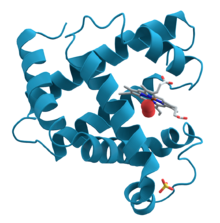
**Protein**

From Wikipedia, the free encyclopedia

[](http://en.wikipedia.org/wiki/File:Myoglobin.png)

A representation of the 3D structure of the protein [myoglobin](http://en.wikipedia.org/wiki/Myoglobin) showing turquoise [alpha helices](http://en.wikipedia.org/wiki/Alpha_helix). This protein was the first to have its structure solved by [X-ray crystallography](http://en.wikipedia.org/wiki/X-ray_crystallography). Towards the right-center among the coils, a[prosthetic group](http://en.wikipedia.org/wiki/Prosthetic_group) called a [heme group](http://en.wikipedia.org/wiki/Heme_group)(shown in gray) with a bound oxygen molecule (red).

**Proteins** ([/](http://en.wikipedia.org/wiki/Help:IPA_for_English)[ˈproʊˌtiːnz](http://en.wikipedia.org/wiki/Help:IPA_for_English#Key)[/](http://en.wikipedia.org/wiki/Help:IPA_for_English) or [/](http://en.wikipedia.org/wiki/Help:IPA_for_English)[ˈproʊti.ɨnz](http://en.wikipedia.org/wiki/Help:IPA_for_English#Key)[/](http://en.wikipedia.org/wiki/Help:IPA_for_English)) are large [biological molecules](http://en.wikipedia.org/wiki/Biomolecule), or [macromolecules](http://en.wikipedia.org/wiki/Macromolecule), consisting of one or more long chains of [amino acid](http://en.wikipedia.org/wiki/Amino_acid) residues. Proteins perform a vast array of functions within living organisms, including [catalyzing metabolic reactions](http://en.wikipedia.org/wiki/Enzyme_catalysis), [replicating DNA](http://en.wikipedia.org/wiki/DNA_replication), [responding to stimuli](http://en.wikipedia.org/wiki/Cell_signaling), and transporting molecules from one location to another. Proteins differ from one another primarily in their sequence of amino acids, which is dictated by the [nucleotide sequence](http://en.wikipedia.org/wiki/Nucleotide_sequence) of their [genes](http://en.wikipedia.org/wiki/Genes), and which usually results in [folding](http://en.wikipedia.org/wiki/Protein_folding) of the protein into a specific [three-dimensional structure](http://en.wikipedia.org/wiki/Protein_structure) that determines its activity.

A linear chain of amino acid residues is called a [polypeptide](http://en.wikipedia.org/wiki/Polypeptide). A protein contains at least one long polypeptide. Short polypeptides, containing less than about 20-30 residues, are rarely considered to be proteins and are commonly called [peptides](http://en.wikipedia.org/wiki/Peptide), or sometimes oligopeptides. The individual amino acid residues are bonded together by [peptide bonds](http://en.wikipedia.org/wiki/Peptide_bond) and adjacent amino acid [residues](http://en.wikipedia.org/wiki/Residue_(chemistry)). The [sequence](http://en.wikipedia.org/wiki/Peptide_sequence) of amino acid residues in a protein is defined by the [sequence](http://en.wikipedia.org/wiki/DNA_sequence) of a [gene](http://en.wikipedia.org/wiki/Gene), which is encoded in the [genetic code](http://en.wikipedia.org/wiki/Genetic_code). In general, the genetic code specifies 20 standard amino acids; however, in certain organisms the genetic code can include [selenocysteine](http://en.wikipedia.org/wiki/Selenocysteine) and—in certain[archaea](http://en.wikipedia.org/wiki/Archaea)—[pyrrolysine](http://en.wikipedia.org/wiki/Pyrrolysine). Shortly after or even during synthesis, the residues in a protein are often chemically modified by [posttranslational modification](http://en.wikipedia.org/wiki/Posttranslational_modification), which alters the physical and chemical properties, folding, stability, activity, and ultimately, the function of the proteins. Sometimes proteins have non-peptide groups attached, which can be called [prosthetic groups](http://en.wikipedia.org/wiki/Prosthetic_group) or [cofactors](http://en.wikipedia.org/wiki/Cofactor_(biochemistry)). Proteins can also work together to achieve a particular function, and they often associate to form stable [protein complexes](http://en.wikipedia.org/wiki/Protein_complex).

Once formed proteins only exist for a certain period of time and are then [degraded](http://en.wikipedia.org/wiki/Proteolysis#Protein_degradation) and recycled by the cell's machinery through the process of [protein turnover](http://en.wikipedia.org/wiki/Protein_turnover). A protein's lifespan is measured in terms of its [half-life](http://en.wikipedia.org/wiki/Half-life) and covers a wide range. They can exist for minutes or years with an average lifespan of 1-2 days in mammalian cells. Abnormal and or misfolded proteins are degraded more rapidly either due to being targeted for destruction or due to being unstable.

