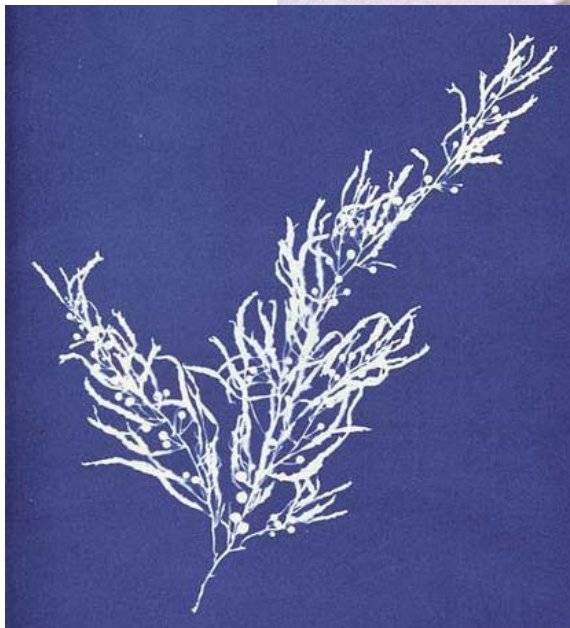
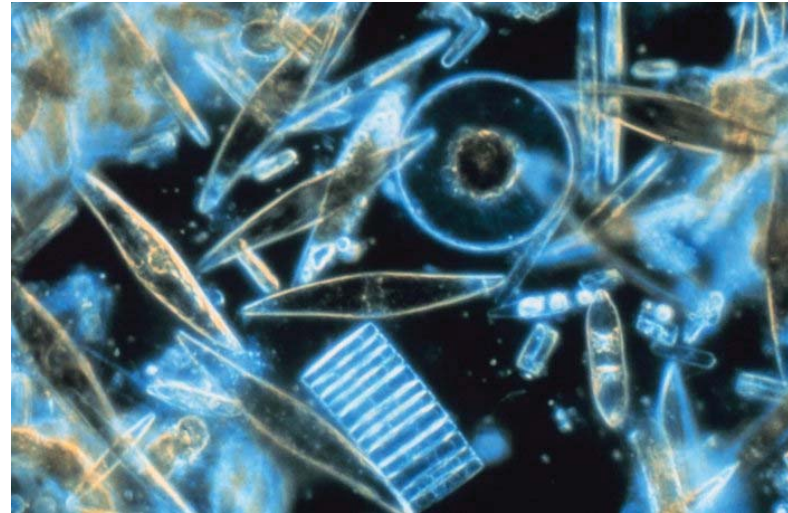


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Please see

<http://tolweb.org/tree?group=Stramenopiles&contgroup=Eukaryotes>

Diatoms

BACILLARIOPHYTA

Diatoms are unicells that share the feature of having a cell wall made of silicon dioxide. This opaline or glass frustule is composed of two parts (valves), which fit together with the help of a cingulum or set of girdle bands.

The taxonomy of diatoms is based in large part on the shape and structure of the siliceous valves. Although some species can be identified in the living state, and some genera were and have been erected based on the organization and fate of cytoplasmic organelles, species-level identification usually requires examination with oil immersion objectives of permanently-mounted specimens.

Two major groups of diatoms are generally recognized: the **centric diatoms** exhibit radial symmetry (symmetry about a point) and have oogamous sexual reproduction.

The **pennate diatoms** are bilaterally symmetrical (symmetry about a line) and produce ameboid gametes that are morphologically similar but may be physiologically different.

Chloroplasts of diatoms are variable, but consistent within most taxa. Chloroplasts may be many small discs, a condition found in most centric diatoms and some (araphid) pennates, or few large, plate-like chloroplasts are found in the majority of pennate taxa.

Diatoms

Oldest fossils are Jurassic. Some lower Cretaceous and an excellent record from the Late Cretaceous

Diatoms have found a resource (SiO_2) that few other groups exploit and have taken advantage. 6% as costly as cellulose to make SiO_2 frustule

Their lifecycles often involve sedimentation when nutrients decline and later resuspension. Rhizosolenia (?) Sinks to low O_2 water to collect NO_3^-
Significant N-fixation by heterocystous N-fixing cyanobacterial symbionts of Rhizosolenia

CaCO_3 will dissolve at depth whereas silica is more resistant. Huge areas of the sea floor are covered in diatomaceous material.

Amorphous silica has interesting optical properties, unlike CaCO_3 which is largely opaque. Why does a photosynthetic organism like a coccolithophorid choose to bury itself in opaque material? Some believe silica frustules can refract light to make it more available for diatoms.

