2011

CURRICULUM VITAE

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Date and Place of Birth	November 8, 1946, Moscow, Russia
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Academic Appointments and Education:

1970:	B.S. in Chemistry, Moscow University, Moscow, Russia.
1973:	Ph.D. in Biochemistry, Institute of Molecular Biology, Moscow.
1973-1976:	Research Fellow, Institute of Molecular Biology, Moscow.
1977-1980:	Assistant Professor, Dept. of Biology, M. I. T., Cambridge, MA.
1980-1986:	Associate Professor, Department of Biology, M. I. T.
1986-1992:	Professor of Biology, Department of Biology, M. I. T.
1992-present:	Howard & Gwen Laurie Smits Professor of Cell Biology, Division of Biology, California Institute of Technology, Pasadena, CA.

Other Appointments

Member, Molecular Cytology Study Section, NIH, 1983-1987.
Co-organizer, Banbury Conference on the Ubiquitin System, Cold Spring Harbor Laboratory, NY, 1993.
Visiting Fellow, International Institute for Advanced Studies, Kyoto, Japan, 2001.
Board Member, Encyclopedia of Molecular Cell Biology and Mol. Medicine, 2002-2005.
Member, Medical Advisory Board, Gairdner Foundation, Canada, 2002-2006.
Member, O'Connor Advisory Committee, March of Dimes Foundation, 2007-present.

Honorary Memberships

Fellow, American Academy of Arts and Sciences, 1987.
Member, National Academy of Sciences, 1995.
Fellow, American Academy of Microbiology, 2000.
Foreign Associate, European Molecular Biology Organization, 2001.
Member, American Philosophical Society, 2001.
Fellow, American Association for Advancement of Science, 2002.
Foreign Member, Academia Europaea, 2005.

Awards

Merit Award, National Institutes of Health, 1998.
Novartis-Drew Award in Biomedical Science, Novartis, Inc. and Drew University, 1998.
Gairdner International Award, Gairdner Foundation, Canada, 1999.
(with A. Hershko)
Sloan Prize, General Motors Cancer Research Foundation, 2000.
(with A. Hershko)
Lasker Award in Basic Medical Research, Albert and Mary Lasker Foundation, 2000.
(with A. Hershko and A. Ciechanover)
Shubitz Prize in Cancer Research, University of Chicago, 2000.
Hoppe-Seyler Award, Society for Biochemistry and Molecular Biology, Germany, 2000.
Pasarow Award in Cancer Research, Pasarow Foundation, 2001.
Max Planck Award, Germany, 2001.
Merck Award, American Society for Biochemistry and Molecular Biology, 2001.
(with A. Hershko)
Wolf Prize in Medicine, Wolf Foundation, Israel, 2001.
(with A. Hershko)
Massry Prize, Massry Foundation, 2001.
(with A. Hershko)
Horwitz Prize, Columbia University, 2001.
(with A. Hershko)
Wilson Medal, American Society for Cell Biology, 2002.
(with A. Hershko)
Stein and Moore Award, Protein Society, 2005.
(with A. Hershko)
March of Dimes Prize in Developmental Biology, March of Dimes Foundation, 2006.
Griffuel Prize in Cancer Research, Association pour la Recherche sur le Cancer, France, 2006.
Gagna and Van Heck Prize, Fonds National de la Recherche Scientifique, Belgium, 2006.
Weinstein-AACR Distinguished Award and Lectureship, Am. Assoc. for Cancer Research, 2007.
Schleiden Medal, Deutsche Akademie der Naturforscher Leopoldina, Germany, 2007.
Gotham Prize in Cancer Research, Gotham Foundation, 2008.
Vilcek Prize in Biomedical Research, Vilcek Foundation, 2010.
Otto Warburg Prize, Society for Biochemistry and Molecular Biology, Germany, 2011.