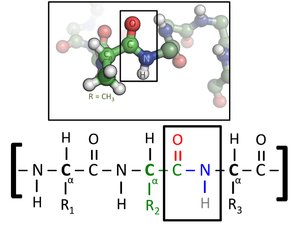
Like other biological [macromolecules](http://en.wikipedia.org/wiki/Macromolecules) such as [polysaccharides](http://en.wikipedia.org/wiki/Polysaccharide) and [nucleic acids](http://en.wikipedia.org/wiki/Nucleic_acid), proteins are essential parts of organisms and participate in virtually every process within [cells](http://en.wikipedia.org/wiki/Cell_(biology)). Many proteins are [enzymes](http://en.wikipedia.org/wiki/Enzyme) that [catalyze](http://en.wikipedia.org/wiki/Catalysis)biochemical reactions and are vital to [metabolism](http://en.wikipedia.org/wiki/Metabolism). Proteins also have structural or mechanical functions, such as [actin](http://en.wikipedia.org/wiki/Actin) and [myosin](http://en.wikipedia.org/wiki/Myosin) in muscle and the proteins in the [cytoskeleton](http://en.wikipedia.org/wiki/Cytoskeleton), which form a system of [scaffolding](http://en.wikipedia.org/wiki/Scaffolding) that maintains cell shape. Other proteins are important in [cell signaling](http://en.wikipedia.org/wiki/Cell_signaling), [immune responses](http://en.wikipedia.org/wiki/Antibody), [cell adhesion](http://en.wikipedia.org/wiki/Cell_adhesion), and the [cell cycle](http://en.wikipedia.org/wiki/Cell_cycle). Proteins are also necessary in animals' diets, since animals cannot [synthesize](http://en.wikipedia.org/wiki/Amino_acid_synthesis) all the amino acids they need and must obtain [essential amino acids](http://en.wikipedia.org/wiki/Essential_amino_acid) from food. Through the process of [digestion](http://en.wikipedia.org/wiki/Digestion), animals break down ingested protein into free amino acids that are then used in metabolism.

Proteins may be [purified](http://en.wikipedia.org/wiki/Protein_purification) from other cellular components using a variety of techniques such as [ultracentrifugation](http://en.wikipedia.org/wiki/Ultracentrifugation), [precipitation](http://en.wikipedia.org/wiki/Precipitation_(chemistry)), [electrophoresis](http://en.wikipedia.org/wiki/Electrophoresis), and [chromatography](http://en.wikipedia.org/wiki/Chromatography); the advent of [genetic engineering](http://en.wikipedia.org/wiki/Genetic_engineering) has made possible a number of methods to facilitate purification. Methods commonly used to study protein structure and function include [immunohistochemistry](http://en.wikipedia.org/wiki/Immunohistochemistry), [site-directed mutagenesis](http://en.wikipedia.org/wiki/Site-directed_mutagenesis), [X-ray crystallography](http://en.wikipedia.org/wiki/X-ray_crystallography), [nuclear magnetic resonance](http://en.wikipedia.org/wiki/Nuclear_magnetic_resonance) and[mass spectrometry](http://en.wikipedia.org/wiki/Mass_spectrometry).

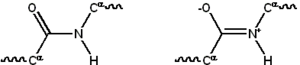
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  + [5.4 Bioinformatics](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#Bioinformatics)
    - [5.4.1 Structure prediction and simulation](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#Structure_prediction_and_simulation)
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* [10 References](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#References)
* [11 External links](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#External_links)
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  + [11.2 Tutorials and educational websites](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#Tutorials_and_educational_websites)

**Biochemistry**

[](http://en.wikipedia.org/wiki/File:Peptide-Figure-Revised.png)

Chemical structure of the peptide bond (bottom) and the three-dimensional structure of a peptide bond between an [alanine](http://en.wikipedia.org/wiki/Alanine) and an adjacent amino acid (top/inset)

[](http://en.wikipedia.org/wiki/File:Peptide_group_resonance.png)

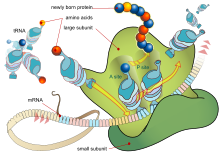
[Resonance](http://en.wikipedia.org/wiki/Resonance_(chemistry)) structures of the [peptide bond](http://en.wikipedia.org/wiki/Peptide_bond) that links individual amino acids to form a protein [polymer](http://en.wikipedia.org/wiki/Polymer)