Opal changes volume when heated so diatomaceous sediments can make good oil reservoirs

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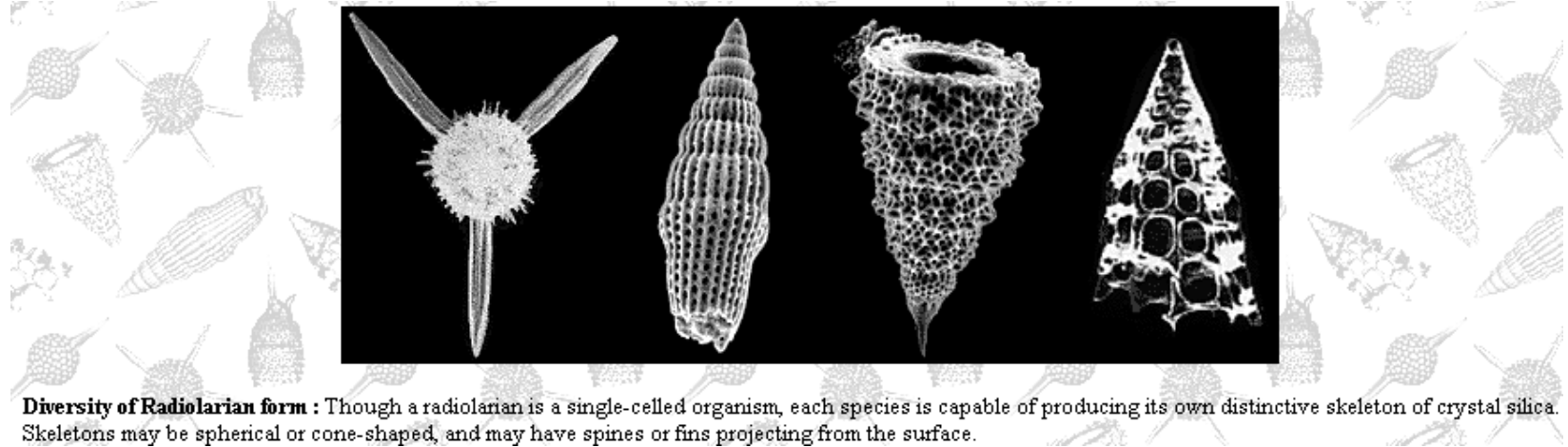
Please see Figure 1 and Figure 2 on the Science article, DOI: [10.1126/science.1096806](https://doi.org/10.1126/science.1096806).

Captions are on the next two pages.

Fig. 1. Neighbor-joining phylogenetic tree based on nearly complete 18S rRNA sequences of diatoms. Some of the sequences were published before (5); 86 others (see table S1 for details) were determined in this study. The sequences of *Coccolid haptophyte* and *Emiliana huxleyi* were used as outgroups but were pruned from the tree. *Bolidomonas mediterranea* is a sister group of the diatoms. The tree was created with the use of the Jukes Cantor model. HBI-biosynthesizing strains are indicated in red. Diatoms in green were tested but did not contain HBI alkenes; diatoms in black were not tested for the presence of HBI alkenes. The scale bar indicates 10% sequence variation. The inset shows the structure of C25 HBI alkane (27) and parent skeleton of C25 HBI unsaturated alkenes (7–11) produced by diatoms. Note that the odd non HBI-biosynthesizing *Rhizosolenia* strain, *R. robusta*, falls completely out of the *Rhizosolenia* phylogenetic cluster, indicating that its morphological classification as a *Rhizosolenia* diatom is probably wrong

Fig. 2. The occurrence of the C25 HBI skeleton in marine sediments (**A**) and petroleum (**B**) through geological time based on the analysis of over 400 sediment and 81 petroleum samples. For marine sediments, the relative abundance of the C25 HBI alkane is indicated by the ratio of the HBI alkane to phytane (Ph) (HBI/Ph+1) plotted on a log scale. Phytane is derived from the side chain of chlorophyll, which can be derived from all photosynthetic algae and cyanobacteria. For petroleum, the C25 HBI alkane concentration is presented on a log scale in $\mu\text{g g}^{-1}$ (parts per million) of the total saturated alkanes of each petroleum. The detection limit is 100 ppm, and all samples plotted on the 100 ppm line, thus, do not contain detectable amounts of C25 HBI alkane. Uncertainties in the ages of the petroleum samples are indicated by error bars. Both plots clearly show that the HBI biosynthetic pathway did not exist before ca. 90 Ma. (Inset) shows the more exact timing of this event.

Radiolaria (not algae)



Diversity of Radiolarian form : Though a radiolarian is a single-celled organism, each species is capable of producing its own distinctive skeleton of crystal silica. Skeletons may be spherical or cone-shaped, and may have spines or fins projecting from the surface.

Image courtesy of Museum of Paleontology, University of California. Used with permission.

With their glassy skeletons of often perfect geometric form and symmetry, radiolarians are among the most beautiful of all protists. They are also an ancient group, going back all the way to the early Cambrian Period. Their abundance in many rocks, their long geologic history, and their diversity through time make them important sources of information on the geologic age and structure of many deposits.

Radiolaria can range anywhere from 30 microns to 2 mm in diameter. Their skeletons tend to have arm-like extensions that resemble spikes, which are used both to increase surface area for buoyancy and to capture prey. Most radiolarians are **planktonic**, and get around by coasting along ocean currents. Most are somewhat spherical, but there exist a wide variety of shapes, including cone-like and tetrahedral forms (see the image above). Besides their diversity of form, radiolarians also exhibit a wide variety of behaviors. They can reproduce sexually or asexually; they may be filter feeders or predators; and may even participate in symbiotic relations with unicellular algae.

