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STRUCTURAL BIOLOGY:

Enhanced: The Ribosome Is a Ribozyme

Thomas R. Cech [HN17] *

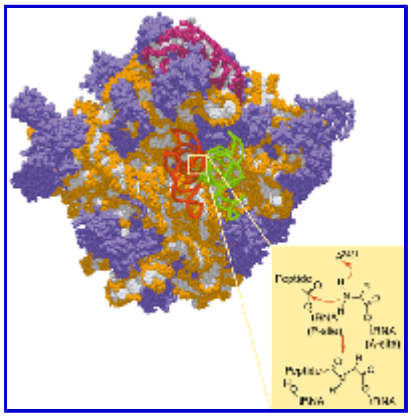
The amino acids we obtain by digestion of steak, salmon, or a lettuce salad are loaded onto transfer RNAs (tRNAs) and rebuilt into proteins in the ribosome [HN1], the cell's macromolecular protein-synthesis factory. The bacterial ribosome [HN2] is composed of three RNA molecules and more than 50 proteins. Its key components are so highly conserved among all of Earth's species that a similar entity must have fueled protein synthesis [HN3] in the common ancestor of all extant life. Although the chemical reaction catalyzed by the ribosome is simple--the joining of amino acids through amide (peptide) linkages--it performs the remarkable task of choosing the amino acids to be added to the growing polypeptide chain by reading successive messenger RNA (mRNA) codons. On page 905 of this issue, Steitz, Moore, and colleagues [HN4] (1) now provide the first atomic-resolution view of the larger of the two subunits of the ribosome. From this structure they deduce on page 920 that RNA components of the large subunit accomplish the key peptidyl transferase reaction (2). Thus, ribosomal RNA (rRNA) does not exist as a framework to organize catalytic proteins. Instead, the proteins are the structural units and they help to organize key ribozyme (catalytic RNA) [HN5] elements, an idea long championed by Harry Noller, Carl Woese, [HN6] and others.

These landmark publications are but the latest chapter in a progression of ribosome structural studies that have spanned four decades. Early electron micrographs of ribosomes in action led to immunoelectron microscopy and ultimately to cryo-electron microscopy images of about 20 Å resolution [HN7]. Proteins were also located within the ribosome by neutron scattering. However, to achieve atomic resolution, x-ray crystallography [HN8] is required, a daunting task given the huge size (2.6 x 10^6 daltons) and asymmetry of the ribosome. The pioneering crystallization of ribosomes from the bacterium *Haloarcula marismortui* [HN9] in the 1980s by Ada Yonath [HN10] and H. G. Wittmann provided the first rays of hope, but it is only in the past few years that crystal structures have been determined for the large subunit (5 Å resolution) (3), the small subunit (5.5 Å resolution) (4), and the whole ribosome complexed with tRNAs (7.8 Å resolution) [HN11] (5).

Now, at 2.4 Å, almost the entire chain of the 23*S* rRNA and its tiny 5*S* rRNA partner, totaling 3043 nucleotides, have been fitted into the electron density map of the *H. marismortui* large ribosomal subunit (1). The RNA secondary structure [HN12] (intramolecular base-pairing pattern) of the large-subunit rRNA had been determined previously (6), and is present as predicted in the x-ray structure. In addition, a large number of unpredicted RNA tertiary structure interactions are now seen. Overall, the RNA forms a huge single mass of tightly packed helices, not six discrete domains connected by floppy linkers as a naïve observer might predict from looking at the secondary structure diagram.

Where, then, are all of the proteins, and what is their function? The globular domains of 26 proteins are found largely on the exterior of the subunit (see the figure). Twelve of these proteins have unusual snake-like extensions, devoid of tertiary

structure and in some cases even secondary structure, and an additional protein is entirely extended; their shapes are molded by their interactions with the RNA. From these pictures, and from what is known about protein cofactors that facilitate the action of some other ribozymes, it is likely that these ribosomal proteins buttress, stabilize, and orient the otherwise floppy RNA into a specific, active structure.