Most proteins consist of linear [polymers](http://en.wikipedia.org/wiki/Polymer) built from series of up to 20 different L-α-[amino acids](http://en.wikipedia.org/wiki/Amino_acid). All [proteinogenic amino acids](http://en.wikipedia.org/wiki/Proteinogenic_amino_acid) possess common structural features, including an [α-carbon](http://en.wikipedia.org/wiki/Alpha_carbon) to which an [amino](http://en.wikipedia.org/wiki/Amino) group, a[carboxyl](http://en.wikipedia.org/wiki/Carboxyl) group, and a variable [side chain](http://en.wikipedia.org/wiki/Side_chain) are [bonded](http://en.wikipedia.org/wiki/Chemical_bond). Only [proline](http://en.wikipedia.org/wiki/Proline) differs from this basic structure as it contains an unusual ring to the N-end amine group, which forces the CO–NH amide moiety into a fixed conformation.[[1]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Nelson2005-1) The side chains of the standard amino acids, detailed in the [list of standard amino acids](http://en.wikipedia.org/wiki/List_of_standard_amino_acids), have a great variety of chemical structures and properties; it is the combined effect of all of the amino acid side chains in a protein that ultimately determines its three-dimensional structure and its chemical reactivity.[[2]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Gutteridge2005-2) The [amino acids](http://en.wikipedia.org/wiki/Amino_acids) in a polypeptide chain are linked by [peptide bonds](http://en.wikipedia.org/wiki/Peptide_bond). Once linked in the protein chain, an individual amino acid is called a *residue,* and the linked series of carbon, nitrogen, and oxygen atoms are known as the *main chain* or *protein backbone.*[[3]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-3)

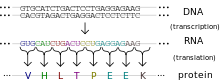
The peptide bond has two [resonance](http://en.wikipedia.org/wiki/Resonance_(chemistry)) forms that contribute some [double-bond](http://en.wikipedia.org/wiki/Double-bond) character and inhibit rotation around its axis, so that the alpha carbons are roughly [coplanar](http://en.wikipedia.org/wiki/Coplanar). The other two [dihedral angles](http://en.wikipedia.org/wiki/Dihedral_angle) in the peptide bond determine the local shape assumed by the protein backbone.[[4]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-4) The end of the protein with a free carboxyl group is known as the [C-terminus](http://en.wikipedia.org/wiki/C-terminus) or carboxy terminus, whereas the end with a free amino group is known as the [N-terminus](http://en.wikipedia.org/wiki/N-terminus) or amino terminus. The words *protein*, *polypeptide,* and [*peptide*](http://en.wikipedia.org/wiki/Peptide) are a little ambiguous and can overlap in meaning. *Protein* is generally used to refer to the complete biological molecule in a stable [conformation](http://en.wikipedia.org/wiki/Tertiary_structure), whereas *peptide* is generally reserved for a short amino acid oligomers often lacking a stable three-dimensional structure. However, the boundary between the two is not well defined and usually lies near 20–30 residues.[[5]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Lodish2004-5) *Polypeptide* can refer to any single linear chain of amino acids, usually regardless of length, but often implies an absence of a defined [conformation](http://en.wikipedia.org/wiki/Tertiary_structure).

**Synthesis**

**Biosynthesis**

[](http://en.wikipedia.org/wiki/File:Ribosome_mRNA_translation_en.svg)

A ribosome produces a protein using mRNA as template.

[](http://en.wikipedia.org/wiki/File:Genetic_code.svg)

The [DNA](http://en.wikipedia.org/wiki/DNA) sequence of a gene [encodes](http://en.wikipedia.org/wiki/Genetic_code)the [amino acid](http://en.wikipedia.org/wiki/Amino_acid) sequence of a protein.

