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Letter to the Editor

Francis Theodore Haxo (March 9, 1921–June 10, 2010): Innovator, Dedicated Biologist, and Grand Master of the Carotenoids in Marine Organisms

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Francis Haxo has been known to us as a thoughtful, patient, and dedicated scientist of the highest order. As a genuine scholar, he meticulously mulled over ideas for years before publishing his research. One of us (GG) knew him through three other friends: Barbara B. Prézelin, 1948-2021; David (Dave) C. Fork, 1929-2020; Beatrice (Beazy) M. Sweeney, 1914-1989; additionally, Anitra Thorhaug (AT) knew him as she was the last student of Larry Blinks, with whom Haxo had worked with. Francis Haxo was generous to his students, but he took a long time to finalize and submit their papers—to ensure that all was well. We provide here a glimpse of his research after a brief note on his personal life—remembering him more than a decade after his death. He was an unsung hero and he deserves to be remembered by algal, marine, and plant biologists throughout the world. A thorough and detailed memorial to Francis Haxo and his research, will soon be published by Anitra Thorhaug, Graeme Berlyn, and Synnøve Liaaen-Jensen (2023).

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PERSONAL LIFE

Francis Theodore Haxo was born on March 9, 1921, in Grand Forks, North Dakota; his parents were Henry Emile and Florence Shull Haxo, who were immigrants from France. Henry was a brilliant linguist, and a professor of French at the University of North Dakota. Francis married Nan Bolander in 1946, they had 2 children, and divorced in the mid-1950s. In 1961, he married Judith McLaughlin, with whom he had 3 children. Francis died of pneumonia on June 10, 2010, in San Diego/La Jolla, California. Figure 1 shows a photograph of F. T. Haxo aged about 50.

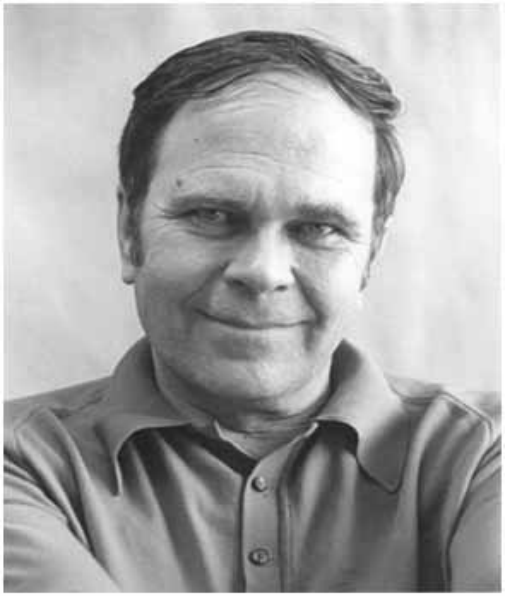

Fig. 1: A 1970s photograph of Francis T. Haxo taken at Brookhaven National Laboratory; Haxo was then a professor at the Scripps Institution of Oceanography.
Source: **https://library.ucsd.edu/dc/object/bb12638060/zoom/0**

ACADEMIC LIFE AND RESEARCH: PRE-1960 PERIOD

In 1937, Francis graduated from Central High School in Grand Forks, North Dakota. In 1941, he obtained his BS (Biology) from the University of North Dakota, the state's oldest and largest university. Then, during

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World War II (1941-1945), while in the USA, Francis investigated biochemical formulae for the best "sunscreens" to protect military persons from damaging UV light, especially in the South Pacific. He had joined Stanford University as a graduate student in Biology in the early 1940s. He obtained his PhD in Biology from Stanford, in 1947; here, he had the benefit of learning from top authorities such as Arthur C. Giese (1905-1994; Photobiology); George Beadle (1903-1989; Genetics; <https://en.wikipedia.org/wiki/George_Beadle>); Cornelis Van Niel (1897-1985; Microbiology; <https://en.wikipedia.org/wiki/C._B._van_Niel>); and Lazlo Zechmeister (1890-1972; Organic Chemistry; see Ettre, 1989). At Stanford, Francis was introduced to work on *Neurospora*, then a highly popular organism, a fungus (Zechmeister and Haxo, 1946). Haxo (1949) made pioneering observations on the yellow-orange pigments (the carotenoids) in this organism. Soon thereafter, he was offered a post-doctorate position at the Hopkins Marine Station of Stanford University with Professor Lawrence R. Blinks, where he became known for designing and using the Haxo-Blinks electrode for accurately measuring photosynthesis, as well as for the original work on *chromatic transients* in oxygenic photosynthesis (Haxo and Blinks, 1950). For a full understanding of this research, especially in light of the discovery of the two-light effect (the Emerson Enhancement Effect: Emerson et al., 1957; Emerson and Rabinowitch, 1960), see Blinks, 1954, 1960, but, especially Haxo, 1960. Further, excellent tributes to Blinks (Thorhaug and Berlyn, 2009, and Abbott and Smith, 2010) provide additional nuances to Haxo's research of this time.