Special Lectures (2000-present):

Honors Program Lecture, New York University School of Medicine, New York, New York, 2000.
Gordon Lecture, Brandeis University, Waltham, Massachusetts, 2000.
Harvey Society Lecture, Rockefeller University, New York, New York, 2001.
Nelson Lecture, Yale University, New Haven, Connecticut, 2001.
Edsall Lecture, Harvard University, Cambridge, Massachusetts, 2001.
Keynote Lecture, Symposium on Growth Control, Salk Institute for Biol. Studies, La Jolla, 2001.
Dean's Lecture, Mount Sinai School of Medicine, New York, New York, 2002.
University Lecture, University of Texas, Southwestern Medical Center, Dallas, Texas, 2002.
Keynote Lecture, Symp. on Ubiquitin in Normal & Cancer Cells, Vancouver, Canada, 2002.
Chiron Lecture, University of California, Berkeley, California, 2002.

Special Lectures (cont.):

Keynote Lecture, Symp. on the Ubiquitin System in Health & Disease, NIH, Bethesda, 2003.
Hofmann Lecture, University of Pittsburgh, Pittsburgh, Pennsylvania, 2004.
Distinguished Guest Lecture, Baylor College of Medicine, Houston, Texas, 2005.
Opening Lecture, FASEB Conference on Ubiquitin and Cellular Regulation, 2006.
Dulbecco Lecture, Salk Institute for Biological Studies, La Jolla, California, 2008.
President's Lecture, Sanford/Burnham Medical Research Institute, La Jolla, California, 2010.
Distinguished Lecture in Signal Transduction, University of California, Irvine, California, 2010.
Alexander Rich Lecture, MIT, Cambridge, Massachusetts, 2011.

Selected Publications (1968-present)

(grouped by the fields; numbered chronologically)

Chromosome Structure and Gene Expression

1. Varshavsky, A. (1968) Regulation of synthesis of genetic repressors in bacteria. **Mol. Biol**. (Russia) 2, 13-20.
4. Ilyin, Y. V., Varshavsky, A., Mickelsaar, U. N. and Georgiev, G. P. (1971) Redistribution of proteins in mixtures of nucleoproteins, DNA and RNA. **Eur**. **J**. **Biochem**. 22, 235-245.
5. Varshavsky, A. and Georgiev, G. P. (1972) Clustered arrangement of histones F2a1 and F3 in chromosomal deoxyribonucleoproteins. **Biochim**. **Biophys**. **Acta** 281, 449-674.
9. Varshavsky, A. and Georgiev, G. P. (1973) Redistribution of histones during unfolding of chromosomal DNA. **Mol**. **Biol**. **Reports** 1, 143-148.
12. Varshavsky, A. and Ilyin, Y. V. (1974) Salt treatment of chromatin induces redistribution of histones. **Biochim**. **Biophys**. **Acta** 340, 207-217.
14. Ilyin, Y. V., Bayev, A. A. Jr., Zhuse, A. L. and Varshavsky, A. (1974) Histone-histone proximity in chromatin as revealed by imidoester crosslinking. **Mol**. **Biol**. **Reports** 1, 343-348.
17. Varshavsky, A. and Bakayev, V. V. (1975) Nu-bodies and free DNA in chromatin lacking histone H1. **Mol**. **Biol**. **Reports** 2, 209-217.
18. Varshavsky, A., Bakayev, V. V. and Georgiev, G. P. (1976) Heterogeneity of chromatin subunits *in vitro* and location of histone H1. **Nucl. Acids Res.** 3, 477-492.
23. Varshavsky, A., Bakayev, V. V., Chumackov, P. M. and Georgiev, G. P. (1976) Minichromosome of simian virus 40: presence of histone H1. **Nucl. Acids Res**. 3, 2101-2114.
27. Varshavsky, A. (1976) Structural and functional organization of eukaryotic chromosomes. **Biol**. **Zentralblatt** 95, 301-316.
30. Bakayev, V. V., Bakayeva, T. G. and Varshavsky, A. (1977) Nucleosomes and subnucleosomes: heterogeneity and composition. **Cell** 11, 619-630.
31. Varshavsky, A., Nedospasov, S. A., Bakayev, V. V., Bakayeva, T. G. and Georgiev, G. P. (1977) Histone-like proteins in the *E. coli* chromosome. **Nucl. Acids Res**. 4, 2725-2745.
33. Varshavsky, A., Bakayev, V. V., Nedospasov, S. A. and Georgiev, G. P. (1977) On the structure of eukaryotic, prokaryotic and viral chromatin. **Cold Spring Harbor Symp. Quant. Biol**. 42, 457-472.
37. Varshavsky, A., Sundin, O. and Bohn, M. (1978) SV40 viral minichromosome: preferential exposure of the origin of replication. **Nucl. Acids Res**. 5, 3469-3478.

