THE JOURNAL OF BIOLOGICAL CHEMISTRY

Vol. 285, No. 20, Issue of May 14, p. e6, 2010
Printed in U.S.A.

Classics

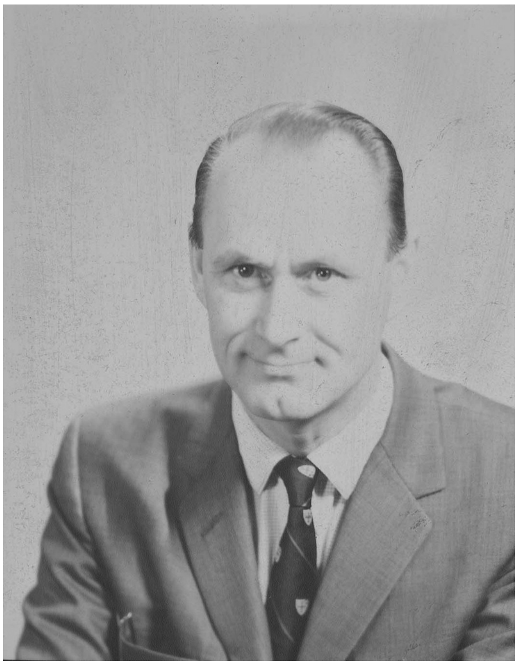
A PAPER IN A SERIES REPRINTED TO CELEBRATE THE CENTENARY OF THE JBC IN 2005

JBC Centennial
1905–2005
100 Years of Biochemistry and Molecular Biology

The Discovery of Glyoxysomes: the Work of Harry Beevers

Sucrose Synthesis from Acetate in the Germinating Castor Bean: Kinetics and Pathway
(Canvin, D. T., and Beevers, H. (1961) *J. Biol Chem.* 236, 988–995)

Mitochondria and Glyoxysomes from Castor Bean Endosperm. Enzyme Constituents and Catalytic Capacity
(Cooper, T. G., and Beevers, H. (1969) *J. Biol. Chem.* 244, 3507–3513)



Harry Beevers. Photograph courtesy of Purdue University Libraries, Karnes Archives and Special Collections.

Harry Beevers (1924–2004) was born in Shildon, a small industrial town in County Durham, England. He initially wanted to become a schoolteacher who taught woodworking and arts and crafts but was forced to choose an alternate career when wartime shortages of materials prevented his school from stocking the supplies necessary for those courses. Fortunately, in secondary school he was inspired by a biology teacher who took his students on field trips to study the local ecology of the nearby moors. Encouraged by this teacher to do independent research, Beevers borrowed a microscope from the school and analyzed the flora and fauna of local ponds. This project inspired Beevers to pursue a career in science.

In 1942, Beevers entered the accelerated wartime university program and received a B.Sc. in botany from King's College in Newcastle upon Tyne (then part of Durham University). He remained at King's College for graduate school, studying CO_2 fixation with Meirion Thomas, which led him to a lifelong interest in plant metabolism.

After earning his doctoral degree, Beevers moved to Oxford University. He became first assistant, and later chief research assistant, in plant physiology in the medicinal plant research laboratory of W. O. James, an authority on plant respiration. Beevers' research in Oxford centered on the biosynthesis of tropane alkaloids. He also looked into the uptake of weak acids and weak bases by plant organs.

In 1950, Beevers attended a meeting on CO_2 fixation organized by the Society for Experimental Biology. There he realized that radioactive $^{14}CO_2$ would help answer some of his research questions. Because this isotope was more readily available in the United States and job prospects were limited in postwar England, Beevers obtained an appointment as an assistant professor in the department of biology at Purdue University.

At Purdue, Beevers continued his studies on plant respiration but also decided to look at the pathway involved in the conversion of fat to sugar in castor bean seedlings. His initial work centered on "feeding" labeled precursors to castor bean endosperm and analyzing the products

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and on isolating mitochondria and studying their metabolic properties. However, his major breakthrough occurred when he was on sabbatical leave at Oxford University in 1956 and Hans Krebs suggested that Beevers collaborate with Hans Kornberg on the conversion of fat to carbohydrate in plants. Working together, Beevers and Kornberg showed that malate synthase and isocitrate lyase, the two enzymes that characterize the glyoxylate cycle, were present in the endosperm of castor beans (1, 2). This discovery set the course of Beevers' research for the next 25 years.

To prove that the glyoxylate cycle was converting fat to sugar in castor bean endosperm, Beevers and David Canvin provided a variety of ^{14}C-labeled substrates to slices of castor bean endosperm. As reported in the first *Journal of Biological Chemistry* (JBC) Classic reprinted here, the resulting labeling patterns were in agreement with the postulated pathways: succinate produced from acetate served as a precursor for glucose by a reversal of glycolysis. The experiments also showed that the classic tricarboxylic acid cycle did not operate during germination, and instead, acetate was metabolized into sugars via the newly discovered glyoxalate shunt. Because considerable amounts of carbohydrates are required by plants for cell wall synthesis during growth, the glyoxalate shunt provided sugars from the acetyl-CoA generated by β-oxidation of fatty acids in the absence of available carbohydrates.

The next big discovery in was made by Beevers' postdoctoral fellow Bill Breidenbach, who analyzed the linear sucrose gradients of endosperm homogenates and showed that the glyoxylate cycle enzymes were found in an organelle fraction that was not mitochondria (3). Beevers and Breidenbach called these new organelles glyoxysomes.

Following up on this finding, Beevers and T. G. Cooper set about showing that all of the enzymes necessary for the glyoxylate cycle were present in glyoxysomes. To do this, they assayed each of the 16 enzymes of the citric acid and glyoxylate cycles in preparations of mitochondria and glyoxysomes from 5-day-old castor bean endosperm. They found that 85% of isocitrate lyase and malate synthetase activities, the two enzymes unique to the glyoxalate shunt, were confined to the glyoxysomes. In addition, a new enzyme was found, glutamate: oxalacetate transaminase, and shown to be in high concentrations in both glyoxysomes and mitochondria. Beevers and Cooper (4) also noted that both succinate dehydrogenase and fumarase activities were not present in glyoxysomes, leading them to conclude that the succinate produced in glyoxysomes must be transported to the mitochondria (where succinate dehydrogenase and fumarase activities are high) before being metabolized to malate.

Beevers' discovery of glyoxysomes led to others finding similar organelles, leaf peroxysomes, and also greatly improved our understanding of peroxysomal metabolism in animals.

In 1969, Beevers joined the faculty of the new campus of the University of California, Santa Cruz, where he remained for the rest of his career. He earned many awards and honors for his research, including the American Society of Plant Physiologists' Stephen Hales Prize in 1970 and its Charles Reid Barnes Life Membership Award in 1999. He was also elected to the U.S. National Academy of Sciences and the American Academy of Arts and Sciences and served as the president of the American Society of Plant Physiologists. In 1995, Oxford University named a building in his honor, the Harry Beevers Laboratory in the Plant Sciences Department.[1,2]

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DOI 10.1074/jbc.O110.000228

[1] We thank Neil P. J. Price for providing background information on Harry Beevers.
[2] Additional background information on Harry Beevers was taken from Ref. 5.