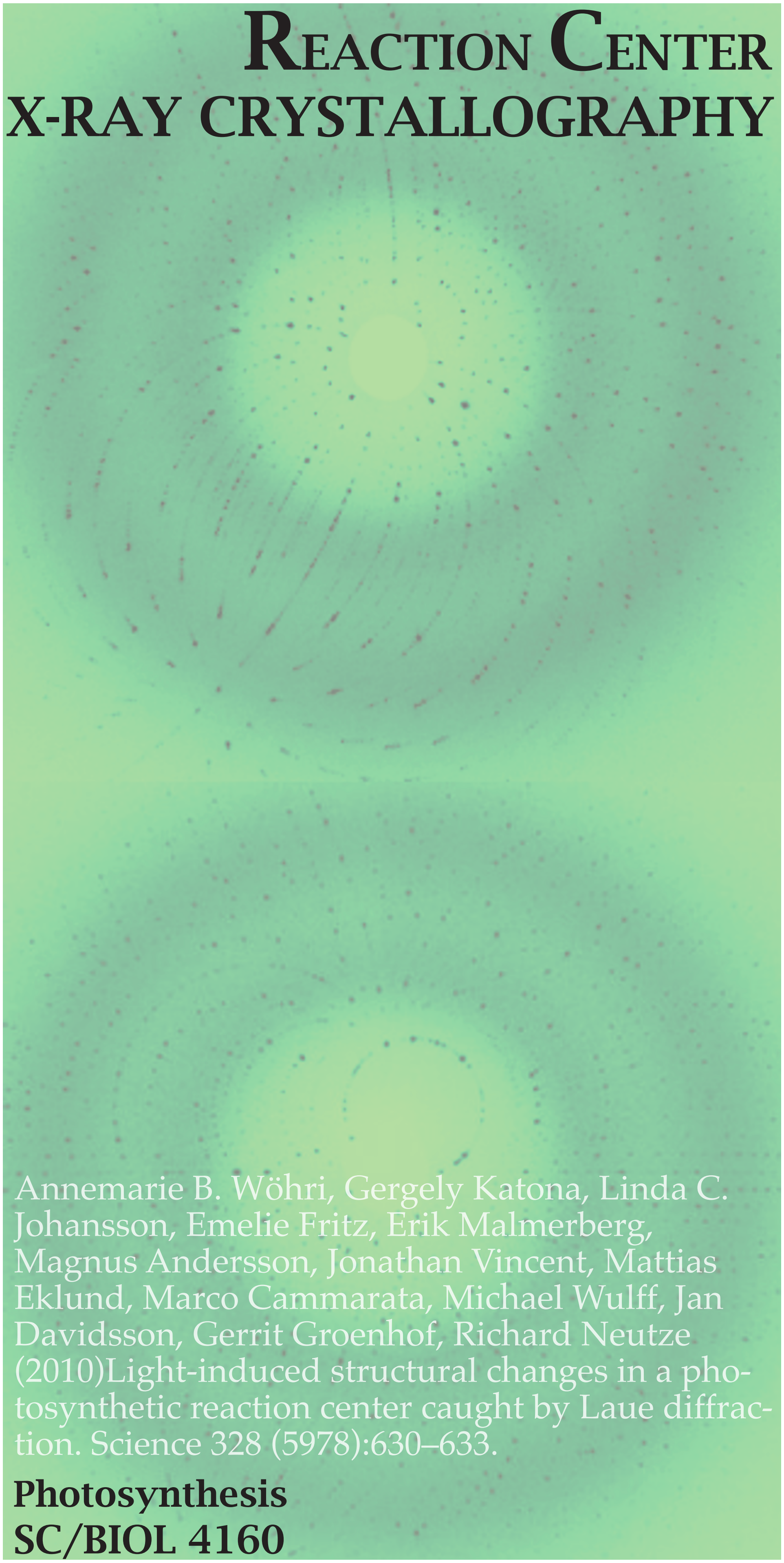
Reaction Center
X-RAY CRYSTALLOGRAPHY



Annemarie B. Wöhri, Gergely Katona, Linda C. Johansson, Emelie Fritz, Erik Malmerberg, Magnus Andersson, Jonathan Vincent, Mattias Eklund, Marco Cammarata, Michael Wulff, Jan Davidsson, Gerrit Groenhof, Richard Neutze (2010)Light-induced structural changes in a photosynthetic reaction center caught by Laue diffraction. Science 328 (5978):630–633.

Photosynthesis
SC/BIOL 4160

Looking for a Clean Energy Source?
Try Photosynthesis.

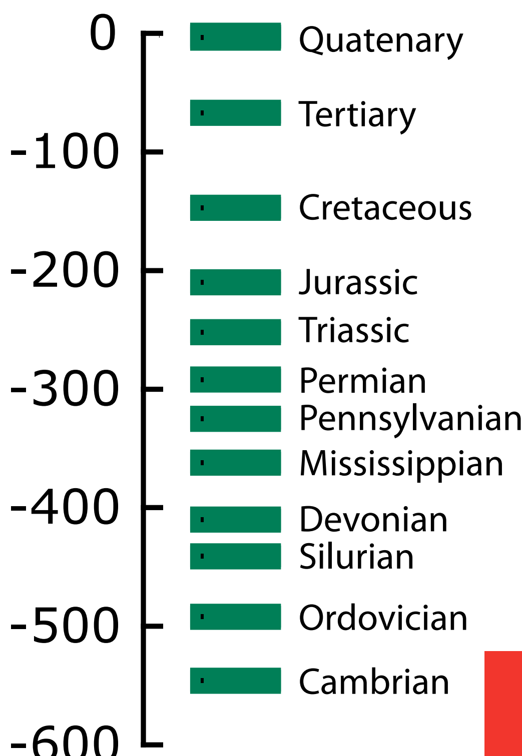
Want Oxygen?
Try Photosynthesis.