A ribosome's true colors. (**Top**) The large subunit of the ribosome (1) seen from the viewpoint of the small subunit, with proteins in purple, 23*S* rRNA in orange and white, 5*S* rRNA (at the top) in burgundy and white, and A-site tRNA (green) and P-site tRNA (red) docked according to (5). (**Bottom**) The peptidyl transfer mechanism catalyzed by RNA (2). The general base (adenine 2451 in *Escherichia coli* 23*S* rRNA) is rendered unusually basic by its environment within the folded structure; it could abstract the proton at any of several steps, one of which is shown here.

The part of the subunit's surface that is most devoid of protein is the active-site region. This was precisely located by soaking the crystals in a small-molecule inhibitor provided by Michael Yarus [HN13] (7). This inhibitor is an analog of the anionic tetrahedral intermediate formed when a nucleophile attacks a planar carbonyl (see the figure). (In protein synthesis, the nucleophile is the amino group of the amino acid in the ribosome's A-site, and the carbonyl belongs to the P-site amino acid esterified to the 3'-ribose of tRNA.) It is the absence of any protein moiety within 18 Å of the correctly bound inhibitor in their structure, coupled with earlier work that defined this conserved part of the large-subunit rRNA as the "peptide transferase center," that led the authors to conclude that RNA (and not protein) must be responsible for catalysis. The ribosome is a ribozyme, admittedly one dependent on structural support from protein components--substantially deproteinized large subunits still carry out peptidyl transfer, although complete deproteinization destroys this reactivity (8).

The authors propose a detailed mechanism for catalysis (2) that will undoubtedly be the subject of much analysis and experimental testing. One key feature of the mechanism is a particular adenine base (conserved at this position in thousands of sequenced rRNAs) that acts as a general acid-base catalyst, deprotonating the nucleophilic amine (see the figure) and protonating the 3'-oxygen of the ribose reaction product. The ability of RNA to provide general acid-base catalysis was discovered only last year (9, 10) in studies involving the hepatitis delta virus ribozyme [HN14] (11).

Efficient general acid-base catalysis requires that the acid-base have a pK_a around pH 7.0, whereas the adenine base titrates at or below pH 3.5. However, it is already known that certain RNA structures can perturb the pK_a of adenine toward a neutral pH (12). In addition, as Muth *et al*. [HN15] (13) report on page 947 of this issue, experimental analysis of the nucleotides within the peptidyl transferase center demonstrates that the adenine implicated by the crystal structure has an unusual pK_a of 7.6. Remarkably, two RNAs--identified by in vitro evolution for their ability to catalyze peptidyl transfer (14) or to bind the analog of the reaction intermediate (15)--have adenines in a local sequence and secondary structure similar to that of the critical adenine in the ribosome. So, this pair of RNAs may recapitulate the key feature of the rRNA reaction mechanism.

Of course, general acid-base catalysis can easily be provided in the active site of a protein enzyme, which leads to the question: Why does nature use RNA catalysis to achieve protein synthesis? One argument is evolutionary. If, indeed, there was an early RNA world [HN16] where RNA provided both genetic information and catalytic function, then the earliest protein synthesis would have had to be catalyzed by RNA. Later, the RNA-only ribosome/ribozyme may have been

embellished with additional proteins; yet, its heart of RNA functioned sufficiently well that it was never replaced by a protein catalyst. But there are persuasive chemical arguments as well. The substrates of the ribosome are RNAs--aminoacylated tRNAs and an mRNA--and RNA is particularly well suited for specific recognition of other RNAs through formation of base pairs, base triples, and other interactions. Furthermore, RNA is well suited to perform very large-scale conformational changes, and such movements are required for protein synthesis.

These most recent contributions of Steitz, Moore, and colleagues provide a milestone, but not the finish line. This one structure contains more RNA-RNA and RNA-protein interactions than all previous atomic-level structures combined, so ribophiles can look forward to years of additional analysis. The whole ribosome needs to be brought to this same atomic level of resolution, and the proposed reaction mechanism deserves critical testing. Finally, the molecular basis of the mRNA translocation step that must occur after each peptidyl transfer event remains obscure. Thus, although the current crystal structure provides one beautiful frame, we still look forward to seeing the entire movie.