Proteins are assembled from amino acids using information encoded in [genes](http://en.wikipedia.org/wiki/Gene). Each protein has its own unique amino acid sequence that is specified by the [nucleotide](http://en.wikipedia.org/wiki/Nucleotide) sequence of the gene encoding this protein. The [genetic code](http://en.wikipedia.org/wiki/Genetic_code) is a set of three-nucleotide sets called [codons](http://en.wikipedia.org/wiki/Codon) and each three-nucleotide combination designates an amino acid, for example AUG ([adenine](http://en.wikipedia.org/wiki/Adenine)-[uracil](http://en.wikipedia.org/wiki/Uracil)-[guanine](http://en.wikipedia.org/wiki/Guanine)) is the code for [methionine](http://en.wikipedia.org/wiki/Methionine). Because [DNA](http://en.wikipedia.org/wiki/DNA)contains four nucleotides, the total number of possible codons is 64; hence, there is some redundancy in the genetic code, with some amino acids specified by more than one codon.[[6]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-vanHolde1996-6) Genes encoded in DNA are first [transcribed](http://en.wikipedia.org/wiki/Transcription_(genetics)) into pre-[messenger RNA](http://en.wikipedia.org/wiki/Messenger_RNA) (mRNA) by proteins such as [RNA polymerase](http://en.wikipedia.org/wiki/RNA_polymerase). Most organisms then process the pre-mRNA (also known as a *primary transcript*) using various forms of [Post-transcriptional modification](http://en.wikipedia.org/wiki/Post-transcriptional_modification) to form the mature mRNA, which is then used as a template for protein synthesis by the [ribosome](http://en.wikipedia.org/wiki/Ribosome). In [prokaryotes](http://en.wikipedia.org/wiki/Prokaryote) the mRNA may either be used as soon as it is produced, or be bound by a ribosome after having moved away from the [nucleoid](http://en.wikipedia.org/wiki/Nucleoid). In contrast, [eukaryotes](http://en.wikipedia.org/wiki/Eukaryote) make mRNA in the [cell nucleus](http://en.wikipedia.org/wiki/Cell_nucleus) and then [translocate](http://en.wikipedia.org/wiki/Protein_translocation) it across the [nuclear membrane](http://en.wikipedia.org/wiki/Nuclear_membrane) into the [cytoplasm](http://en.wikipedia.org/wiki/Cytoplasm), where [protein synthesis](http://en.wikipedia.org/wiki/Protein_biosynthesis)then takes place. The rate of protein synthesis is higher in prokaryotes than eukaryotes and can reach up to 20 amino acids per second.[[7]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Pain2000-7)

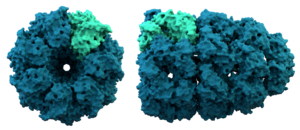
The process of synthesizing a protein from an mRNA template is known as [translation](http://en.wikipedia.org/wiki/Translation_(genetics)). The mRNA is loaded onto the ribosome and is read three nucleotides at a time by matching each codon to its [base pairing](http://en.wikipedia.org/wiki/Base_pair) [anticodon](http://en.wikipedia.org/wiki/Anticodon)located on a [transfer RNA](http://en.wikipedia.org/wiki/Transfer_RNA) molecule, which carries the amino acid corresponding to the codon it recognizes. The enzyme [aminoacyl tRNA synthetase](http://en.wikipedia.org/wiki/Aminoacyl_tRNA_synthetase) "charges" the tRNA molecules with the correct amino acids. The growing polypeptide is often termed the *nascent chain*. Proteins are always biosynthesized from [N-terminus](http://en.wikipedia.org/wiki/N-terminus) to [C-terminus](http://en.wikipedia.org/wiki/C-terminus).[[6]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-vanHolde1996-6)

The size of a synthesized protein can be measured by the number of amino acids it contains and by its total [molecular mass](http://en.wikipedia.org/wiki/Molecular_mass), which is normally reported in units of *daltons* (synonymous with [atomic mass units](http://en.wikipedia.org/wiki/Atomic_mass_unit)), or the derivative unit kilodalton (kDa). [Yeast](http://en.wikipedia.org/wiki/Yeast) proteins are on average 466 amino acids long and 53 kDa in mass.[[5]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Lodish2004-5) The largest known proteins are the [titins](http://en.wikipedia.org/wiki/Titin), a component of the [muscle](http://en.wikipedia.org/wiki/Muscle) [sarcomere](http://en.wikipedia.org/wiki/Sarcomere), with a molecular mass of almost 3,000 kDa and a total length of almost 27,000 amino acids.[[8]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Fulton1991-8)

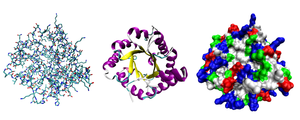
**Chemical synthesis**

Short proteins can also be synthesized chemically by a family of methods known as [peptide synthesis](http://en.wikipedia.org/wiki/Peptide_synthesis), which rely on [organic synthesis](http://en.wikipedia.org/wiki/Organic_synthesis) techniques such as [chemical ligation](http://en.wikipedia.org/wiki/Chemical_ligation) to produce peptides in high yield.[[9]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Bruckdorfer2004-9) Chemical synthesis allows for the introduction of non-natural amino acids into polypeptide chains, such as attachment of [fluorescent](http://en.wikipedia.org/wiki/Fluorescent) probes to amino acid side chains.[[10]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Schwarzer2005-10) These methods are useful in laboratory [biochemistry](http://en.wikipedia.org/wiki/Biochemistry) and [cell biology](http://en.wikipedia.org/wiki/Cell_biology), though generally not for commercial applications. Chemical synthesis is inefficient for polypeptides longer than about 300 amino acids, and the synthesized proteins may not readily assume their native [tertiary structure](http://en.wikipedia.org/wiki/Tertiary_structure). Most chemical synthesis methods proceed from C-terminus to N-terminus, opposite the biological reaction.[[11]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kent2009-11)

**Structure**

[](http://en.wikipedia.org/wiki/File:Chaperonin_1AON.png)

The crystal structure of the chaperonin. Chaperonins assist protein folding.