<http://www.ucmp.berkeley.edu/protista/radiolaria/rads.html>

Though their silica skeletons have allowed us to find numerous fossils, scientists still have not been able to successfully develop a complete classification scheme for them. The evolution of the Radiolaria can be easily traced on the broad scale, with major transitions in the global fauna, but a concise taxonomy reflecting the evolutionary relationships of major groups is still elusive. Until comparatively recently, radiolarians were primarily studied by **micropaleontologists**, and only at the end of the 20th century have scientists from other fields begun to study these fascinating protists as well.

Radiolaria exhibit several different types of behavior that should be noted. They often share relationships with [dinoflagellate](#) symbionts. These dinoflagellate **symbionts** are enclosed in a thin envelope of cytoplasm produced by the host's rhizopodial system. Radiolaria provide ammonium and carbon dioxide for the dinoflagellate symbionts, and in return the dinoflagellates provide their radiolarian host with a jelly-like layer that serves as both for protection and capturing prey. Another symbiotic relationship for radiolarians is with **algal symbionts**. When food is scarce, an algal symbiont can provide its host radiolarian with much needed nourishment. There is very little known about the Radiolaria-algal symbiont symbiotic relationship, but it is known that algal symbionts are found in the [extracapsulum](#) of many radiolarians, and can provide a host with enough nourishment to allow it to maintain nutritional **autonomy**. This simply means that the radiolarian can go several weeks without food. Algal symbionts can also alleviate competition among individuals of a Radiolaria colony. Algal symbionts are generally found only within Radiolaria who dwell in areas that receive sufficient light

<http://www.ucmp.berkeley.edu/protista/radiolaria/rads.html>

Foraminifera (forams) – not algae



<http://www.ucmp.berkeley.edu/foram/foramintro.html>



Image courtesy of Museum of Paleontology, University of California. Used with permission.

Foraminifera (forams for short) are single-celled [protists](#) with shells. Their shells are also referred to as **tests** because in some forms the protoplasm covers the exterior of the shell. The shells are commonly divided into chambers which are added during growth, though the simplest forms are open tubes or hollow spheres. Depending on the species, the shell may be made of organic compounds, sand grains and other particles cemented together, or crystalline calcite.

Fully grown individuals range in size from about 100 micrometers to almost 20 centimeters long. A single individual may have one or many nuclei within its cell. The largest living species have a symbiotic relationship with [algae](#), which they "farm" inside their shells. Other species eat foods ranging from dissolved organic molecules, [bacteria](#), [diatoms](#) and other single celled phytoplankton, to small animals such as copepods. They move and catch their food with a network of thin extensions of the cytoplasm called **reticulopodia**, similar to the pseudopodia of an amoeba, although much more numerous and thinner.

Foraminifera (forams)

- Each of the major groups of foraminifera uses different materials to build their shells. The basic types of wall structures are:
- agglutinated -- test made of particles cemented together. Some species use whatever particles are available, while other species may select only sponge spicules or mica flakes or a certain size particle to build their test.
- calcareous hyaline -- interlocking crystals of calcite about 1 micrometer in diameter.
- microgranular -- equidimensional, subspherical particles of calcite closely packed together without cement.
- porcellaneous -- wall made of apparently randomly arranged microscopic rods of calcite, with ordered inner and outer surface layers.
- <http://www.ucmp.berkeley.edu/foram/foramintro.html>

VIRIDAEPLANTAE

**Richard M. McCourt,
R. L. Chapman,
M. A. Buchheim and
Brent D. Mishler**

- ◆ Chlamydomonas (Chlorophyceae)
- ◆ Spirogyra (Zygnemetales)
- ◆ Coleochaete (Coleochaetales)
- ◆ Hepatica (an embryophyte)

Algal photographs copyright © 1995, Rick McCourt; Hepatica photograph copyright © 1995, Wayne P. Maddison.

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Please see:

http://tolweb.org/tree?group=Green_plants

VIRIDAEPLANTAE

http://tolweb.org/tree?group=Green_plants

- Green plants as defined here includes a broad assemblage of photosynthetic organisms that all contain chlorophylls a and b, store their photosynthetic products as starch inside the double-membrane-bounded chloroplasts in which it is produced, and have cell walls made of cellulose (Raven et al., 1992). In this group are several thousand species of what are classically considered green algae, plus several hundred thousand land plants.