The above research was followed by the discovery of a new carotenoid, peridinin, in Haxo's next position, when he joined the *Plant Physiology* Department at Johns Hopkins University (Baltimore, Maryland). This carotenoid has been widely used in coloration of food [e.g., Pinckaed et al., (1953); for a general review on this topic, see Gordon and Bauernfeind (1982)].

In 1952, Francis joined the Scripps Institute of Oceanography (San Diego, California) where he worked on a broad range of marine algal topics. Haxo et al., (1955) provided new information on the antenna pigments (both on the red phycoerythrins, and the blue phycocyanins) of many algae. With David Fork, Haxo provided novel information on the accessory pigments of the cryptomonads in a paper published in *Nature* (Haxo and Fork, 1959). With Beazy Sweeney, and Woody Hastings, the topmost circadian rhythm folks, *Gonyaulax polyedra* was added to his research, in which this team provided novel information on the role of pigments in its photosynthesis (Sweeney et al., 1959, which is a highly cited publication). Much later, together with Beazy Sweeney and Barbara Prézelin, Govindjee established circadian rhythm in chlorophyll *a* fluorescence in the same organism (Govindjee et al., 1979; Sweeney et al., 1979).

Before we discuss Haxo's research beyond 1960, we provide here a connection of one of us (Govindjee) with Haxo through his own background and interest in photosynthesis. Even when Govindjee (Gov) was a graduate student, he respected the research of Francis Haxo.

In 1960, he had obtained his PhD in Biophysics under the guidance of Eugene Rabinowitch, and had read the Sweeney et al., (1959) paper, on circadian rhythm, mentioned above, as soon as it was available at the UIUC Library. For his PhD, Gov had worked on the role of pigments in the two-light reactions of photosynthesis, following the discovery of the two-light reactions by Emerson et al., (1957); e.g., Govindjee and Rabinowitch, (1960). Govindjee served on the faculty at UIUC from 1961-1999 (see < https://www.life.illinois.edu/govindjee/ >), and during all his teaching in various courses in plant physiology, biophysics, and photobiology, he always cited and discussed the research of Francis Haxo and Larry Blinks.

ACADEMIC LIFE: HAXO'S RESEARCH DURING THE 1960s AND BEYOND

In this *Letter to the Editor*, we simply list chronologically, the various topics that Haxo worked on with his many collaborators during the rest of his life. For details, the readers need to examine, in depth, the publications cited below.

In the 1960s, Haxo published, working with many algae, on circadian rhythm (Sweeney and Haxo,

1961), on pigment proteins (Óh Eocha and Haxo, 1960), on the carotenes and carotenoids (Chapman and Haxo, 1963, 1966; Mallams et al., 1967), as well as on the pigments in dinoflagellates (Jeffrey and Haxo, 1968).

In the 1970s, Haxo's research activities focused on the carotenoids in many algal and other organisms: See e.g., Strain et al., 1971, 1976; Johansen et al., 1974; Haxo et al., 1976; Kiosen et al., 1976; Prézelin and Haxo, 1976; Siegelman et al., 1976; and Song et al., 1976. His research on the carotenoids was extended to include work on invertebrates such as anemones (Fox et al., 1978). Further, Haxo began to identify pigments such as various chlorophyll *c*'s (Withers and Haxo, 1975), and cytochrome *f* (Mehand et al., 1975). In addition, Withers and Haxo (1978) examined the functional presence and the composition of lipid globules in some of these organisms. From our perspective, Prézelin et al., (1976) provided important information on the effect of different light intensities on the functioning of various pigment-proteins in photosynthesis (cf. Sayre et al., (2020) where photosynthesis was improved by regulating antenna size in a green alga; and a review on *Light and Photosynthesis* by Lazar et al., 2022). These primary investigations of pigments by Haxo and colleagues investigating various algae and invertebrates were to become useful as satellites attained better visual light-spectra coverage so that algal and invertebrate groups could be defined in extent and location at oceanic depths by their pigments.