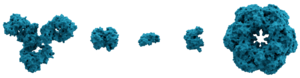
[](http://en.wikipedia.org/wiki/File:Proteinviews-1tim.png)

Three possible representations of the three-dimensional structure of the protein [triose phosphate isomerase](http://en.wikipedia.org/wiki/Triose_phosphate_isomerase). Left: all-atom representation colored by atom type. Middle: Simplified representation illustrating the backbone conformation, colored by secondary structure. Right: Solvent-accessible surface representation colored by residue type (acidic residues red, basic residues blue, polar residues green, nonpolar residues white)

Most proteins [fold](http://en.wikipedia.org/wiki/Protein_folding) into unique 3-dimensional structures. The shape into which a protein naturally folds is known as its [native conformation](http://en.wikipedia.org/wiki/Native_conformation).[[12]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-12) Although many proteins can fold unassisted, simply through the chemical properties of their amino acids, others require the aid of molecular [chaperones](http://en.wikipedia.org/wiki/Chaperone_(protein)) to fold into their native states.[[13]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-13) Biochemists often refer to four distinct aspects of a protein's structure:[[14]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-14)

* [*Primary structure*](http://en.wikipedia.org/wiki/Primary_structure): the [amino acid sequence](http://en.wikipedia.org/wiki/Peptide_sequence). A protein is a [polyamide](http://en.wikipedia.org/wiki/Polyamide).
* [*Secondary structure*](http://en.wikipedia.org/wiki/Secondary_structure): regularly repeating local structures stabilized by [hydrogen bonds](http://en.wikipedia.org/wiki/Hydrogen_bond). The most common examples are the [alpha helix](http://en.wikipedia.org/wiki/Alpha_helix), [beta sheet](http://en.wikipedia.org/wiki/Beta_sheet) and [turns](http://en.wikipedia.org/wiki/Turn_(biochemistry)). Because secondary structures are local, many regions of different secondary structure can be present in the same protein molecule.
* [*Tertiary structure*](http://en.wikipedia.org/wiki/Tertiary_structure): the overall shape of a single protein molecule; the spatial relationship of the secondary structures to one another. Tertiary structure is generally stabilized by nonlocal interactions, most commonly the formation of a [hydrophobic core](http://en.wikipedia.org/wiki/Hydrophobic_core), but also through [salt bridges](http://en.wikipedia.org/wiki/Salt_bridge_(protein)), hydrogen bonds, [disulfide bonds](http://en.wikipedia.org/wiki/Disulfide_bond), and even [posttranslational modifications](http://en.wikipedia.org/wiki/Posttranslational_modification). The term "tertiary structure" is often used as synonymous with the term *fold*. The tertiary structure is what controls the basic function of the protein.
* [*Quaternary structure*](http://en.wikipedia.org/wiki/Quaternary_structure): the structure formed by several protein molecules (polypeptide chains), usually called [*protein subunits*](http://en.wikipedia.org/wiki/Protein_subunit) in this context, which function as a single [protein complex](http://en.wikipedia.org/wiki/Protein_complex).

Proteins are not entirely rigid molecules. In addition to these levels of structure, proteins may shift between several related structures while they perform their functions. In the context of these functional rearrangements, these tertiary or quaternary structures are usually referred to as "[conformations](http://en.wikipedia.org/wiki/Chemical_conformation)", and transitions between them are called *conformational changes.* Such changes are often induced by the binding of a [substrate](http://en.wikipedia.org/wiki/Substrate_(biochemistry)) molecule to an enzyme's [active site](http://en.wikipedia.org/wiki/Active_site), or the physical region of the protein that participates in chemical catalysis. In solution proteins also undergo variation in structure through thermal vibration and the collision with other molecules.[[15]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-15)

[](http://en.wikipedia.org/wiki/File:Protein_composite.png)

Molecular surface of several proteins showing their comparative sizes. From left to right are:[immunoglobulin G](http://en.wikipedia.org/wiki/Immunoglobulin_G) (IgG, an [antibody](http://en.wikipedia.org/wiki/Antibody)), [hemoglobin](http://en.wikipedia.org/wiki/Hemoglobin),[insulin](http://en.wikipedia.org/wiki/Insulin) (a hormone), [adenylate kinase](http://en.wikipedia.org/wiki/Adenylate_kinase) (an enzyme), and [glutamine synthetase](http://en.wikipedia.org/wiki/Glutamine_synthetase) (an enzyme).