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Please see: http://tolweb.org/tree?group=Green_plants

VIRIDAEPLANTAE- CHLOROPHYCEAE

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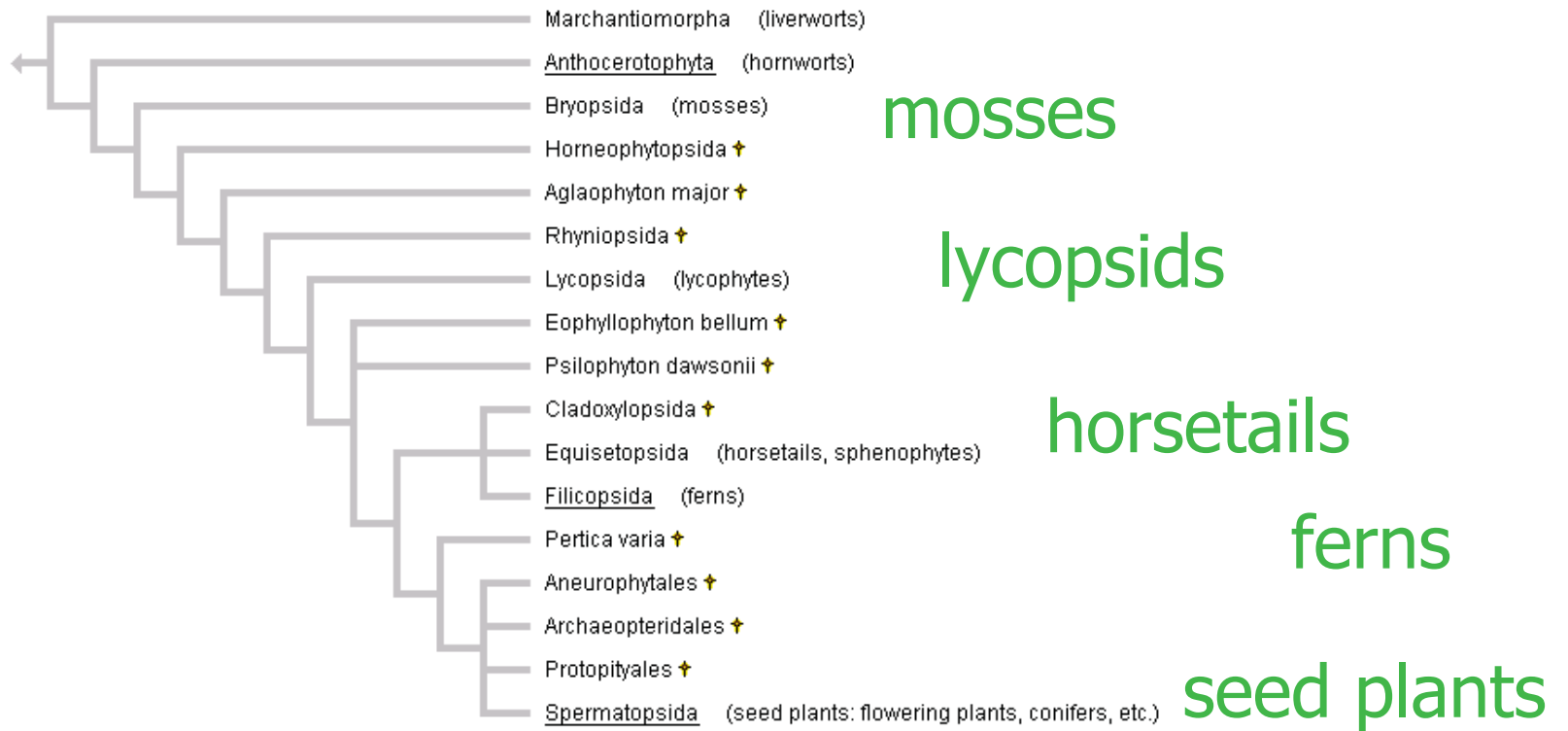
Please see

<http://www.ucmp.berkeley.edu/greenalgae/chlorophyceae.html>

Chlorellales, especially *Chlorella* are an important group because of their role as **endosymbionts** inside the tissues of sponges, ciliates and formams. Green algae produce biopolymers, algeanans, which are recalcitrant, non-hydrolysable biopolymers and feedstock for crude oil.

http://tolweb.org/tree?group=Green_plants

Paul Kenrick and Peter Crane



Oldest evident land plant = Late Ordovician spore

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<http://www.ucmp.berkeley.edu/IB181/VPL/Elp/Elp1.html>,

<http://www.ucmp.berkeley.edu/IB181/VPL/Elp/ElpP/Elp91.jpeg>,

<http://www.ucmp.berkeley.edu/IB181/VPL/Elp/ElpP/Elp101.jpeg>

Oldest N. Hemisphere
vascular plant = Late
Silurian *Cooksonia*

Earliest Land Plants - Lycopsoids



Image by MIT OpenCourseWare.

Baragwanathia longifolia

Upper Silurian and Lower Devonian of Australia

To the left a fossil, to the right a reconstruction of a part of the plant. The sporangia are in the axils of the leaves. Drawing J. Hulst

<http://www.xs4all.nl/~steurh/eng/ebaragw.html>

Ferns

Kathleen M. Pryer and Alan R. Smith

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Please see

<http://tolweb.org/tree?group=Filicopsida&contgroup=Embryophytes>



FERNS

FERNS date back to at least the Middle Devonian. They include four living groups: **Marattiales**, **Ophioglossales**, **Psilotales** and **leptosporangiate ferns**.