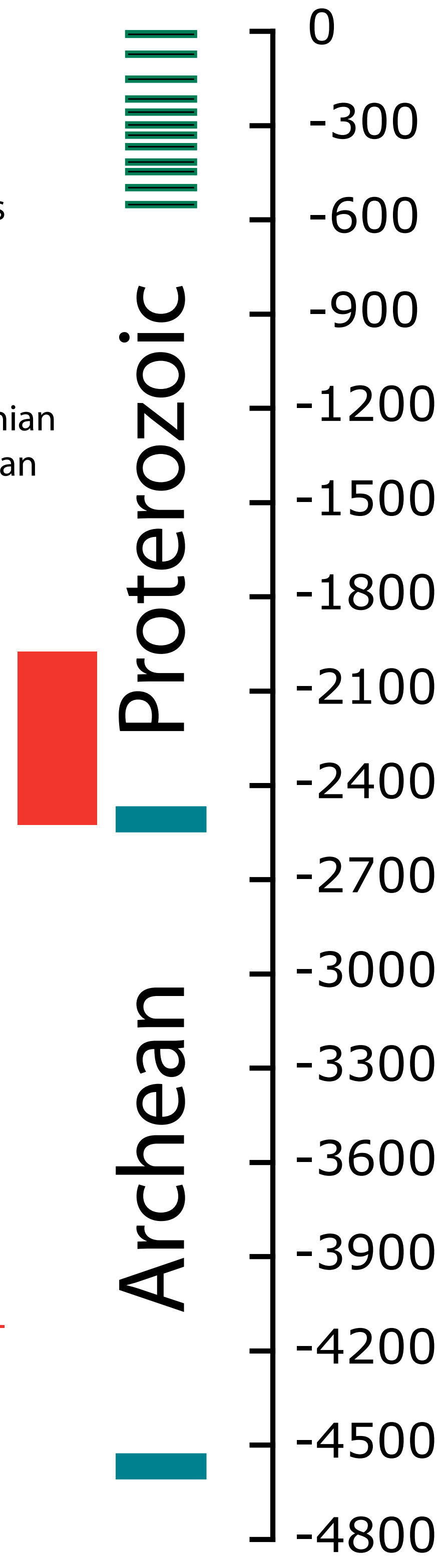
Want to Remove Excess Carbon Dioxide?
Try Photosynthesis.

Want to Eat?
Try Photosynthesis.

Although life had begun in the form of anaerobic bacteria early in the Archean Eon, photosynthetic bacteria did not appear until the middle Archean and were not abundant until the start of the Proterozoic. The bacteria emitted oxygen. The atmosphere changed. The oceans changed. The oceans had been rich in dissolved ferrous iron, in large part put into the seas by the extruding lavas of two billion years. Now with the added oxygen, the iron became ferric, insoluble and dense. Precipitating out, it sank to the bottom as ferric sludge, where it joined the lime muds and silica muds and other seafloor sediments to form, worldwide, the banded-iron formations that were destined to become rivets, motorcars, and cannons. This was the iron of the Mesabi Range, the Australian iron of the Hammerslee Basin, the iron of Michigan, Wisconsin, Brazil. More than ninety percent of the iron ever mined in the world has come from Precambrian banded-iron formations. Their ages date broadly from twenty-five hundred to two thousand million years before the present. The transition that produced them—from a reducing to an oxidizing atmosphere and the associated radical changes in the chemistry of the oceans—would be unique. It would never repeat itself. The earth would not go through that experience twice.

John McPhee. Annals of the Former World





Plant Biology

SC/BIOL 2010

GO Green

A GEOLOGICAL HISTORY OF PHOTOSYNTHESIS.

Much of the evidence of the origins of photosynthesis is indirect.

In great part, this is because of a dearth of fossil evidence. While the sedimentary rocks, in which fossils are preserved, are abundant for the time period 500 million years ago to the present, Prior to that time, geological upheaval has destroyed much of the fossil record. There are, however, examples of sedimentary rocks which date to about 3500 million years ago. From these, there is evidence in the form of <u>microfossils</u>.

There is also "macro-evidence": PreCambrian Stromatolites.

These are columnar or mound-shaped finely layered rock structures which were recognized as part of the geological record in the mid-1800's.

In the 1960's, their biological origins were verified with the discovery of living stromatolites in a hypersaline lagoon on the western coast of Australia.

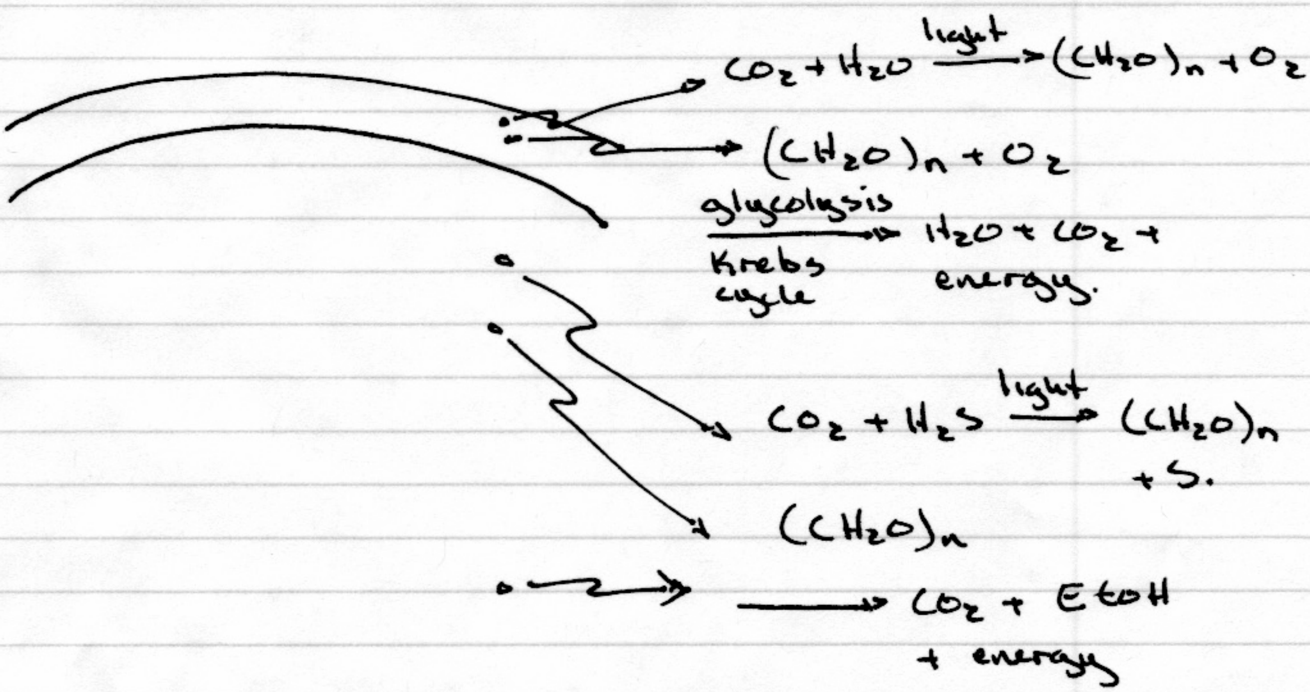
Modern stromatolites are rare, because they 'grow' (accrete) very slowly and would normally be grazed (in the modern era) by invertebrates, such as snails.