Proteins can be informally divided into three main classes, which correlate with typical tertiary structures: [globular proteins](http://en.wikipedia.org/wiki/Globular_protein), [fibrous proteins](http://en.wikipedia.org/wiki/Fibrous_protein), and [membrane proteins](http://en.wikipedia.org/wiki/Membrane_protein). Almost all globular proteins are [soluble](http://en.wikipedia.org/wiki/Soluble) and many are enzymes. Fibrous proteins are often structural, such as [collagen](http://en.wikipedia.org/wiki/Collagen), the major component of connective tissue, or [keratin](http://en.wikipedia.org/wiki/Keratin), the protein component of hair and nails. Membrane proteins often serve as [receptors](http://en.wikipedia.org/wiki/Receptor_(biochemistry))or provide channels for polar or charged molecules to pass through the [cell membrane](http://en.wikipedia.org/wiki/Cell_membrane).[[16]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-16)

A special case of intramolecular hydrogen bonds within proteins, poorly shielded from water attack and hence promoting their own [dehydration](http://en.wikipedia.org/wiki/Dehydration), are called [dehydrons](http://en.wikipedia.org/wiki/Dehydron).[[17]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Fernandez2003-17)

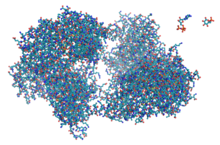
**Structure determination**

Discovering the tertiary structure of a protein, or the quaternary structure of its complexes, can provide important clues about how the protein performs its function. Common experimental methods of structure determination include [X-ray crystallography](http://en.wikipedia.org/wiki/X-ray_crystallography) and [NMR spectroscopy](http://en.wikipedia.org/wiki/Protein_NMR), both of which can produce information at [atomic](http://en.wikipedia.org/wiki/Atom) resolution. However, NMR experiments are able to provide information from which a subset of distances between pairs of atoms can be estimated, and the final possible conformations for a protein are determined by solving a [distance geometry](http://en.wikipedia.org/wiki/Distance_geometry) problem. [Dual polarisation interferometry](http://en.wikipedia.org/wiki/Dual_polarisation_interferometry) is a quantitative analytical method for measuring the overall protein [conformation](http://en.wikipedia.org/wiki/Protein_conformation) and [conformational changes](http://en.wikipedia.org/wiki/Conformational_change) due to interactions or other stimulus. [Circular dichroism](http://en.wikipedia.org/wiki/Circular_dichroism) is another laboratory technique for determining internal beta sheet/ helical composition of proteins. [Cryoelectron microscopy](http://en.wikipedia.org/wiki/Cryoelectron_microscopy) is used to produce lower-resolution structural information about very large protein complexes, including assembled [viruses](http://en.wikipedia.org/wiki/Virus);[[18]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-18) a variant known as[electron crystallography](http://en.wikipedia.org/wiki/Electron_crystallography) can also produce high-resolution information in some cases, especially for two-dimensional crystals of membrane proteins.[[19]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Gonen2005-19) Solved structures are usually deposited in the [Protein Data Bank](http://en.wikipedia.org/wiki/Protein_Data_Bank) (PDB), a freely available resource from which structural data about thousands of proteins can be obtained in the form of [Cartesian coordinates](http://en.wikipedia.org/wiki/Cartesian_coordinates) for each atom in the protein.[[20]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Standley2008-20)

Many more gene sequences are known than protein structures. Further, the set of solved structures is biased toward proteins that can be easily subjected to the conditions required in [X-ray crystallography](http://en.wikipedia.org/wiki/X-ray_crystallography), one of the major structure determination methods. In particular, globular proteins are comparatively easy to [crystallize](http://en.wikipedia.org/wiki/Crystallize) in preparation for X-ray crystallography. Membrane proteins, by contrast, are difficult to crystallize and are underrepresented in the PDB.[[21]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Walian2004-21) [Structural genomics](http://en.wikipedia.org/wiki/Structural_genomics) initiatives have attempted to remedy these deficiencies by systematically solving representative structures of major fold classes. [Protein structure prediction](http://en.wikipedia.org/wiki/Protein_structure_prediction) methods attempt to provide a means of generating a plausible structure for proteins whose structures have not been experimentally determined.[[22]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Sleator2012-22)

**Cellular functions**

Proteins are the chief actors within the cell, said to be carrying out the duties specified by the information encoded in genes.[[5]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Lodish2004-5) With the exception of certain types of [RNA](http://en.wikipedia.org/wiki/RNA), most other biological molecules are relatively inert elements upon which proteins act. Proteins make up half the dry weight of an [*Escherichia coli*](http://en.wikipedia.org/wiki/Escherichia_coli) cell, whereas other macromolecules such as DNA and RNA make up only 3% and 20%, respectively.[[23]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Voet-23) The set of proteins expressed in a particular cell or cell type is known as its [proteome](http://en.wikipedia.org/wiki/Proteome).