In the 1980s, Haxo continued his wide-ranging research into the understanding of the structure and function of carotenoids in various marine invertebrates including clams and starfish (see e.g. Bjørnland et al., 1984; Skjenstad et al., 1984; Pennington et al., 1985; Zagalsky et al., 1989; for clams, see <https://en.wikipedia.org/wiki/Giant_clam>). Further, Balch and Haxo (1984) provided important quantitative information on the pigment-protein components of dinoflagellates, and importantly, Vernet et al., (1989) focused on deciphering spectral properties of, for example, *Gonyaulax polyedra.* From our personal perspective, the work of Neori et al., (1986) provided an important support to the relationship between chlorophyll *a* fluorescence and photosynthesis in the marine organisms they worked on—something of great interest and value to current thinking in this field in all oxygenic photosynthesis (see e.g., Khan et al., 2020).

In the 1990s, and 2000s, Professor Francis Theodore Haxo had begun to participate in Emeritus academic life at the University of California, San Diego. We recognize Neori and Haxo (1990) where they focused on what (and how) photo adaptation plays a key role in increasing photosynthesis and, thus, in principle, productivity—something of great interest to all of us today and in the future. Further, Bjørnland et al., (2003) remind us all not to forget the importance of carotenoids in photosynthetic organisms, and thus, in the global context we are living in—these pigments being the focus and life-long contribution of Haxo to both basic and applied aspects of algae and plants.

We conclude by mentioning that Francis T. Haxo was not only an active researcher, but he especially enjoyed oceanography and the trips on the 'Scripps research vessel'; he was on the Australian Voyage, and on Alpha-Helix in 1966, and many have told us that he was great fun to be with. For his interest in patenting some ideas, he was involved with in his later life, we have provided them in the Appendix. A detailed and wonderful Tribute to Francis Haxo, and his research, will soon be published by Thorhaug et al., (2023).

On behalf of many friends in the 'photosynthesis community', we want the readers to know that we all miss Francis Theodore Haxo- it was more than 12 years ago that he left this world.

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Appendix:

On patents by F. T. Haxo and collaborators.

Along with other colleagues, F. T. Haxo filed for several patents—some were still under review and consideration when he passed away, but some were

granted. We list here the names of some of his collaborators and some of the titles (or the topics) to give the readers an idea of his wide interest in biotechnology; applicants included several companies. *Source:* https://patents.justia.com/inventor/francis-t-haxo. The following list is chronologically presented from the latest to the earliest considerations of patents for ideas.

M. J. Kimzey; F. T. Haxo;* and *V. Sharma*: Kits for using bispyridines to improve labeling of nucleophiles; *F. T. Haxo*,* and *M. J. Kimzey:* Use of quaternary and tertiary ammonium cations to denature proteins; *F. T. Haxo*,* and *M. J. Kimzey*: Use of polyamines as resolving agents for capillary electrophoresis of labeled glycans using gels; *F. U. Limjap, M. J. Kimzey and F. T. Haxo**: Methods and kits for using blocked 2-AA for glycan analysis; *S. Vlasenko, F. T. Haxo** and *A. Guerrero Navarro*: Use of tri- and tetra- hydroxyl quaternary ammonium compounds as resolving agents for electrophoretic separations; *M. J. Kimzey, F. U. Limjap, F. T. Haxo** and *S. Vlasenko*: Use of quaternary and tertiary ammonium cations to denature proteins; *M. J. Kimzey, F. T. Haxo*,* and *V. Sharma*: Use of bispyridines to improve labeling of nucleophiles; *F. T. Haxo** and *M. J. Kimzey:* Use of bile detergents to denature glycoproteins prior to enzymatic digestion*; M. J. Kimzey* and *F. T. Haxo**: [On the use of] nitro-substituted non-fluorescent asymmetric cyanine dye compounds; and *L. G. Lee, R. J. Graham, K. B. Mullah,* and *F. T. Haxo**: [On the use of] Nitro-substituted non-fluorescent asymmetric cyanine dye compounds – [useful for quenching reporter dyes].

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