They exhibit a well-defined layering.

uppermost felt-like mat (the growth surface) formed by a meshwork of filamentous cyanobacteria that are oxygen-producing photosynthetic micro-organisms and other oxygen-requiring (aerobic) microbes.

A thin undermat containing non-oxygen-producing photosynthetic micro-organisms and facultative aerobes.

A thick lowermost oxygen-depleted zone that contains a "menagerie" of anaerobic micro-organisms.



source: Schopf, J W 1992. The oldest fossils and what they mean. In Major Events in the History of Life.

"living stromatolites" and fossil stromatolites are one line of evidence in support of the archaic origins of photosynthesis
Another has to do with a property of the primary CO_2 - fixing enzyme, Ribulose 1,5 - diphosphate carboxylase: Discriminating between the two isotopes of carbon ~~&~~ $^{13}CO_2$ & $^{12}CO_2$.

<u>nota bene</u>* There are three isotopes in carbon.
Carbon-12 is the predominate stable isotope, about 99% of total carbon.
Carbon-13 is a minor stable isotope, about 1% of total carbon
Carbon-14 is the unstable radioactive isotope (about 10^{-12} %) naturally produced by cosmic ray interactions in the atmosphere. Its half-life is 5730 years.

Photosynthetic discrimination is slight (about 0.1%) but measureable using gas isotope ratio mass spectrometry.

^{12}C enrichment at 17 ‰ (17 parts per thousand) has been observed in PreCambrian rocks as old as 3500 million years ago, consistent with archaic photosynthesis.

* source: http://www.cstl.nist.gov/div837/837.01/index.html (NIST Atmospheric Chemistry Group)

NOTA BENE ^{12}C / ^{13}C isotopic discrimination

^{12}C & ^{13}C are naturally occurring carbon isotopes in the atmosphere: 98.89% and 1.11%, respectively.

RuBisCO reacts with $^{12}CO_2$ more rapidly due to a kinetic isotope effect.

$^{13}C/^{12}C$ ratios are lower in products of C_3 photosynthesis than in the atmosphere

The $^{13}C/^{12}C$ ratio is expressed as $\delta^{13}C$ [‰].

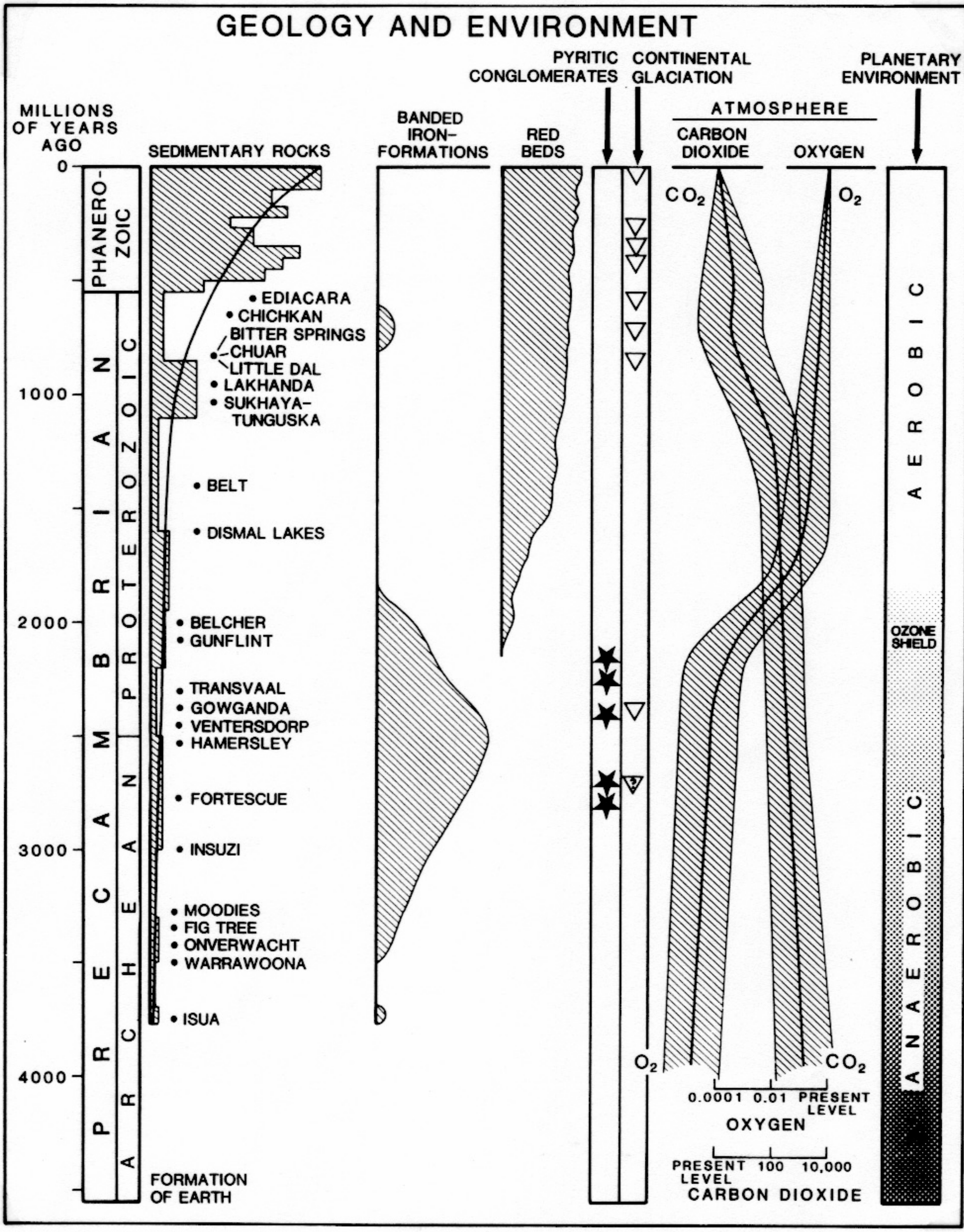
$$\delta^{13}C\,[‰] = \left[\left(\frac{^{13}C/^{12}C \text{ in sample}}{^{13}C/^{12}C \text{ in reference}}\right) - 1\right] \times 10^3$$