38. Varshavsky, A., Sundin, O. and Bohn, M. (1979) A 400 bp region of SV40 viral DNA that includes the origin of replication is exposed in SV40 minichromosomes. **Cell** 16, 453-466.
39. Sundin, O. and Varshavsky, A. (1979) Staphylococcal nuclease makes a single nonrandom cut in the SV40 viral minichromosome. **J. Mol. Biol.** 132, 535-546.
45. Levinger, L. and Varshavsky, A. (1981) *Drosophila* heat shock proteins are associated with nuclease-resistant, high salt-resistant nuclear structures. **J. Cell Biol.** 90, 793-796.
50. Barsoum, J., Levinger, L. and Varshavsky, A. (1982) On the chromatin structure of the amplified, transcriptionally active gene for dihydrofolate reductase in mouse cells. **J**. **Biol**. **Chem**. 257, 5274-5282.
51. Levinger, L. and Varshavsky, A. (1982) Protein D1 preferentially binds AT-DNA and is a component of *Drosophila melanogaster* nucleosomes containing AT-rich satellite DNA. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 79, 7152-7156.
54. Wu, K., Strauss, F. and Varshavsky, A. (1983) Nucleosome arrangement in green monkey alpha-satellite chromatin. **J. Mol. Biol.** 170, 93-117.
67. Barsoum, J. and Varshavsky, A. (1985) Preferential localization of variant nucleosomes near the 5'-end of the mouse dihydrofolate reductase gene. **J. Biol. Chem.** 260, 7688-7697.
73. Solomon, M. J., Strauss, F. and Varshavsky, A. (1986) A mammalian HMG protein recognizes a stretch of six AT base pairs in duplex DNA. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 83, 1276-1289.
80. Peck, L. J., Millstein, L., Eversole-Cire, P., Gottesfeld, J. M. and Varshavsky, A. (1987) Transcriptionally inactive oocyte-type 5S RNA genes of *Xenopus laevis* are complexed with TFIIIA *in vitro*. **Mol**. **Cell**. **Biol**. 7, 3503-3510.
91. Winter, E. and Varshavsky, A. (1989) A DNA-binding protein that recognizes oligo dA-oligo dT tracts. **EMBO J**. 8, 1867-1877.

Chromosome Segregation and Replication

41. Sundin, O. and Varshavsky, A. (1980) Terminal stages of SV40 DNA replication proceed via multiply intertwined catenated dimers. **Cell** 21, 103-114.
46. Sundin, O. and Varshavsky, A. (1981) Arrest of segregation leads to accumulation of highly intertwined catenated dimers: dissection of the final stages of SV40 DNA replication. **Cell** 25, 659-669.
55. Varshavsky, A., Sundin, O., Özkaynak, E., Pan, R., Solomon, M. and Snapka, R. (1983) Final stages of SV40 DNA replication: multiply intertwined catenated dimers as SV40 segregation intermediates. In: ***Mechanisms of DNA Replication and Recombination***, Liss, Inc., New York, pp. 463-494.
56. Varshavsky, A., Levinger, L., Sundin, O., Barsoum, J., Özkaynak, E., Swerdlow, P. and Finley, D. (1983) Cellular and SV40 chromatin: replication, segregation, and ubiquitination. **Cold Spring Harbor Symp. Quant. Biol.** 47, 511-528.
81. Solomon, M. J. and Varshavsky, A. (1987) A nuclease-hypersensitive region forms *de novo* after chromosome replication. **Mol**. **Cell**. **Biol**. 7, 3822-3825.

Gene Amplification, Multidrug Transporters, and Drug Resistance

43. Varshavsky, A. (1981) On the possibility of metabolic control of replicon "misfiring": relationship to emergence of malignant phenotypes in mammalian cell lineages.

Proc. **Natl**. **Acad**. **Sci**. **USA** 78, 3673-3677.