References

1. N. Ban, P. Nissen, J. Hansen, P. B. Moore, T. A. Steitz, *Science* **289**, 905 (2000).
2. P. Nissen, J. Hansen, N. Ban, P. B. Moore, T. A. Steitz, *Science* **289**, 920 (2000).
3. N. Ban *et al*., *Nature* **400**, 841 (1999) [Medline].
4. W. M. Clemons Jr., *et al*., *Nature* **400**, 833 (1999) [Medline].
5. J. H. Cate, M. M. Yusupov, G. Z. Yusupova, T. N. Earnest, H. F. Noller, *Science* **285**, 2095 (1999).
6. H. F. Noller *et al.*, *Nucleic Acids Res.* **9**, 6167 (1981) [Medline].
7. M. Welch, J. Chastang, M. Yarus, *Biochemistry* **34**, 385 (1995) [Medline].
8. H. F. Noller, V. Hoffarth, L. Zimniak, *Science* **256**, 1416 (1992) [Medline].
9. A. T. Perrotta, I.-H. Shih, M. D. Been, *Science* **286**, 123 (1999).
10. S. Nakano, D. M. Chadalavada, P. C. Bevilacqua, *Science* **287**, 1493 (2000).
11. A. R. Ferre-D'Amare, K. Zhou, J. A. Doudna, *Nature* **395**, 567 (1998) [Medline].
12. P. Legault and A. Pardi, *J. Am. Chem. Soc.* **119**, 6621 (1997).
13. G. W. Muth, L. Ortoleva-Donnelly, S. A. Strobel, *Science* **289**, 947 (2000).
14. B. Zhang and T. R. Cech, *Chem. Biol.* **5**, 539 (1998) [Medline].
15. M. Welch, I. Majerfeld, M. Yarus, *Biochemistry* **36**, 6614 (1997) [Medline].

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HyperNotes

Related Resources on the World Wide Web

General Hypernotes

P. Gannon's Cell & Molecular Biology Online offers lists of Web resources for cell and molecular biologists.

The CMS Molecular Biology Resource is a compendium of electronic and Internet-accessible tools and resources for molecular biology, biotechnology, molecular evolution, biochemistry, and biomolecular modeling.

The Hypermedia Glossary of Genetic Terms is provided by B. Schlindwein, Weihenstephan Information and Documentation Centre, Freising, Germany.

Kimball's Biology Pages provides presentations on types of RNA, ribosomes, and protein synthesis.

U. Melcher, Department of Biochemistry and Molecular Biology, Oklahoma State University, provides a tutorial on molecular genetics.

BUBL LINK, a catalog of selected Internet resources covering all academic subject areas maintained by the

Strathclyde University Library, UK, offers links to Internet resources on biochemistry and molecular biology and crystallography.

The American Crystallographic Association provides links to crystallographic Web sites and crystallography education Web resources.

The International Union of Crystallography provides a collection of teaching pamphlets, a directory of crystallographers, and Crystallography Online, a guide to Internet resources. The journal *Acta Crystallographica Section D: Biological Crystallography* is available on the Web.

CrystaLinks: A Crystallographer's Miscellany is maintained by E. Merritt, Biomolecular Structure Center at the University of Washington School of Medicine.

The Nucleic Acid Database Project, Rutgers University, assembles and distributes structural information about nucleic acids. An introduction to nucleic acids is presented.

The Protein Data Bank is an international repository for the processing and distribution of 3D macromolecular structure data. Educational and other Web links for macromolecular structure-related resources are provided, as is a presentation on the nature of 3D structural data and x-ray crystallography.

The RNA World Website, provided by the Institut für Molekulare Biotechnologie (IMB), Jena, Germany, provides links to Internet resources on RNA-related topics.

The Ribosomal Database Project from the Center for Microbial Ecology, Michigan State University, provides a collection of Internet links.

The rRNA WWW Server is maintained by P. De Rijk, Department of Biochemistry, University of Antwerp, Belgium.

Crystallography 101 is a an introductory course on the Web provided by B. Rupp on his Macromolecular Crystallography Web Site.

The Principles of Protein Structure is a Web-based course presented by the School of Crystallography, Birkbeck College, University of London. The glossary for the course is available from the Virtual Hyperglossary Web site.