[](http://en.wikipedia.org/wiki/File:Hexokinase_ball_and_stick_model,_with_substrates_to_scale_copy.png)

The enzyme [hexokinase](http://en.wikipedia.org/wiki/Hexokinase) is shown as a conventional ball-and-stick molecular model. To scale in the top right-hand corner are two of its substrates, [ATP](http://en.wikipedia.org/wiki/Adenosine_triphosphate)and [glucose](http://en.wikipedia.org/wiki/Glucose).

The chief characteristic of proteins that also allows their diverse set of functions is their ability to bind other molecules specifically and tightly. The region of the protein responsible for binding another molecule is known as the[binding site](http://en.wikipedia.org/wiki/Binding_site) and is often a depression or "pocket" on the molecular surface. This binding ability is mediated by the tertiary structure of the protein, which defines the binding site pocket, and by the chemical properties of the surrounding amino acids' side chains. Protein binding can be extraordinarily tight and specific; for example, the [ribonuclease inhibitor](http://en.wikipedia.org/wiki/Ribonuclease_inhibitor) protein binds to human [angiogenin](http://en.wikipedia.org/wiki/Angiogenin) with a sub-femtomolar [dissociation constant](http://en.wikipedia.org/wiki/Dissociation_constant) (<10−15 M) but does not bind at all to its amphibian homolog [onconase](http://en.wikipedia.org/wiki/Onconase) (>1 M). Extremely minor chemical changes such as the addition of a single methyl group to a binding partner can sometimes suffice to nearly eliminate binding; for example, the [aminoacyl tRNA synthetase](http://en.wikipedia.org/wiki/Aminoacyl_tRNA_synthetase) specific to the amino acid [valine](http://en.wikipedia.org/wiki/Valine) discriminates against the very similar side chain of the amino acid [isoleucine](http://en.wikipedia.org/wiki/Isoleucine).[[24]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Sankaranarayanan2001-24)

Proteins can bind to other proteins as well as to [small-molecule](http://en.wikipedia.org/wiki/Small_molecule) substrates. When proteins bind specifically to other copies of the same molecule, they can [oligomerize](http://en.wikipedia.org/wiki/Oligomer) to form fibrils; this process occurs often in structural proteins that consist of globular monomers that self-associate to form rigid fibers. [Protein–protein interactions](http://en.wikipedia.org/wiki/Protein%E2%80%93protein_interaction) also regulate enzymatic activity, control progression through the [cell cycle](http://en.wikipedia.org/wiki/Cell_cycle), and allow the assembly of large [protein complexes](http://en.wikipedia.org/wiki/Protein_complex) that carry out many closely related reactions with a common biological function. Proteins can also bind to, or even be integrated into, cell membranes. The ability of binding partners to induce conformational changes in proteins allows the construction of enormously complex [signaling](http://en.wikipedia.org/wiki/Cell_signaling) networks.[[25]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-25) Importantly, as interactions between proteins are reversible, and depend heavily on the availability of different groups of partner proteins to form aggregates that are capable to carry out discrete sets of function, study of the interactions between specific proteins is a key to understand important aspects of cellular function, and ultimately the properties that distinguish particular cell types.[[26]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Copland2009-26)[[27]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Samarin2009-27)

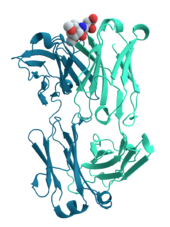
**Enzymes**

The best-known role of proteins in the cell is as [enzymes](http://en.wikipedia.org/wiki/Enzyme), which [catalyze](http://en.wikipedia.org/wiki/Catalysis) chemical reactions. Enzymes are usually highly specific and accelerate only one or a few chemical reactions. Enzymes carry out most of the reactions involved in [metabolism](http://en.wikipedia.org/wiki/Metabolism), as well as manipulating DNA in processes such as [DNA replication](http://en.wikipedia.org/wiki/DNA_replication), [DNA repair](http://en.wikipedia.org/wiki/DNA_repair), and [transcription](http://en.wikipedia.org/wiki/Transcription_(genetics)). Some enzymes act on other proteins to add or remove chemical groups in a process known as posttranslational modification. About 4,000 reactions are known to be catalyzed by enzymes.[[28]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-EXPASY2000-28) The rate acceleration conferred by enzymatic catalysis is often enormous—as much as 1017-fold increase in rate over the uncatalyzed reaction in the case of [orotate decarboxylase](http://en.wikipedia.org/wiki/Orotate_decarboxylase) (78 million years without the enzyme, 18 milliseconds with the enzyme).[[29]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Radzicka1995-29)

The molecules bound and acted upon by enzymes are called [substrates](http://en.wikipedia.org/wiki/Substrate_(biochemistry)). Although enzymes can consist of hundreds of amino acids, it is usually only a small fraction of the residues that come in contact with the substrate, and an even smaller fraction—three to four residues on average—that are directly involved in catalysis.[[30]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-urlEBI-30) The region of the enzyme that binds the substrate and contains the catalytic residues is known as the [active site](http://en.wikipedia.org/wiki/Active_site).