44. Varshavsky, A. (1981) Phorbol ester dramatically increases incidence of methotrexate-resistant cells: possible mechanisms and relevance to tumor promotion. **Cell** 25, 561-572.
55. Barsoum, J. and Varshavsky, A. (1983) Mitogenic hormones and tumor promoters greatly increase the incidence of cells bearing amplified dihydrofolate reductase genes. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 80, 5330-5334.
56. Varshavsky, A. (1983) Diadenosine 5', 5'",-P^1,P^4-tetraphosphate: a pleiotropically acting alarmone? **Cell** 34, 711-712.
58. Varshavsky, A. (1983) Do stalled replication forks synthesize a specific alarmone? **J**. **Theoret**. **Biol**. 105, 707-714.
59. Snapka, R. and Varshavsky, A. (1983) Loss of unstably amplified dihydrofolate reductase genes from mouse cells is accelerated by hydroxyurea. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 80, 7533-7537.
63. Roninson, I., Abelson, H. T., Housman, D. E., Howell, N. and Varshavsky, A. (1984) Amplification of specific DNA sequences correlates with multidrug resistance in Chinese hamster cells. **Nature** 30, 626-628.
71. Ciccarelli, R. B., Solomon, J. J., Varshavsky, A. and Lippard, S. J. (1985) *In vivo* effects of cis- and trans diaminedichloroplatinum (II) on SV40 chromosomes: differential repair, DNA-protein crosslinking, and inhibition of replication. **Biochemistry** 24, 7533-7540.
72. Gros, P., Croop, J., Roninson, I., Varshavsky, A. and Housman, D. E. (1986) Isolation and characterization of DNA sequences amplified in multidrug-resistant hamster cells. **Proc. Natl. Acad. Sci. USA** 83, 337-341.
93. McGrath, J. P. and Varshavsky, A. (1989) The yeast *STE6* gene encodes a homolog of the mammalian multidrug resistance P-glycoprotein. **Nature** 340, 400-404.

New Biochemical and Genetic Methods

16. Bakayev, V. V., Melnickov, A. A., Osicka, V. A. and Varshavsky, A. (1975) Isolation and characterization of chromatin subunits. **Nucl. Acids Res**. 2, 1401-1419. *(Low ionic strength electrophoretic technique for separation of DNA-protein complexes.)*
22. Varshavsky, A., Bakayev, V. V. and Georgiev, G. P. (1976) Heterogeneity of chromatin subunits and location of histone H1. **Nucl. Acids Res**. 3, 477-492. *(Fractionation of nucleosomes by low ionic strength electrophoresis, the forerunner of gel shift assay.)*
42. Levinger, L., Barsoum, J. and Varshavsky, A. (1981) Two-dimensional hybridization mapping of nucleosomes. **J**. **Mol**. **Biol**. 146, 287-304.
49. Boyce, F., Sundin, O., Barsoum, J. and Varshavsky, A. (1982) New way to isolate SV40 viral minichromosomes: use of a thiol-specific reagent. **J**. **Virol**. 42, 292-296.
64. Strauss, F. and Varshavsky, A. (1984) A protein binds to a satellite DNA repeat at three sites which would be brought into proximity by DNA folding in the nucleosome. **Cell** 37, 889-901. *(The first use of gel shift assay to detect specific DNA-binding proteins in cell extracts.)*
69. Solomon, M. J. and Varshavsky, A. (1985) Formaldehyde-mediated DNA-protein crosslinking: a probe for *in vivo* chromatin structures. **Proc**. **Nat**. **Acad**. **Sci**. **USA** 82, 6470-6474.
74. Swerdlow, P. S., Finley, D. and Varshavsky, A. (1986) Enhancement of immunoblot sensitivity by heating of hydrated filters. **Analyt**. **Biochem**. 156, 147-153.