(measured with mass spectrometry)

C_3 $\delta^{13}C$ is −28 ‰

C_4 $\delta^{13}C$ is −14 ‰

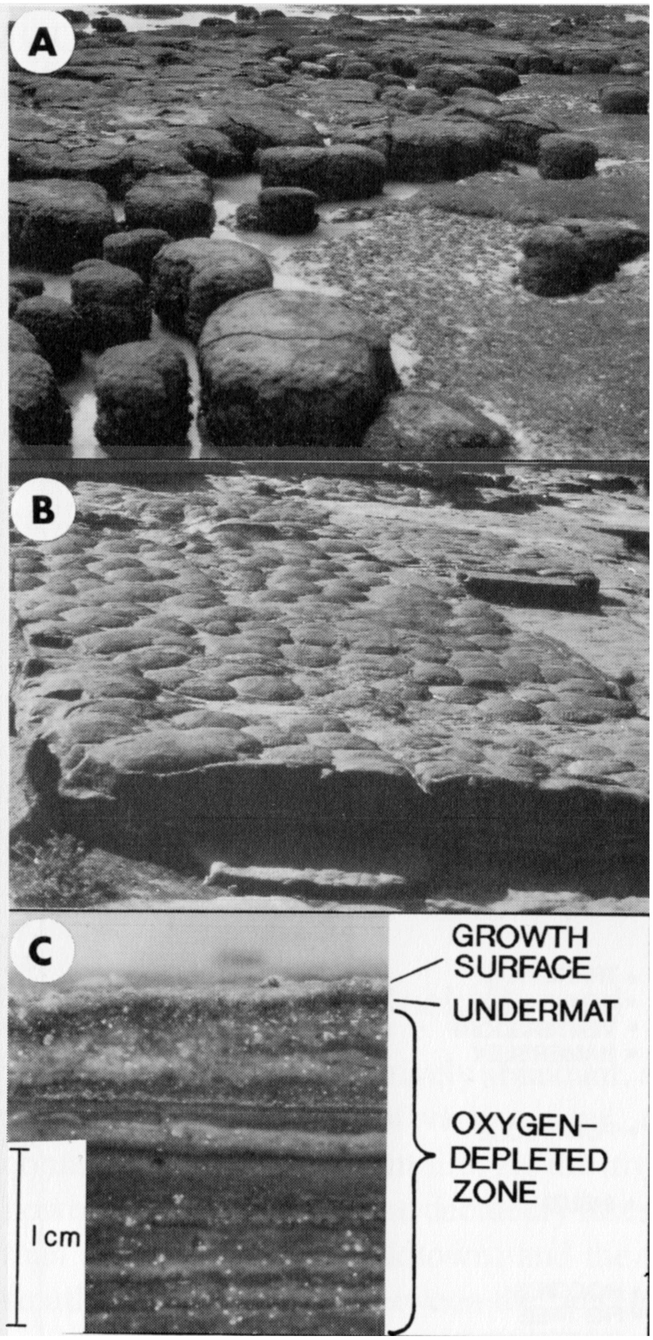
source: H-W Heldt Plant Biochemistry and Molecular Biology. Oxford Univ. Press. page 212.



Source: J. W. Schopf (1992) The oldest fossils and what they mean. *In* Major Events in the History of Life (ed. J. W. Schopf). Jones and Bartlett. Boston

FIGURE 2.3

Modern and fossil stromatolites. (A) Living stromatolitic reef composed of solitary and interconnected columnar and mound-shaped carbonate stromatolites at Shark Bay (Hamelin Pool), 650 km north-northwest of Perth, Western Australia; stromatolites are 30 to 40 cm in height. (B) Precambrian stromatolitic reef composed of interconnected columnar and mound-shaped carbonate stromatolites, about 2300 Ma in age, from the Transvaal Supergroup (Campbellrand Subgroup, Transvaal Dolomite) at Groot Boetsap River, 50 km northwest of Warrenton, northern Cape Province, South Africa; stromatolitic reef is about 40 cm in height. (C) Vertical section of a living stromatolitic microbial mat, showing stratified organization of the photic zone—the uppermost growth surface and the immediately underlying undermat layer—and of the thick, underlying oxygen-depleted zone, from "North Pond," Laguna Mormona-Figueroa, 15 km northwest of San Quintin, Baja California del Norte, Mexico.



