

ALBERT S. MILDVAN
CURRICULUM VITAE

TITLE: Professor of Biological Chemistry and Chemistry

DATE OF BIRTH: March 3, 1932

PLACE OF BIRTH: Philadelphia, PA

EDUCATION:

University of Pennsylvania	A.B.	1953	Chemistry, Mathematics
Johns Hopkins Medical School, Baltimore, MD	M.D.	1957	Medicine
Johns Hopkins Medical Service, Baltimore City Hospitals	-	1958	Medical Internship

HONORS:

Phi Beta Kappa; Pi Mu Epsilon (Mathematics); Established Investigatorship from the American Heart Association (1965-1970); Editor, Arch. Biochem. Biophys. (1968-92), Biochemistry (1972-1977), Biophysical Journal (1975-1978), Journal of Biological Chemistry (1979-1991); Co-Chairman, Gordon Conf. on Enzymes (1971); Member of NSF Molecular Biol. Panel (1971-1974) and Council on Basic Science, American Heart Association; Personnel Committee, American Cancer Society (1975-1977); Program Chairman, Biol. Div., American Chemical Society (1979-1981); PAABS Lecture of the American Chemical Society (1982); Director, Johns Hopkins M.D./Ph.D. Program (1982-1985); Council Member NIGMS (1986-1990); Councilor, American Chemical Society, Div. of Biological Chemistry (1988-1990); Herbert Sober Prize, American Society for Biochemistry and Molecular Biology (1988); Executive Committee, American Chemical Society, Division of Biological Chemistry (1993-95); Organizing Committee, International Meeting on Horizons in Hydrogen Bond Research, Berlin (2003), Roskilde, (2005); Session Organizer and Session Chair, Gordon Conference on Isotopes (2002); Frontier Lecture, Gordon Conference on Enzymes, Coenzymes, and Metabolic Pathways (2002); R.R Fisher Memorial Lecture, U. South Carolina (2004).

MAJOR RESEARCH INTEREST:

The mechanism of enzyme action and its relevance to neoplastic, cardiovascular and metabolic disease

RESEARCH AND/OR PROFESSIONAL EXPERIENCE:

The Johns Hopkins University, School of Medicine, Professor of Biological Chemistry and Chemistry	1981-present
The Institute for Cancer Research, Senior Member	1972-1981
The Institute for Cancer Research, Associate Member	1968-1972
The University of Pennsylvania, Professor of Physical Biochemistry	1974-present
The University of Pennsylvania, Associate Professor of Physical Biochemistry, EPR, pulsed and continuous wave, NMR, DNA polymerase, lyases, kinases, dehydrogenases	1968-1974
Johnson Foundation, The University of Pennsylvania, Assistant Professor of Physical Biochemistry	1965-1968
Established Investigator (American Heart Association) Enzyme kinetics, EPR, pulsed and continuous wave, NMR, carboxylases, dehydrogenases, kinases	1965-1970
Johnson Foundation, The University of Pennsylvania Advanced Postdoctoral Fellow (American Heart Association), Dr. Mildred Cohn Enzyme kinetics, pulsed NMR, EPR spectroscopy, kinases	1962-1965
Institute of Animal Physiology, Cambridge, England Postdoctoral Fellow, Dr. G.D. Greville Enzyme kinetics, ultracentrifugation, electrophoresis, dehydrogenases	1960-1962
National Heart Institute, Research Associate	1958-1960

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Dr. N.W. Shock and Dr. B.L. Strehler
Mathematical theories of aging, fluorimetry, spectroscopy, clinical medicine

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MAJOR SCIENTIFIC CONTRIBUTIONS

Methods Introduced

1. Developed the quantitative use of proton relaxation rate (PRR) measurements of water for the determination of binding stoichiometries and dissociation constants describing metal and substrate interactions with enzymes (6, 9, 10, 29, 52).
2. Introduced the use of spin-labeled substrate analogs of NAD, CoA-esters Cr(ATP) for measuring intersubstrate distances on enzymes, and solvent access to bound substrates (21, 23, 46, 57, 80, 114, 117).
3. Developed the longitudinal substrate relaxation rate ($1/T_1$) method for determining metal-substrate and intersubstrate distances on enzymes (15, 17, 18, 23, 95).
4. Developed the use of longitudinal ($1/T_1$) and transverse ($1/T_2$) relaxation rate methods for determining the rates of substrate dissociation and binding to enzyme complexes (17, 18).
5. Developed the kinetic protection method for measuring metal and substrate dissociation constants from enzymes (7, 9).
6. Combined the use of T_1 method and Nuclear Overhauser Effects to deduce conformations of enzyme-bound substrates (ATP, peptides). Applications to many enzymes.
7. Use of T_1 and Enzyme-Substrate NOE's to position substrates into X-ray structure of enzymes (NMR-Docking).
8. Developed, with J. Peisach, pulsed EPR methods to detect enzyme- Mn^{2+} -nucleotide bridge complexes (176, 254), subsequently confirmed by X-ray crystallography (262).
9. Established NMR criteria for the detection of short, strong hydrogen bonds on proteins (238), and for measuring their lengths with high precision (238, 241, 245, 249, 251).