76. Snapka, R. M., Kwok, K., Bernard, J. A., Harling, O. and Varshavsky, A. (1986) Post-separation detection of nucleic acids and proteins by neutron activation. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 83, 9320-9324.
82. Varshavsky, A. (1987) An electrophoretic assay for DNA-binding proteins. **Meth. Enzymol.** 151, 551-565.
83. Bartel, B. and Varshavsky, A. (1988) Hypersensitivity to heavy water: a new conditional phenotype. **Cell** 52, 935-941. *(A generally applicable alternative to temperature-sensitive conditional mutants.)*
86. Solomon, M. J., Larsen, P. L. and Varshavsky, A. (1988) Mapping protein-DNA interactions *in vivo* with formaldehyde. **Cell** 53, 937-947. *(Invention of the chromatin immunoprecipitation assay (ChIP), for localizing DNA-bound proteins of interest at specific DNA sequences in chromosomes, through the in vivo crosslinking, DNA fragmentation, immunoprecipitation, and DNA hybridization).*
112. Dohmen, R. J., Wu, P. P. and Varshavsky, A. (1994) Heat-inducible degron: a method for constructing temperature-sensitive mutants. **Science** 263, 1273-1276. (*A generally applicable method for making a temperature-sensitive protein without altering its ORF*.)
113. Johnsson, N. and Varshavsky, A. (1994) Ubiquitin-assisted dissection of protein transport across membranes. **EMBO J.** 13, 2686-2698. *(A ubiquitin-based method for analyzing kinetic aspects of protein translocation across membranes in vivo.)*
115. Johnsson, N. and Varshavsky, A. (1994) Split ubiquitin as a sensor of protein interactions *in vivo*. **Proc. Natl. Acad. Sci. USA** 91, 10340-10344. *(The first split-protein method for detecting protein-protein interactions in living cells. The central idea of this in vivo technique has been extended, by now, from ubiquitin to a number of split protein reporters, including GFP and DHFR. Another current name for the split-protein assay is protein complementation assay (PCA)).*
123. Lévy, F., Johnsson, N., Rümenapf, T. and Varshavsky, A. (1996) Using ubiquitin to follow the metabolic fate of a protein. **Proc. Natl. Acad. Sci. USA** 93, 4907-4912. *(A method for producing equimolar amounts of a reference and a test protein in vivo.)*
127. Johnson, N. and Varshavsky, A. (1997) Split ubiquitin: a sensor of protein interactions *in vivo*. In: **The Yeast Two-Hybrid System** (P. L. Bartel and S. Fields, eds.), pp. 316-332, Oxford University Press, N. Y.
137. Dünnwald, M., Varshavsky, A. and Johnsson, N. (1999) Detection of transient *in vivo* interactions between substrate and transporter during protein translocation into the endoplasmic reticulum. **Mol. Biol. Cell** 10, 329-344.
147. Varshavsky, A. (2000) Ubiquitin fusion technique and its descendants. **Meth. Enzymol.** 327, 578-593.
148. Turner, G. C. and Varshavsky, A. (2000) Detecting and measuring cotranslational protein degradation *in vivo*. **Science** 289, 2117-2120.
169. Dohmen, R. J. and Varshavsky, A. (2005) Heat-inducible degron and the making of conditional mutants. **Meth. Enzymol.** 399, 799-822.
170. Varshavsky, A. (2005) Ubiquitin fusion technique and related methods. **Meth. Enzymol.** 399, 777-799.

Multitarget Designs

117. Varshavsky, A. (1995) Codominance and toxins: a path to drugs of nearly unlimited selectivity. **Proc. Natl. Acad. Sci. USA** 92, 3663-3667.

132. Varshavsky, A. (1998) Codominant interference, antieffectors, and multitarget drugs. **Proc. Natl. Acad. Sci. USA** 95, 2094-2099.