Source: JW Schopf (1992) The oldest fossils and what they mean. *In* Major Events in the History of Life (ed. JW Schopf). Jones and Bartlett. Boston.

Principal Biochemical Pathways of Heterotrophic and Autotrophic Metabolism.

HETEROTROPHY

Anaerobic Fermentation (Primitive):

GLUCOSE SUGAR	———> "Glycolysis"	PYRUVATE	(No addition of Molecular Oxygen) ———>	ETHYL ALCOHOL + CARBON DIOXIDE + HEAT	+	2 UNITS OF ENERGY

Aerobic Respiration (Advanced):

GLUCOSE SUGAR	———> "Glycolysis"	PYRUVATE	(Addition of Molecular Oxygen) ———> "Citric Acid Cycle"	WATER + CARBON DIOXIDE + HEAT	+	36 UNITS OF ENERGY

AUTOTROPHY

Anoxic Bacterial Photosynthesis (Primitive):

CARBON DIOXIDE	+	HYDROGEN SULFIDE	(Light Energy) ———> Bacteriochlorophylls	GLUCOSE SUGAR	+	SULFUR

Oxygenic Cyanobacterial Photosynthesis (Advanced):

CARBON DIOXIDE	+	WATER	(Light Energy) ———> Chlorophyll *a*	GLUCOSE SUGAR	+	OXYGEN

Source: J. W. Schopf (1992) The oldest fossils and what they mean. *In* Major Events in the History of Life (ed. J. W. Schopf). Jones and Bartlett. Boston

Indirect evidence for archaic photosynthesis comes from the appearence of iron oxides.

For our purposes, we can consider two oxidation states of iron. the reduced Fe(II)(+) which is highly soluble in water, and the oxidized Fe(III)(x)

(+) ferrous

(x) ferric

As photosynthesis produced oxygen, it would react with ferrous (Fe(II)) iron to produce ferric oxide That is, rust. For example, hematite Fe_2O_3 and magnetite Fe_3O_4.

These are observed in banded iron formations, which appeared about 3500 million years ago, peaking about 2500 million years ago.

Note that the banded iron formations would have been an enormous sink ~~of~~ for oxygen: O_2 would have reacted with oceanic ferrous iron and precipitated to form iron deposits.
To quote Schopf: "... the photosynthetically produced oxygen was scavenged from the oceans and buried forever in the form of rust".

Iron-containing sediments, called red beds appeared from about 1800 million years ago. These originate on land (unlike the subaqueous banded iron formations) and contain only a small amount of iron oxide which coats the sand or silt particles.

To summarize:

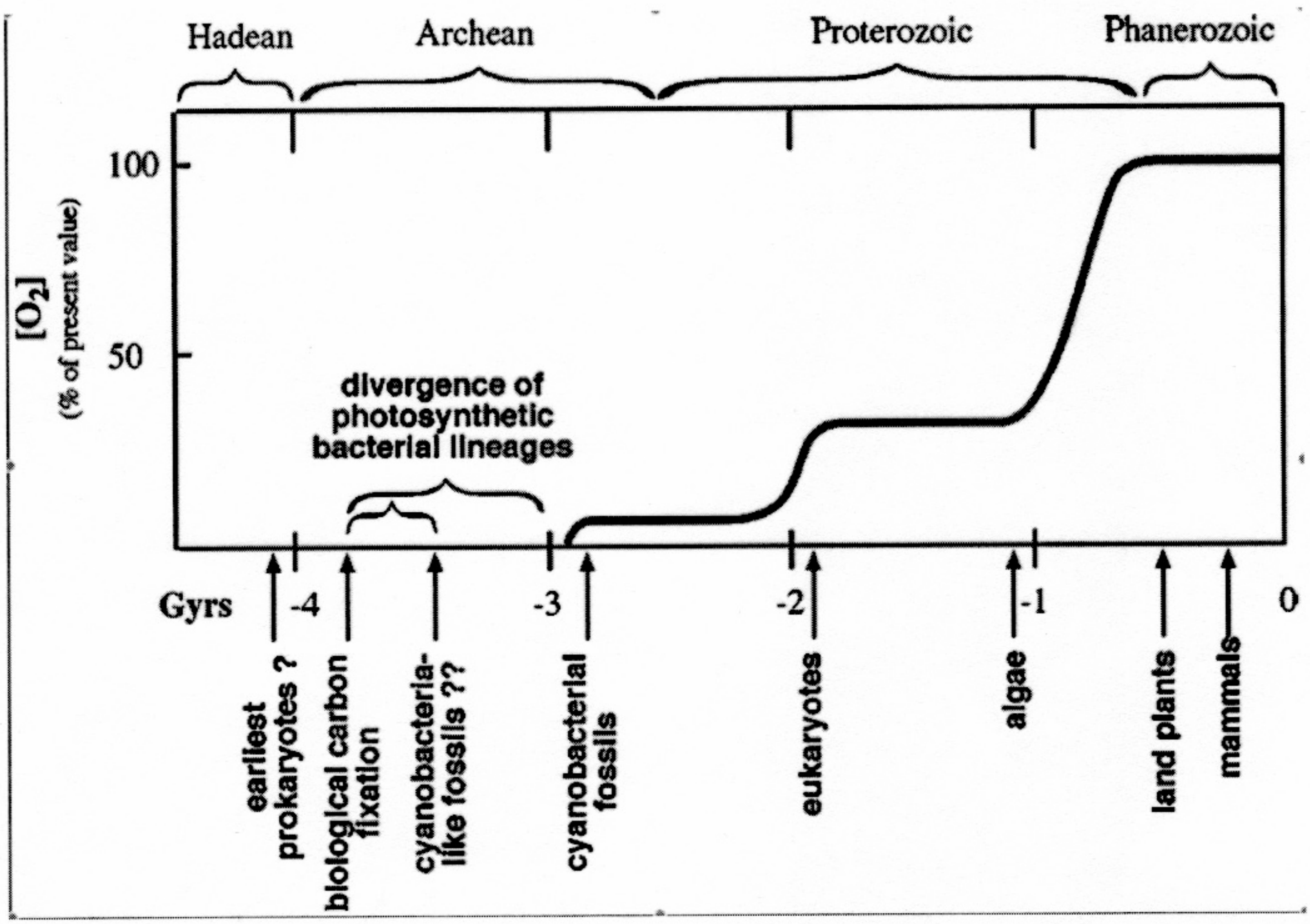
stromatolites, micro-fossils & $^{12}CO_2$ discrimination date from about 3500 million years ago.

oxygen production was consumed by burial in iron-rich layers of banded iron formations

2000 to 1800 million years ago, atmospheric oxygen began to rise.
This timeframe corresponds to fossil-evidence of the RISE OF THE EUKARYOTIC CELL.