Major Findings

1. Determined the coordination scheme, stoichiometry and binding constants of metal activators and substrates to numerous enzymes including eight ATP-utilizing enzymes, seven carbonyl-polarizing enzymes, three lyases, and four oxidoreductases.
2. Discovered that pyruvate carboxylase was a Mn^{2+} -metalloenzyme, the first Mn^{2+} containing metalloenzyme (11, 12).
3. Showed that the added divalent cation in DNA polymerase activates by increasing the tendency of pyrophosphate to leave, and predicted stereochemical inversion on phosphorus (76) which was confirmed by others. Designed a suicidal inactivator of DNA polymerases based on mechanistic considerations: epoxy ATP (100). Showed kinetically, that two divalent cations are needed to activate a reverse transcriptase (255).
4. Determined the conformations and arrangement of the bound substrates on pyruvate kinase (85), DNA polymerase (76), RNA polymerase (91, 102), PP-Rib-P synthetase (109, 124), protein kinase (108, 126),

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transcarboxylase (63, 80, 81), and alcohol dehydrogenase (23, 64, 79). These structures provided clues to the chemical mechanisms.

5. Showed that glucose 1,6-diphosphate must interchange its 2 phosphates at a single site on phosphoglucomutase during catalysis (58, 59, 96).
6. Established the existence of second sphere metal complexes on enzymes (55, 63, 65, 71, 74, 86, 93) in which a ligand (usually water) intervenes between the metal and substrate. These complexes function either as intermediates in forming inner sphere complexes in some cases, or, in other cases are themselves catalytically active.
7. Established the requirement for and clarified the structure of dual-divalent cation activated enzymes: pyruvate kinase (85, 87) and PP-Rib-P synthetase (101, 124).
8. Detected a new type of charge relay system on yeast aldolase (119), enzyme-Zn-histidine substrate.
9. Established that enzymes alter the conformation of flexible substrates, upon binding them (93).
10. Showed that certain enzymes freeze or immobilize those atoms of the substrate at which bond breaking will occur (48, 72, 96).
11. Showed that enzyme-catalyzed displacement at the β -P of ATP (in PP-Rib-P synthetase) occurs with inversion at phosphorus, yielding the first absolute stereochemistry of an ATP reaction (101).
12. Showed that the role of the metal in the lyases, enolase and aconitase, is to coordinate the leaving OH group of the substrate (41, 56). Such a role appears general.
13. Established the asymmetric Pauling-type coordination of oxygen in oxyhemoglobin (82).
14. Established a correlation between the glycosidic torsional angle of enzyme-bound ATP with the adenine base specificity of 8 ATP-utilizing enzymes (120, 131).
15. Detected half-site stoichiometry in the binding of the divalent metal activator to $\text{Na}^+ + \text{K}^+$ ATPase and to malic enzyme (66, 88) establishing extreme negative cooperativity in these enzymes.
16. Established that coenzyme B-12 undergoes homolytic cleavage in the diol-dehydrase reaction resulting in radical forms of the coenzyme and substrate (53, 67).
17. Showed that the regulatory subunit inhibits cAMP activated protein kinase by occluding the protein substrate binding site (117, 120).
18. Detected extended conformations for enzyme-bound tripeptide substrates on glyoxalase I (137, 140), and heptapeptide substrates on cAMP-dependent protein kinase (126).
19. Showed, by measuring the reaction coordinate distance, that the mechanisms of pyruvate kinase and adenylate kinase are associative (85, 121, 164).
20. Showed, by measuring intersubstrate distances on 5 enzymes, that enzymes control which phosphorus atom of ATP is to undergo nucleophilic substitution by properly orienting the other substrate (i.e. such that its entering atom is closest to the appropriate phosphorus atom of ATP (107, 131, 164)).
21. Showed by "NMR docking" that Tyr 14 and Asp 38 are properly located to be the acid and base catalysts on ketosteroid isomerase (167, 177, 189, 190).
22. Produced a new mechanism of staphylococcal nuclease which quantitatively explains its 10^{16} -fold rate acceleration. Tested this mechanism with mutants produced by D. R. Shortle (163).
23. Determined the solution structure of ketosteroid isomerase complexed with a steroid by NMR methods (231, 239).

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24. Determined the solution structure (219, 230) and mechanism (246) of the MutT pyrophosphohydrolase, a DNA-error-preventing enzyme.
25. Detected short, strong hydrogen bonds on two isomerases (228, 233, 234), a lyase (252), and two cholinesterases (250, 251) and measured their lengths with high precision (241, 245).
26. Showed, with C. P. Whitman, that Proline-1 functions as a general base catalyst on 4-oxalocrotonate tautomerase (220, 221) and as a general acid catalyst on its homolog, *trans*-3-chloroacrylic acid dehalogenase (261).
27. Measured the effective dielectric constants (ϵ) at the active sites of ketosteroid isomerase ($\epsilon = 18$) (202), and 4-oxalocrotonate tautomerase ($\epsilon = 14$) (250).
28. Showed that pairs of mutations of an enzyme can interact quantitatively in only five ways: additive, partially additive, no additional effect, synergistic, and antagonistic (197, 263), and applied these concepts to staphylococcal nuclease (188, 192), ketosteroid isomerase (189), 4-oxalocrotonate tautomerase (243), and GDP-mannose mannosyl hydrolase (266).
29. Showed that members of the same (Nudix) superfamily of enzymes can have differing metal requirements differing catalytic residues, and very different mechanisms (209, 230, 247, 248, 254, 264).

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- 5a. Strehler, B.L. and Mildvan, A.S. (1961) Studies on the chemical properties of lipofuscin age pigment. In *"Biological Aspects of Aging"* (N.W. Shock, ed.) Columbia Univ. Press, p. 174.
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