Some early groups that are now extinct, including the **Stauropteridales** and **Zygopteridales**. The chart below shows the stratigraphic ranges over which each group is known to have existed. The green taxa on the right side of the chart are groups of ferns; the blue taxa to the left are **Sphenophytes or Sphenopsids**; and the purple **Cladoxylopsida** in the center are a closely related group.

Of all living ferns, only the Psilotales has no fossil record

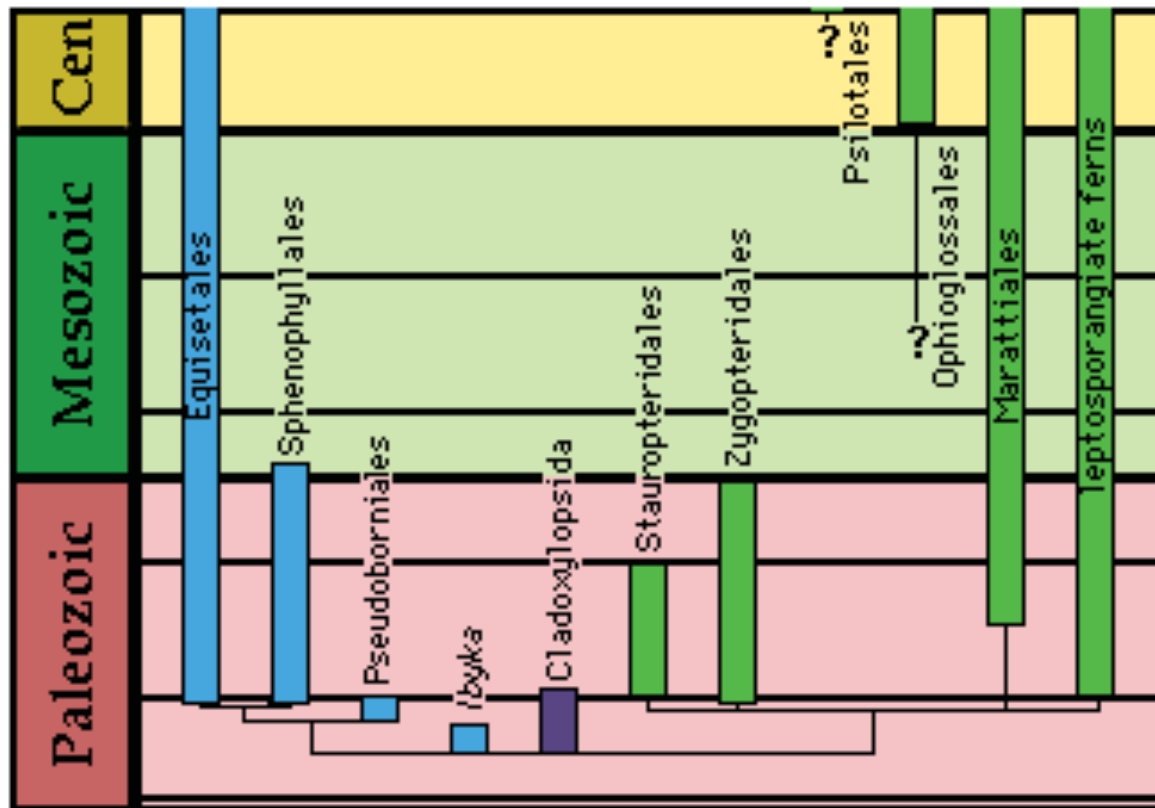


Image courtesy of Museum of Paleontology, University of California. Used with permission.

Conifers

Coniferales

Araucariaceae	Cretaceous to Recent	36 extant species	Southern Hemisphere
Cephalotaxaceae	Jurassic to Recent	5 extant species	Northern Hemisphere
Cupressaceae	Triassic to Recent	157 extant species	both Hemispheres
Pinaceae	Cretaceous to Recent	250 extant species	Northern Hemisphere
Podocarpaceae	Triassic to Recent	131 extant species	Southern Hemisphere
Cheirolepidaceae	Triassic to Cretaceous	extinct	Global
Palissyaceae	Triassic to Jurassic	extinct	Global
Utrechtiaceae	Carboniferous to Permian	extinct	Global

Taxales

Taxaceae	Jurassic to Recent	9 extant species	Northern Hemisphere
----------	--------------------	------------------	----------------------------

Cephalotaxaceae

Amentotaxus

Cephalotaxus

Torreya

Cupressaceae or cypress

cypress

Glyptostrobus,
Metasequoia,
Taxodium) are
deciduous or include
deciduous species.

Pinaceae

firs,
cedar
pines

Podocarpaceae

Dacrydium,
Lepidothamnus,
Nageia, Podocarpus,
Prumnopitys

Araucariaceae → Araucaria

These images have been removed due to copyright restrictions.

Please see the first image on http://www.wollemipine.com/photo_gal.php.

This image has been removed due to copyright restrictions.