The Protein Crystallography Group at the Cambridge Institute for Medical Research, UK, provides lecture notes by R. Read and others for a macromolecular crystallography course. An overview of macromolecular X-ray crystallography and a collection of links to Internet resources are included.

W. Campbell, Department of Biological Sciences, Michigan Technological University, offers lecture notes on protein structure for a biochemistry course. An introduction to ribosome structure is included.

The Department of Biological and Colloidal Structure Research, GKSS Research Centre, Geesthacht, Germany, makes available the proceedings of a September 1998 workshop on the structure research of the ribosome and its functional complexes.

Numbered Hypernotes

1. E. Healy, Department of Chemistry, St. Edward's University, Austin, TX, offers an illustrated list of the amino acids for a biochemistry course. Transfer RNA and ribosome are defined in B. Schlindwein's Hypermedia Glossary of Genetic Terms. The MIT Biology Hypertextbook defines the types of RNA and provides a presentation on ribosomes and protein synthesis. The Cell Biology Graduate Program at the University of Texas Medical Branch makes available a presentation by G. Childs on the role of the ribosome. The Natural Toxins Research Center at Texas A&M University, Kingsville, offers a presentation on ribosome structure and function. L. Smart, Faculty of Environmental and Forest Biology, State University of New York, Syracuse, provides lecture notes on ribosomes, tRNAs, and

translation for a cell physiology course.

2. Cells Alive! provides a diagram with definitions of bacterial cell structure. The Web microbiology textbook by T. Paustian, Department of Bacteriology, University of Wisconsin, includes a section on ribosomes in the chapter on bacterial structure. For a biochemistry course, C. Helbing, Department of Biochemistry and Microbiology, University of Victoria, Canada, provides lecture notes on the features of bacteria ribosomes, as well as an explanation of subunit nomenclature.

3. M. Farabee's On-Line Biology Book has a chapter on protein synthesis. G. Rule, Department of Biological Sciences, Carnegie-Mellon University, provides lecture notes on protein synthesis, ribosomes, and peptide bond formation for a biochemistry course. K. Redding, Department of Chemistry, University of Alabama, provides lecture notes on protein synthesis for a biochemistry course. J. Hardy, Department of Chemistry, University of Akron, offers illustrated lecture summaries on proteins and nucleic acids and protein synthesis in a Web tutorial on general, organic, and biochemistry. T. Terry, Department of Molecular and Cell Biology, University of Connecticut, provides lecture notes on protein synthesis in prokaryotes for a microbiology course.

4. N. Ban, P. Nissen, J. Hansen, P. Moore, and T. Steitz are in the Department of Molecular Biophysics and Biochemistry, Yale University. P. Moore is also in the Department of Chemistry, Yale University. The Moore lab and the Steitz Lab have Web pages. N. Ban provides a collection of links to ribosome and crystallography resources.

5. Ribozyme is defined in the On-line Medical Dictionary. The September 1999 issue of *MPIbpc News* from the Max-Planck-Institut für Biophysikalische Chemie, Göttingen, Germany, had an article by F. Eckstein titled "RNA and DNA as catalysts." The Ribozyme Jump Station provides a collection of links for scientists interested in ribozymes. Sidney Altman and Thomas R. Cech shared the 1989 Nobel Prize in Chemistry "for their discovery of catalytic properties of RNA"; an account of their research is provided. C. Wilson, Department of Biology, University of California, Santa Cruz, provides lecture notes on catalytic RNA for a molecular biology course. A. Fink, Department of Chemistry and Biochemistry, University of California , Santa Cruz, presents lecture notes on catalytic RNA and regulatory control of enzymes for a course on enzyme mechanisms and kinetics. A student project by R. Samuel titled "The structure and function of the hammerhead ribozyme" is made available on the Web by C. Stone of the Chemical Biology Department, Stevens Institute of Technology, Hoboken, NJ.

6. H. Noller is at the Center for Molecular Biology of RNA, University of California, Santa Cruz. C. Woese is in the Department of Microbiology, University of Illinois.