The Ubiquitin System and Regulated Protein Degradation

40. Levinger, L. and Varshavsky, A. (1980) Separation of nucleosomes containing and lacking ubiquitin-H2A semihistone. **Proc**. **Natl**. **Acad**. **Sci**. **USA** 77, 3244-3248.
48. Levinger, L. and Varshavsky, A. (1982) Selective arrangement of ubiquitinated and D1 protein containing nucleosomes in the *Drosophila* genome. **Cell** 28, 375-386.
53. Swerdlow, P. and Varshavsky, A. (1983) Affinity of HMG17 for a nucleosome is not influenced by the presence of ubiquitin-H2A semihistone but depends on DNA fragment size. **Nucl**. **Acids**. **Res**. 11, 387-401.
61. Finley, D., Ciechanover, A. and Varshavsky, A. (1984) Thermolability of ubiquitin-activating enzyme from the mammalian cell cycle mutant ts85. **Cell** 37, 43-55.
62. Ciechanover, A., Finley, D. and Varshavsky, A. (1984) Ubiquitin dependence of selective protein degradation demonstrated in the mammalian cell cycle mutant ts85. **Cell** 37, 57-66.
66. Özkaynak, E., Finley, D. and Varshavsky, A. (1984) The yeast ubiquitin gene: head-to-tail repeats encoding a polyubiquitin precursor protein. **Nature** 312, 663-666.
70. Finley, D. and Varshavsky, A. (1985) The ubiquitin system: functions and mechanisms. **Trends Biochem**. **Sci.** 10, 343-346.
75. Bachmair, A., Finley, D. and Varshavsky, A. (1986) *In vivo* half-life of a protein is a function of its N-terminal residue. **Science** 234, 179-186.
77. Özkaynak, E., Finley, D., Solomon, M. J. and Varshavsky, A. The yeast ubiquitin genes: a family of natural gene fusions. **EMBO J**. 6:1429-1440 (1987).
78. Finley, D., Özkaynak, E. and Varshavsky, A. The yeast polyubiquitin gene is essential for resistance to high temperatures, starvation and other stresses. **Cell** 48:1035-1046 (1987).
79. Jentsch, S., McGrath, J. P. and Varshavsky, A. The yeast DNA repair gene *RAD6* encodes a ubiquitin-conjugating enzyme. **Nature** 329:131-134 (1987).
84. Finley, D., Özkaynak, E., Jentsch, S., McGrath, J. P., Bartel, B., Pazin, M., Snapka, R. M. and Varshavsky, A. Molecular genetics of the ubiquitin system. In: **Ubiquitin** (M. Rechsteiner, ed.), pp. 39-75, Plenum Press, N. Y.(1988).
85. Varshavsky, A., Bachmair, A., Finley, D., Wünning, I. and Gonda, D. The N-end rule of selective protein turnover: mechanistic aspects and functional implications. In: **Ubiquitin** (M. Rechsteiner, ed.), pp. 287-324, Plenum Press, N. Y. (1988).
87. Goebl, M. G., Yochem, J., Jentsch, S., McGrath, J. P., Varshavsky, A. and Byers, B. The yeast cell cycle gene *CDC34* encodes a ubiquitin-conjugating enzyme. **Science** 241:1331-1335 (1988).
88. Bachmair, A. and Varshavsky, A. (1989) The degradation signal in a short-lived protein. **Cell** 56, 1019-1032.
89. Chau, V., Tobias, J. W., Bachmair, A., Mariott, D., Ecker, D., Gonda, D. K., and Varshavsky, A. (1989) A multiubiquitin chain is confined to specific lysine in a targeted short-lived protein. **Science** 243, 1576-1583.
90. Finley, D., Bartel, B. and Varshavsky, A. (1989) The tails of ubiquitin precursors are ribosomal proteins whose fusion to ubiquitin facilitates ribosome biogenesis. **Nature** 338, 394-401.
92. Gonda, D. K., Bachmair, A., Wünning, I., Tobias, J. W., Lane, W. S. and Varshavsky, A.