Family

Araucariaceae

Genus

Wollemia

Number of living species

1 (*Wollemia nobilis* — Wollemi Pine)

Population size

Less than 100 trees

Discovery of Wollemi Pine

1994 (two populations), 2000 (one further population) in the [Wollemi National Park](#)

Discovered by

[David Noble](#), National Parks & Wildlife Service officer, when canyoning

Distribution of fossil remains of Wollemia

Widespread, including Australia, New Zealand and Antarctica

Closest relatives

Agathis (Kauri Pines), Araucaria (Norfolk Island, Hoop, Bunya Bunya and Monkey Puzzle pines) all belong to the family Araucariaceae — see [age and ancestry](#)

Estimated age / lineage

90–200 million years, based on a combination of fossil evidence, known evolutionary relationships of the two genera, biogeography and known timing of the Continental Drift

Oldest known fossil of close relative

90 million years (fossil pollen of dubious identity, known as *Dilwynites*)

Unusual characteristics

Its bark; its bud development; its branching habit — see [appearance](#) and [characteristics](#).

http://www.rbgsyd.nsw.gov.au/plants_info/wollemi_pine

- Wollemi Pine believed to exist naturally in only one location approx 200 km of Sydney,
- Family Araucariaceae
Different features from any known living pine. Closest relatives are probably extinct Araucariaceae of Jurassic and Cretaceous age- between 200 and 65 million years ago and known only from fossils.
- Since the great extinctions at the end of the Cretaceous period, Araucariaceae have survived only in the southern hemisphere.
- May propagate asexually (through root system) since all known trees are genetically identical

ANGIOSPERMS

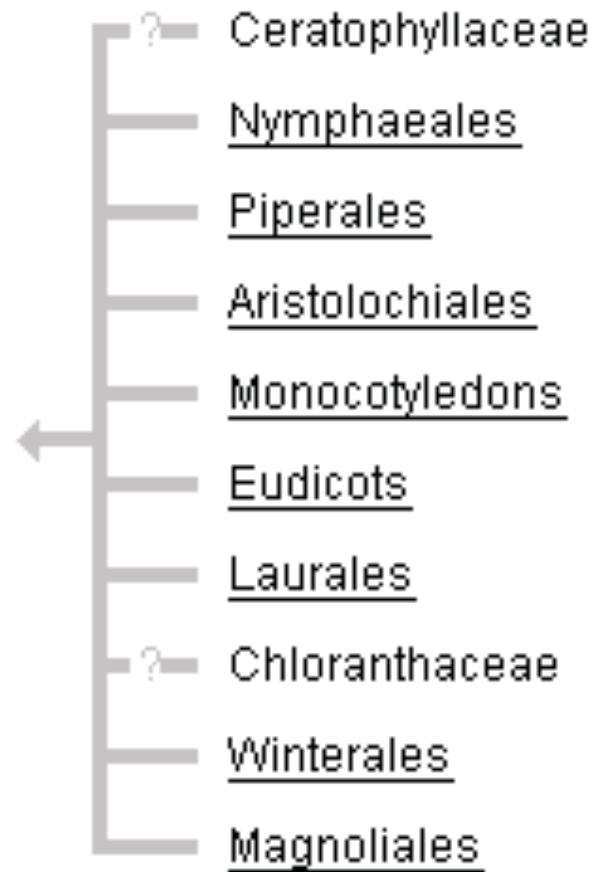
- The rapid diversification of angiosperm taxa began in the Albian (mid-Cretaceous)
- At that time, there was an almost exponential increase in angiosperm diversity, and there does not appear to have been any major extinctions of groups in between.
- Despite the large numbers of taxa that are known from rather early in this diversification, there is no indication of where the taxa are coming from.
- D.I. Axelrod has suggested that we do not find early angiosperm fossils because the earliest angiosperms lived in dry, upland habitats where they were unlikely to be preserved as fossils. This idea remains to be tested.



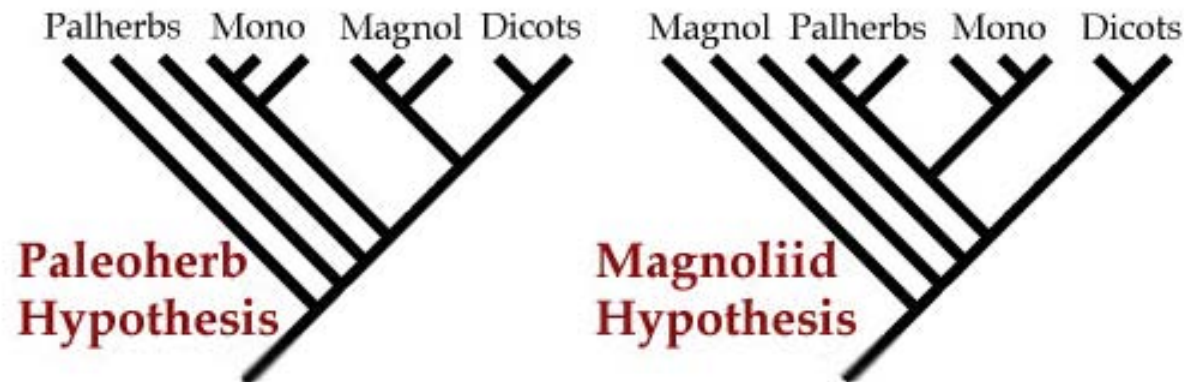
Image courtesy of Museum of Paleontology, University of California. Used with permission.