7. The Electron Microscopy Outreach Program from the San Diego Supercomputer Center provides a Web course on electron microscopy, as well as Web links to structural biology Web resources. Microworld is a guide to online microscopy and microanalysis resources. The Bio-Imaging Center Electron Microscopy Laboratory, SUNY Nassau Community College, Garden City, NY, provides an introduction to electron microscopy, a list of Web sites, and a photomicrograph gallery of images. The Center for Materials Research and Analysis, University of Nebraska at Lincoln, provides an introduction to electron microscopy. The On-line Medical Dictionary defines immunoelectron microscopy. *Access Magazine* Online from the National Center for Supercomputing Applications offers a 31 March 1998 article by M. Schneider tilted "Blueprints of the protein factory" about the cryo-electron microscopy research of J. Frank.

8. B. Rupp provides an introduction to x-ray crystallography. G. Rule provides lecture notes on x-ray crystallography (and part 2) for a course on physical biochemistry. R. Hanson, Department of Chemistry, St. Olaf College, Northfield, MN, provides an introduction to x-ray crystallography. The Wilson-Squier Group, University of California, San Diego, provides an illustrated introduction to x-ray diffraction that includes a section on crystals. The National Synchrotron Light Source at Brookhaven National Laboratory offers a Macromolecular X-Ray Crystallography Web page. The May 1998 issue of the *Journal of Synchrotron Radiation* had an article by K. Holmes and G. Rosenbaum titled "How x-ray diffraction with synchrotron radiation got started." X-Ray Crystallography by D. Edwards, a Web project for a chemistry course at Bristol University, UK, includes a brief history of x-ray crystallography and an introduction to its principles. The 1914 Nobel Prize in Physics was awarded to Max von Laue "for his discovery of the diffraction of X-rays by crystals." William Henry Bragg and William Lawrence Bragg shared the 1915 Nobel Prize in Physics "for their services in the analysis of crystal structure by means of X-rays." The 1962 Nobel Prize in Chemistry

was awarded to Max Ferdinand Perutz and John Cowdery Kendrew "for their studies of the structures of globular proteins" and the 1964 Nobel Prize in Chemistry was awarded to Dorothy Crowfoot Hodgkin "for her determinations by X-ray techniques of the structures of important biochemical substances."

9. A list of bacterial names with standing in nomenclature, made available by J. Euzéby, Ecole Nationale Vétérinaire de Toulouse, France, offers information about the Haloarcula bacteria. The American Type Culture Collection provides catalog information about *Haloarcula marismortui*. M. Weiss, IMB Jena, offers a presentation on the crystallization of biological macromolecules. B. Rupp provides lecture notes on the physical chemistry of protein crystallization.

10. A. Yonath is in the Arbeitsgruppe Ribosomenstruktur, Max-Planck-Arbeitsgruppen für Strukturelle Molekularbiologie, Hamburg, Germany. Yonath is also affiliated with the Department of Structural Biology, Weizmann Institute of Science, Rehovot, Israel. The Max Planck Society issued a research news release about her recent research in producing an electron density map of the small ribosomal subunit from bacterium *Thermus thermophilus*.

11. *Scientific American* offers a 27 September 1999 exploration feature by K. Leutwyler titled "Ribosomes revealed." Access Excellence provides an article by S. Henahan, titled "Imaging the ribosome." The 27 August 1999 issue of *Science* had a news article by Elizabeth Pennisi titled "Ribosome finally begins to yield its complete structure." The Brookhaven National Laboratory issued a news release titled "Landmark progress in understanding ribosome structure - Research done at Brookhaven Lab's Light Source." The November 1999 newsletter of the National Synchrotron Light Source (NSLS) at Brookhaven National Laboratory had an article by M. Capel titled "Ribosome redux at NSLS crystallography stations." The 24 September 1999 issue of *Science* had a report by J. Cate, M. Yusupov, G. Yusupova, T. Earnest, and H. Noller titled "X-ray crystal structures of 70S ribosome functional complexes." The University of California, Santa Cruz, issued a press release titled "UCSC researchers obtain first detailed images of a complete ribosome." The Advanced Light Source at Lawrence Berkeley National Laboratory provides a 22 December 1999 article by L. Tamura titled "Solving the ribosome puzzle." The Winter 2000 *NCRR Reporter*, published by the National Center for Research Resources, National Institutes of Health, had an article by O. Henriksen titled "Looking inside the cellular protein factory."