Coincidence? I have no idea, but think not.

Figure 1 Schematic representation of the rise of oxygen level on Earth during the early history of life [modified from (27)[1]]. Major evolutionary landmarks are indicated by arrows on the lower x-axis, and major geological periods are indicated by brackets on the upper x-axis. Putative stages of early divergence of photosynthetic prokaryotes are indicated by brackets above the lower x-axis: one assumes ~3–3.8 Gyrs and the other 3.5–3.8 Gyrs, depending on what date is accepted as the starting point for oxygenic photosynthesis.



Carl E. Bauer and Jin Xiong (2002) Complex evolution of photosynthesis. Annual Review of Plant Biology 53:503–521.

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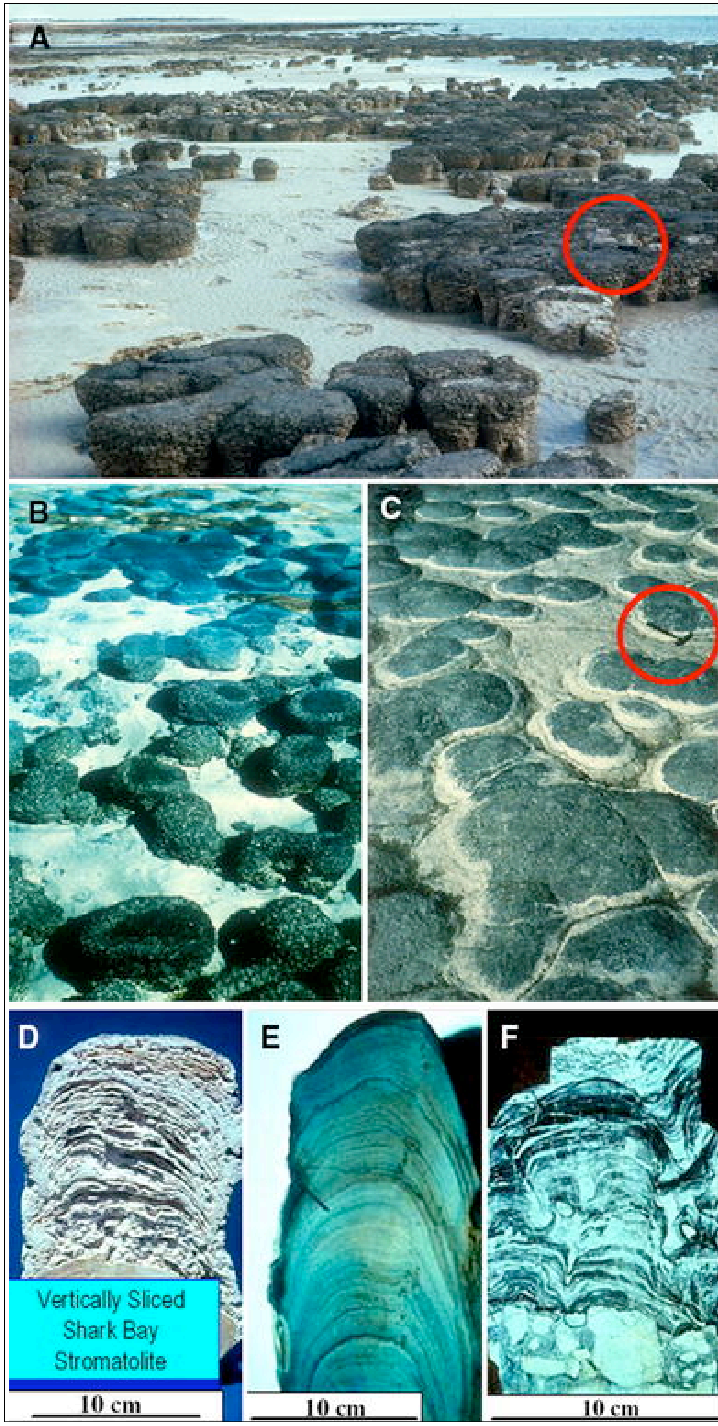
[1] Nitschke W, Muhlenhoff U, Liebl U. 1998. Evolution. In *Photosynthesis: A Comprehensive Treatise*, ed. A. Raghavendra, pp. 286–304. Cambridge, UK: Cambridge Univ. Press

In the beginning photosynthetic systems may have resembled these stromatolites at Shark Bay, Western Australia (Photo Warwick Hillier).



Modern and fossil stromatolites.

A Modern stromatolites at Shark Bay (Hamelin Pool), Western Australia. **B** Modern Shark Bay columnar and domical stromatolites for comparison with (**C**) fossil stromatolites from the ~2,300-Ma-old Transvaal Dolomite, Cape Province, South Africa. **D–F** Modern and fossil vertically sliced columnar to domical stromatolites showing upwardly accreted microbial laminae from Shark Bay (**D**), the ~1,300-Ma-old Belt Supergroup of Montana (**E**), and the ~3,350-Ma-old Fig Tree Group of the eastern Transvaal, South Africa (**F**). Scale for **A** and **C** shown by the geological hammers enclosed by red circles.