Nearly all of our food comes from flowering plants; grains, beans, nuts, fruits, vegetables, herbs and spices almost all come from plants with flowers, as do tea, coffee, chocolate, wine, beer, tequila, and cola. Much of our clothing comes from them as well -- cotton and linen are made from "fibers" of flowering plants, as are rope and burlap, and many commercial dyes are extracted from other flowering plants. We also owe them credit for a large number of our drugs, including over-the-counter medicines such as aspirin, prescribed drugs such as digitalis and atropine, and controlled drugs such as opium, cocaine, marijuana, and tobacco.

Angiosperm Phylogeny ???



<http://www.ucmp.berkeley.edu/anthophyta/anthophyta.html>



Angiosperm Origins: The two competing hypotheses for angiosperm origins paint very different pictures about the biology of the earliest flowering plants.

The Paleoherb Hypothesis suggests that the basal lineages were herbs with rapid lifecycles.

Magnoliid Hypothesis suggests that the basal lineages were small trees with slower lifecycles. (Dicots=tricolpate dicots; Magnol=magnoliids; Mono=monocots; Palherbs=paleoherbs)

<http://www.ucmp.berkeley.edu/anthophyta/anthophytafr.html#origin>

- **The Woody Magnoliid Hypothesis** -- Cladistic analyses by Doyle and Donoghue favor an early angiosperm with morphology similar to living members of the Magnoliales and Laurales.
- These groups are small to medium-sized trees with long broad leaves and large flowers with indeterminate numbers perianth parts. The carpels are imperfectly fused, and make a physical intermediate between a folded leaf and fused pistil. This hypothesis is also favored by molecular studies, and so currently is favored by systematic botanists.
- **It suggests that the earliest angiosperms were understory trees and shrubs, and that the flower was NOT the key innovation for the rapid diversification of angiosperms. In fact woody magnoliids are not particularly diverse, even today.**
- **The Paleoherb Hypothesis** -- The alternative view is an herbaceous origin for the angiosperms. This view has been championed in recent years by Taylor and Hickey, paleobotanists whose cladistic analysis of angiosperms suggests a very different scenario from that previously described. In their analysis, the basal angiosperms are tropical paleoherbs, a group of flowering plants with uncomplicated flowers and a mix of monocot and dicot features.
- **The implication here is that the key innovations of flowers and a rapid life cycle were present in the earliest angiosperms. It has been suggested that changes in climate or geography provided opportunities for these early angiosperms to diversify.**

Molecular Clock data for Plant Evolution

Molecular Evidence for the Early Colonization of Land by Fungi and Plants

Daniel S. Heckman, David M. Geiser, Brooke R. Eidell, Rebecca L. Stauffer, Natalie L. Kardos, S. Blair Hedges

The colonization of land by eukaryotes probably was facilitated by a partnership (symbiosis) between a photosynthesizing organism (phototroph) and a fungus. However, the time when colonization occurred remains speculative. The first fossil land plants and fungi appeared 480 to 460 million years ago (Ma), whereas molecular clock estimates suggest an earlier colonization of land, about 600 Ma. Our protein sequence analyses indicate that green algae and major lineages of fungi were present 1000 Ma and that land plants appeared by 700 Ma, possibly affecting Earth's atmosphere, climate, and evolution of animals in the Precambrian.

Science 293, 1129 (2001)

Mesozoic Era: Stratigraphy

You can find out more about the Mesozoic by clicking on the chart below!