12. The Center for Molecular Biology of RNA, University of California, Santa Cruz, provides presentations titled What is RNA? and Why study RNA structure? RNABase, an RNA structure database, provides an RNA structure primer. The Molecular Biology Notebook, a tutorial from the BioInformatics Department of the Institute of Arable Crops Research, Rothamsted, UK, provides an introduction to RNA structure. M. Zuker, Center for Computational Biology, Washington University, St. Louis, provides a presentation on RNA secondary structure on his RNA Web page. The Comparative RNA Web Site of the laboratory of R. Gutell, Institute for Cellular and Molecular Biology, University of Texas, provides RNA structure definitions.

13. M. Yarus is in the Department of Molecular, Cellular, and Developmental Biology, University of Colorado.

14. The Howard Hughes Medical Institute provides a research news article titled "Ribozymes come ready for action" about J. Doudna and colleagues' research on the hepatitis delta virus ribozyme. The Doudna laboratory, Department of Molecular Biophysics and Biochemistry, Yale University, has a Web page.

15. G. Muth, L. Ortoleva-Donnelly, and S. Strobel are in the Department of Molecular Biophysics and Biochemistry and Department of Chemistry, Yale University. The Strobel laboratory has a Web page.

16. P. Unrau, Whitehead Biomedical Institute, offers a presentation on the RNA world. The February 1998 issue of *BioScience* had an article by L. Landweber, P. Simon, and T. Wagner titled "Ribozyme engineering and early evolution." *New Scientist* offers a presentation on the RNA world theory titled "Let there be life." J. Brown, Department of Microbiology, North Carolina State University, offers lecture notes on the RNA world theory for a course on microbial diversity. The September-October 1995 issue of *American Scientist* had an article by C. de Duve titled "The beginnings of life on Earth" that discussed the RNA world theory.

17. T. R. Cech is in Department of Chemistry and Biochemistry and the Department of Molecular, Cellular, and Developmental Biology, University of Colorado. The Howard Hughes Medical Institute provides information about T.

R. Cech and his appointment as HHMI president. The Cech Laboratory has a Web page.

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- Yarus, M. (2002). PRIMORDIAL GENETICS: Phenotype of the Ribocyte. *Annu. Rev. Genet.* 36: 125-151 [Abstract] [Full Text]
- Zhang, Y., Li, Z., Pilch, D. S., Leibowitz, M. J. (2002). Pentamidine inhibits catalytic activity of group I intron Ca.LSU by altering RNA folding. *Nucleic Acids Res* 30: 2961-2971 [Abstract] [Full Text]
- Woese, C. R. (2002). On the evolution of cells. *Proc. Natl. Acad. Sci. U. S. A.* 99: 8742-8747 [Abstract] [Full Text]
- Zhou, J.-M., Zhou, D.-M., Takagi, Y., Kasai, Y., Inoue, A., Baba, T., Taira, K. (2002). Existence of efficient divalent metal ion-catalyzed and inefficient divalent metal ion-independent channels in reactions catalyzed by a hammerhead ribozyme. *Nucleic Acids Res* 30: 2374-2382 [Abstract] [Full Text]
- Gautschi, M., Mun, A., Ross, S., Rospert, S. (2002). A functional chaperone triad on the yeast ribosome. *Proc. Natl. Acad. Sci. U. S. A.* 99: 4209-4214 [Abstract] [Full Text]
- Schaferkordt, J., Wagner, R. (2001). Effects of base change mutations within an Escherichia coli ribosomal RNA leader region on rRNA maturation and ribosome formation. *Nucleic Acids Res* 29: 3394-3403 [Abstract] [Full Text]

- Takagi, Y., Warashina, M., Stec, W. J., Yoshinari, K., Taira, K. (2001). SURVEY AND SUMMARY: Recent advances in the elucidation of the mechanisms of action of ribozymes. *Nucleic Acids Res* 29: 1815-1834 [Abstract] [Full Text]

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