Figure 1 from J. William Schopf (2010) The paleobiological record of photosynthesis. Photosynthesis Research 107:87–101.

Photosynthesis Research
Official Journal of the International Society of Photosynthesis Research

10.1007/s11120-010-9577-1

Review

The paleobiological record of photosynthesis

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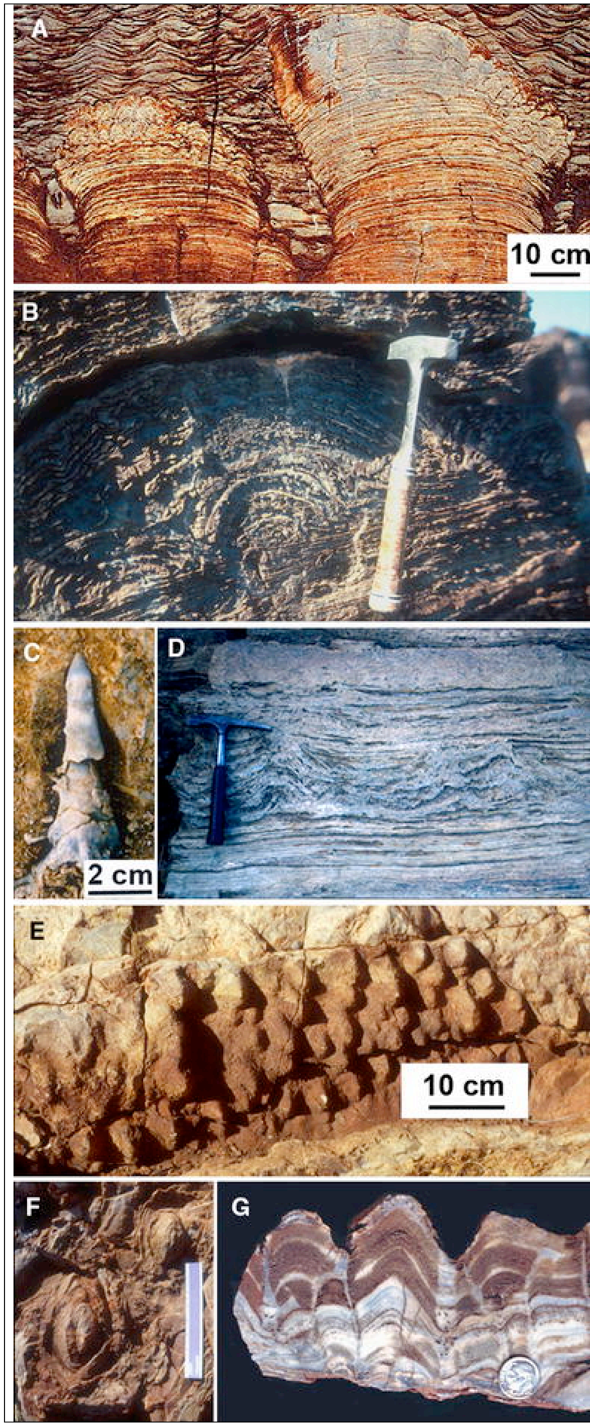

Archean-age microbially laminated stromatolites.

A Domical, pseudocolumnar and branching stromatolites, overlain by rippled sediments, and **B** a domical stromatolite from the ~2,723-Ma-old Tumbiana Formation (Fortescue Group) of Western Australia. **C** Conical stromatolite and **D** stratiform and conical stromatolites, from the ~2,985-Ma-old Insuzi Group, South Africa. **E–G** Laterally linked conical stromatolites from the ~3,388-Ma-old Strelley Pool Chert of Western Australia

Figure 3 from J. William Schopf (2010) The paleobiological record of photosynthesis. Photosynthesis Research 107:87–101.

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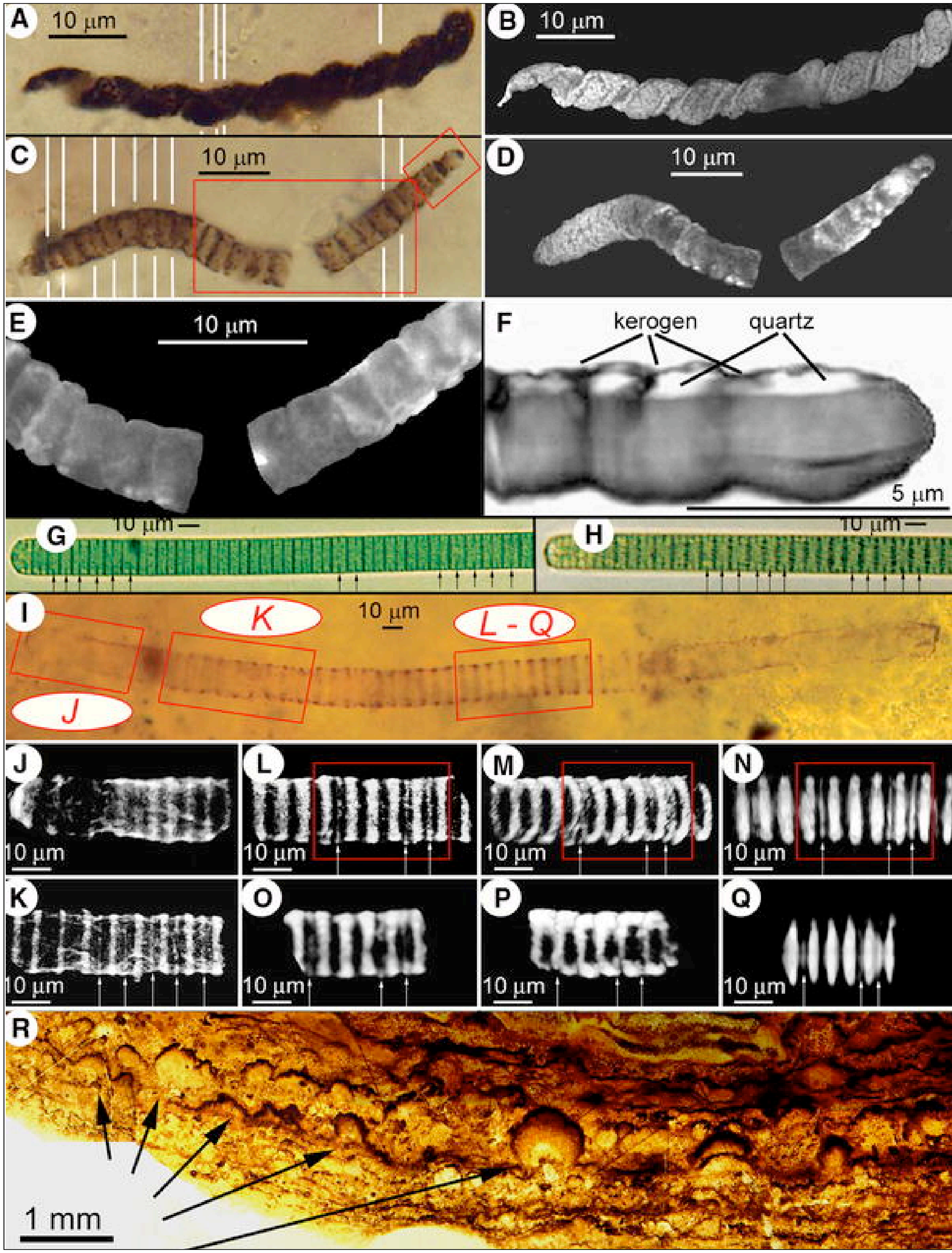