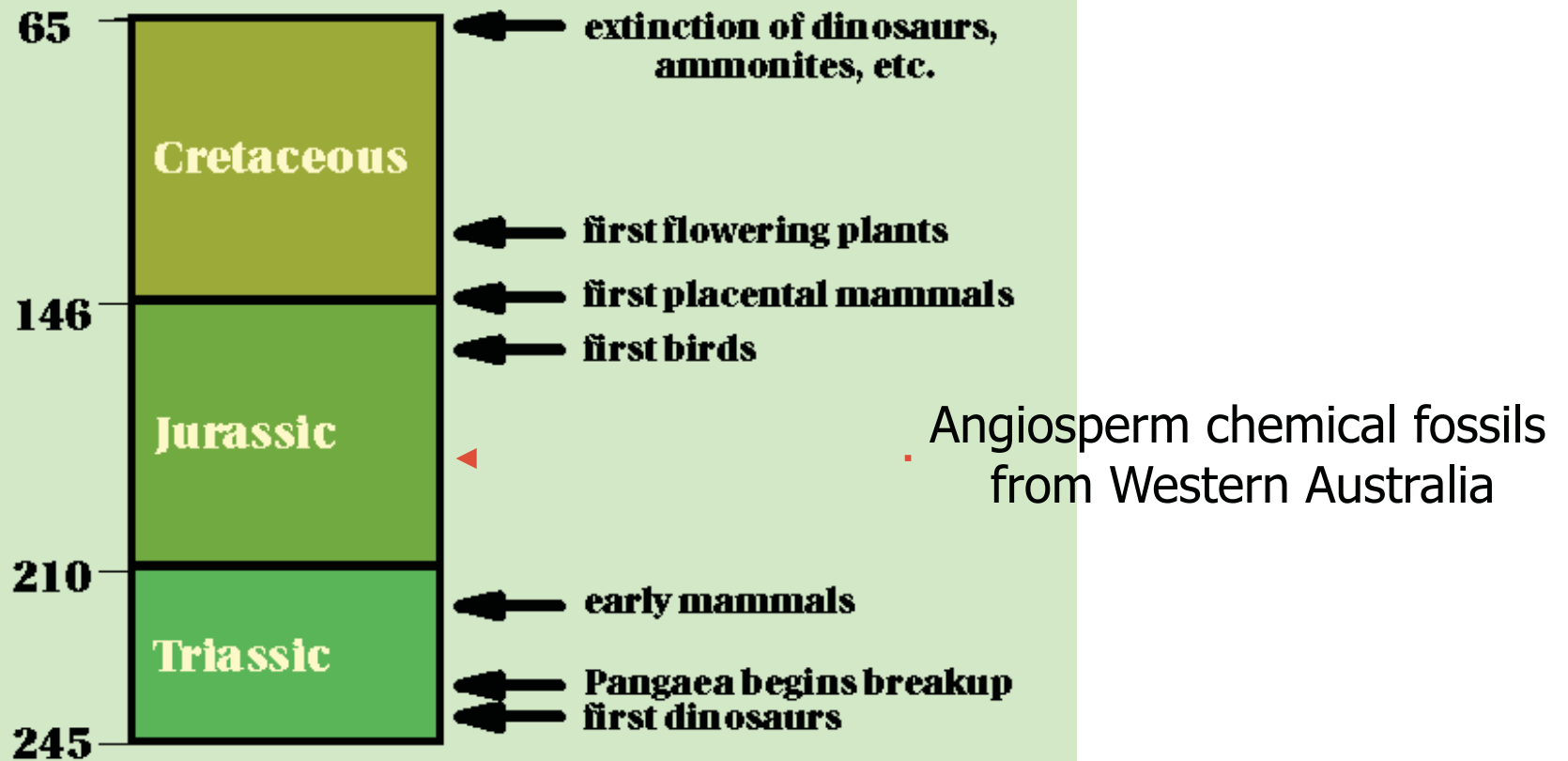


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<http://www.ucmp.berkeley.edu/mesozoic/mesozoicstrat.html>

Innovations and Impacts of Algae and Land Plants

Ability to colonize terrestrial ecosystems →
Changes to the weathering regime & hydrological cycle

New biochemistries for cell wall and structural materials → cellulose, lignin, sporopollenin, algeenan

Recalcitrant organic matter aided preservation →
increase in f_{org} and increase in $p\text{O}_2$

Eocene (?) radiation of C4 plants; grasslands vs forests
Driving forces? Low $p\text{CO}_2$, aridity?

Comparative Responses of Model C3 and C4 Plants to Drought in Low and Elevated CO₂

JOY K. WARD, DAVID T. TISSUE, RICHARD B. THOMAS and BOYD R. STRAIN

Abstract

Interactive effects of CO₂ and water availability have been predicted to alter the competitive relationships between C3 and C4 species over geological and contemporary time scales. We tested the effects of drought and CO₂ partial pressures ($p\text{CO}_2$) ranging from values of the Pleistocene to those predicted for the future on the physiology and growth of model C3 and C4 species. We grew co-occurring *Abutilon theophrasti* (C3) and *Amaranthus retroflexus* (C4) in monoculture at 18 (Pleistocene), 27 (preindustrial), 35 (current), and 70 (future) Pa CO₂ under conditions of high light and nutrient availability. After 27 days of growth, water was withheld from randomly chosen plants of each species until visible wilting occurred. Under well-watered conditions, low $p\text{CO}_2$ that occurred during the Pleistocene was highly limiting to C3 photosynthesis and growth, and C3 plants showed increased photosynthesis and growth with increasing $p\text{CO}_2$ between the Pleistocene and future CO₂ values. Well-watered C4 plants exhibited increased photosynthesis in response to increasing $p\text{CO}_2$, but total mass and leaf area were unaffected by $p\text{CO}_2$. In response to drought, C3 plants dropped a large amount of leaf area and maintained relatively high leaf water potential in remaining leaves, whereas C4 plants retained greater leaf area, but at a lower leaf water potential. Furthermore, drought-treated C3 plants grown at 18 Pa CO₂ retained relatively greater leaf area than C3 plants grown at higher $p\text{CO}_2$ and exhibited a delay in the reduction of stomatal conductance that may have occurred in response to severe carbon limitations.

Image by MIT OpenCourseWare.

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12.007 Geology
Spring 2013

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