In 1951, Calvin published one of the first works in prebiotic chemistry. He reduced carbon dioxide in aqueous solution, by ionizing radiation, to formic acid.

In 1953, Harold Urey rejected this result because of the presence of CO₂. Urey was in favor of a reductive primitive atmosphere without CO₂. However, Calvin maintained his interest for origins of life during the rest of his career, and published his main book on this topic in 1969 (Molecular Evolution towards the Origin of Living Systems on Earth and Elsewhere).

**Keywords**
Biosynthesis, autotrophy, carboxylation, carbon dioxide

**Definition**
A carbon dioxide fixation pathway where a molecule of CO₂ condenses with a 5-C compound (ribulose 1,5-bisphosphate) to yield two molecules of a 3-C compound (3-phosphoglycerate). These 3-C molecules serve both as precursors for biosynthesis and, through a cyclic series of enzymatic reactions, to regenerate the 5-C molecule necessary for the first carboxylating step (Fig. 1). The pathway is present in several bacterial lineages (e.g., cyanobacteria) and its acquisition by eukaryotic cells (chloroplast in algae and plants) was through the endosymbiotic association with ancient cyanobacteria.

**History**
Melvin Calvin (1911–1997) and coworkers established this autotrophic path of carbon in phototrophic organisms using ¹⁴C labelled carbon dioxide and *Chlorella* (a green algae) cultures (Benson & Calvin 1950). Calvin was awarded with the Nobel Prize in Chemistry in 1961 “for his research on the carbon dioxide assimilation in plants.”

**Overview**
The Calvin–Benson cycle allows the synthesis of one triose from three molecules of carbon dioxide (Fig. 1):

![Calvin–Benson Cycle](image)

**Calvin–Benson Cycle. Figure 1** The Calvin–Benson cycle. The stoichiometry of the cycle allows the net synthesis of one molecule of triose from three molecules of carbon dioxide (gray boxes). Other five trioses (5 C₃) are converted into three pentoses (3 C₅) necessary to initiate the cycle again. The energetic cost for the synthesis of one triose is nine ATP molecules and six reducing equivalents (NADH or NADPH). These energetic requirements could be satisfied by a photosynthetic apparatus or a chemolithotrophic metabolism. Except for two key enzymatic steps (1 and 2), all the transformations are a combination of enzymes participating in the Embden–Meyerhof–Parnas pathway and the non-oxidative pentosephosphate pathway. Key enzymatic steps: (1) Rubisco; (2) phosphoribulokinase. Abbreviations: Gd3P, glyceraldehyde 3-phosphate; DHAP, dihydroxyacetonephosphate.
12 electrons (provided by redox coenzymes like NADH or NADPH) and 9 ATP equivalents are required for bringing CO₂ to the oxidation level of the triose glyceraldehyde 3-phosphate. These fueling requirements are supplied by either a phototrophic or a chemolithotroph metabolism. The cycle can be divided into two stages: a reductive carboxylation of the pentose ribulose 1,5-bisphosphate (RuBP) up to glyceraldehyde 3-phosphate and a series of rearrangements of carbon skeletons from trioses to regenerate RuBP throughout 4-, 6-, and 7-C sugar intermediates (Fig. 1). The first step is catalyzed by the key carboxylating enzyme ▶ Rubisco. As other carboxylases, Rubisco also shows a preference for lighter stable isotopes and thus CO₂ fixation results in the depletion of ¹³C(δ¹³C) in the biosynthesized organic matter ranging from −20‰ to −30‰. The second stage of the cycle occurs by the combination of several enzymatic activities from the ▶ Embden–Meyerhof–Parnas pathway and the non-oxidative branch of the pentose phosphate pathway.

The Calvin–Benson cycle was originally described in green plant (i.e., chloroplast) photosynthesis (Benson & Calvin 1950). It is also active in endosymbiotic chemolithotrophic proteobacteria of invertebrates living in close proximity to hydrothermal vents. In free-living prokaryotes, this pathway has been demonstrated in cyanobacteria (the group to which the ancestors of plastids belonged), some aerobic or facultative anaerobic proteobacteria, CO-oxidizing mycobacteria, diverse iron-sulfur-oxidizing firmicutes and in some green sulfur bacteria. Although Rubisco has been isolated from some Archaea, there is no evidence for the operation of the full cycle in autotrophic species from this domain (Berg et al. 2010).

See also
▶ Autotrophy
▶ Embden–Meyerhof–Parnas Pathway
▶ Isotopic Fractionation (Planetary Process)
▶ Rubisco

References and Further Reading

Cambrian Explosion

Synonyms
Cambrian radiation

Definition
The Cambrian explosion was a major evolutionary radiation of organisms, notably multicellular animals (metazoans), that occurred during the Cambrian period (542–588 Ma). Pre-Cambrian fossils reveal a mainly microbial biota, with complex, large-bodied organisms only becoming conspicuous during the latest Proterozoic Eon (the Ediacaran biota). In contrast, Cambrian fossils include abundant evidence for macroscopic motile organisms, and unambiguous examples of most major animal lineages. Exactly what determined the timing of the Cambrian explosion is not clear, and current research aims to disentangle the effects of physical environment, ecological context, and factors related to development and genetics.

See also
▶ Burgess Shale Biota
▶ Chengjiang Biota, China

Cambrian Radiation

▶ Cambrian Explosion

Campbellrand–Malmani Platform, South Africa

Definition
The Campbellrand–Malmani ▶ carbonate platform was deposited in the Kaapvaal craton, South Africa between 2,588 and 2,520 Ma (Neoarchean). This 1.9-km-thick carbonate platform is preserved over at least 190,000 km² and probably originally covered the entire remaining extent of the Kaapvaal craton (600,000 km²). The Campbellrand–Malmani is the first extended carbonate deposit in the Neoarchean ocean, prior of the buildup of the oxygen in the ocean and atmosphere, 2.35 Ga ago. Abundant of aragonite in its deposits suggests a neutral to