Fossil oscillatoriacean cyanobacteria (a through f) **Modern oscillatoriaceans** (g and h) **compared with a morphologically similar fossil trichome** (i through q)

Figure 4 from J. William Schopf (2010) The paleobiological record of photosynthesis. Photosynthesis Research 107:87–101.

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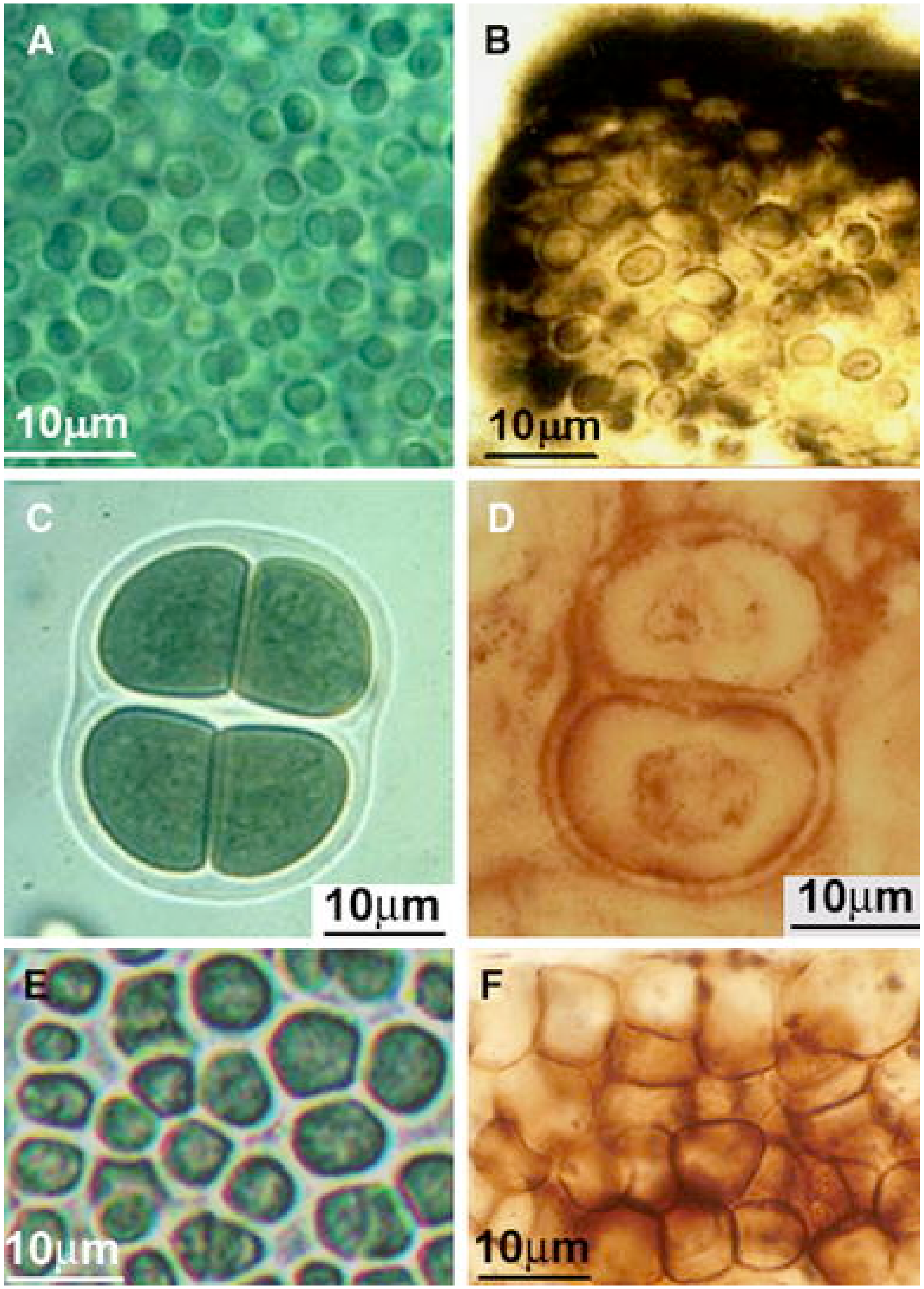

Modern
(left panels)
Fossil
(right panels)
cyanobacteria.

Figure 5 from J. William Schopf (2010) The paleobiological record of photosynthesis. Photosynthesis Research 107:87–101.

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