(1989) Universality and structure of the N-end rule. **J**. **Biol**. **Chem**. 264, 16700-16712.
94. Balzi, E., Choder, M., Chen, W., Varshavsky, A. and Goffeau, A. (1990) Cloning and functional analysis of the arginyl-tRNA-protein transferase gene *ATE1* of *Saccharomyces cerevisiae*. **J**. **Biol**. **Chem**. 265, 7464-7471.
95. Hochstrasser, M. and Varshavsky, A. (1990) *In vivo* degradation of a transcriptional regulator: the yeast α2 repressor. **Cell** 61, 697-708.
96. Johnson, E. S., Gonda, D. K. and Varshavsky, A. (1990) *Cis-trans* recognition and subunit-specific degradation of short-lived proteins. **Nature** 346, 287-291.
97. Bartel, B., Wünning, I. and Varshavsky, A. (1990) The recognition component of the N-end rule pathway. **EMBO J**. 9, 3179-3189.
98. Hochstrasser, M., Ellison, M. J., Chau, V. and Varshavsky, A. (1991) The short-lived MATalpha2 transcriptional regulator is ubiquitinated *in vivo*. **Proc. Nat. Acad. Sci. USA** 88, 4606-4610.
99. Baker, R. T. and Varshavsky, A. (1991) Inhibition of the N-end rule pathway in living cells. **Proc. Natl. Acad. Sci. USA** 88, 1090-1094.
100. Varshavsky, A. (1991) Naming a targeting signal. **Cell** 64, 13-15.
101. Tobias, J. W. and Varshavsky, A. (1991) Cloning and functional analysis of the ubiquitin-specific protease gene *UBP1* of *S. cerevisiae*. **J. Biol. Chem**. 266, 12021-12028.
102. Dohmen, R. J., Madura, K., Bartel, B. and Varshavsky, A. (1991) The N-end rule is mediated by the Ubc2 (Rad6) ubiquitin-conjugating enzyme. **Proc. Natl. Acad. Sci. USA** 88, 7351-7355.
103. McGrath, J. P., Jentsch, S. and Varshavsky, A. (1991) *UBA1*: an essential yeast gene encoding ubiquitin-activating enzyme. **EMBO J**. 10, 227-237.
104. Tobias, J. W., Shrader, T. E., Rocap, G. and Varshavsky, A. (1991) The N-end rule in bacteria. **Science** 254, 1374-1377.
105. Johnson, E. S., Bartel, B., Seufert, W. and Varshavsky, A. (1992) Ubiquitin as a degradation signal. **EMBO J**. 11, 497-505.
106. Ota, I. and Varshavsky, A. (1992) A gene encoding a putative tyrosine phosphatase suppresses lethality of an N-end rule-dependent mutant. **Proc. Natl. Acad. Sci. USA** 89, 2355-2359.
107. Baker, R. T., Tobias, J. W. and Varshavsky, A. (1992) Ubiquitin-specific proteases of *S. cerevisiae:* cloning of *UBP2* and *UBP3*, and functional analysis of the *UBP* gene family. **J. Biol. Chem.** 267, 23363-23375.
108. Varshavsky, A. (1992) The N-end rule. **Cell** 69, 725-735.
109. Shrader, T. E., Tobias, J. W. and Varshavsky, A. (1993) The N-end rule in *Escherichia coli*: cloning and analysis of the leucyl, phenylalanyl-tRNA-protein transferase gene *aat*. **J. Bact**. 175, 4364-4374.
110. Madura, K., Dohmen, R. J. and Varshavsky, A. (1993) N-recognin/Ubc2 interactions in the N-end rule pathway. **J. Biol. Chem.** 268, 12046-12054.
111. Ota, I. M. and Varshavsky, A. (1993) A yeast protein similar to bacterial two-component regulators. **Science** 262, 566-569.
114. Madura, K. and Varshavsky, A. (1994) Degradation of G-alpha by the N-end rule pathway. **Science** 265, 1454-1458.
116. Johnston, J. A., Johnson, E. S., Waller, P. and Varshavsky, A. (1995) Methotrexate inhibits proteolysis of dihydrofolate reductase by the N-end rule pathway. **J. Biol. Chem.** 270, 8172-8178.
118. Baker, R. T. and Varshavsky, A. (1995) N-terminal amidase: a new enzyme and component of a targeting complex in the N-end rule pathway. **J. Biol. Chem.** 270, 12065-12074.

119. Varshavsky, A. The world of ubiquitin. (1995) **Engineering & Science** 58, 26-36.
120. Johnson, E. S., Ma, P. C. M., Ota, I. M. and Varshavsky, A. (1995) A proteolytic pathway that recognizes ubiquitin as a degradation signal. **J. Biol. Chem**. 270, 17442-17456.
121. Dohmen, R. J., Stappen, R., McGrath, J. P., Forrová, H., Kolarov, J., Goffeau, A. and Varshavsky, A. (1995) An essential yeast gene encoding a homolog of ubiquitin-activating enzyme. **J. Biol. Chem**. 270, 18099-18109.
122. Varshavsky, A. (1996) The N-end rule. **Cold Spring Harbor Symp. Quant Biol**. 60, 461-478.
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