[Dirigent proteins](http://en.wikipedia.org/wiki/Dirigent_protein) are members of a class of proteins which dictate the stereochemistry of a compound synthesized by other enzymes.

**Cell signaling and ligand binding**

[](http://en.wikipedia.org/wiki/File:Mouse_cholera_antibody.png)

[Ribbon diagram](http://en.wikipedia.org/wiki/Ribbon_diagram) of a mouse antibody against [cholera](http://en.wikipedia.org/wiki/Cholera) that binds a [carbohydrate](http://en.wikipedia.org/wiki/Carbohydrate) antigen

Many proteins are involved in the process of [cell signaling](http://en.wikipedia.org/wiki/Cell_signaling) and [signal transduction](http://en.wikipedia.org/wiki/Signal_transduction). Some proteins, such as [insulin](http://en.wikipedia.org/wiki/Insulin), are extracellular proteins that transmit a signal from the cell in which they were synthesized to other cells in distant[tissues](http://en.wikipedia.org/wiki/Biological_tissue). Others are [membrane proteins](http://en.wikipedia.org/wiki/Membrane_protein) that act as [receptors](http://en.wikipedia.org/wiki/Receptor_(biochemistry)) whose main function is to bind a signaling molecule and induce a biochemical response in the cell. Many receptors have a binding site exposed on the cell surface and an effector domain within the cell, which may have enzymatic activity or may undergo a [conformational change](http://en.wikipedia.org/wiki/Conformational_change) detected by other proteins within the cell.[[31]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-31)

[Antibodies](http://en.wikipedia.org/wiki/Antibodies) are protein components of an [adaptive immune system](http://en.wikipedia.org/wiki/Adaptive_immune_system) whose main function is to bind [antigens](http://en.wikipedia.org/wiki/Antigen), or foreign substances in the body, and target them for destruction. Antibodies can be [secreted](http://en.wikipedia.org/wiki/Secrete) into the extracellular environment or anchored in the membranes of specialized [B cells](http://en.wikipedia.org/wiki/B_cell) known as [plasma cells](http://en.wikipedia.org/wiki/Plasma_cell). Whereas enzymes are limited in their binding affinity for their substrates by the necessity of conducting their reaction, antibodies have no such constraints. An antibody's binding affinity to its target is extraordinarily high.[[32]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-32)

Many ligand transport proteins bind particular [small biomolecules](http://en.wikipedia.org/wiki/Small_molecule) and transport them to other locations in the body of a multicellular organism. These proteins must have a high binding affinity when their [ligand](http://en.wikipedia.org/wiki/Ligand) is present in high concentrations, but must also release the ligand when it is present at low concentrations in the target tissues. The canonical example of a ligand-binding protein is [haemoglobin](http://en.wikipedia.org/wiki/Haemoglobin), which transports [oxygen](http://en.wikipedia.org/wiki/Oxygen) from the [lungs](http://en.wikipedia.org/wiki/Lung) to other organs and tissues in all [vertebrates](http://en.wikipedia.org/wiki/Vertebrate) and has close [homologs](http://en.wikipedia.org/wiki/Homology_(biology)) in every biological [kingdom](http://en.wikipedia.org/wiki/Kingdom_(biology)).[[33]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-33) [Lectins](http://en.wikipedia.org/wiki/Lectins) are sugar-binding proteins which are highly specific for their sugar moieties. [Lectins](http://en.wikipedia.org/wiki/Lectins) typically play a role in biological [recognition](http://en.wikipedia.org/wiki/Molecular_recognition) phenomena involving cells and proteins.[[34]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Rudiger2000-34) [Receptors](http://en.wikipedia.org/wiki/Receptor_(biochemistry)) and [hormones](http://en.wikipedia.org/wiki/Hormone) are highly specific binding proteins.

[Transmembrane proteins](http://en.wikipedia.org/wiki/Transmembrane_protein) can also serve as ligand transport proteins that alter the [permeability](http://en.wikipedia.org/wiki/Semipermeable_membrane) of the cell membrane to [small molecules](http://en.wikipedia.org/wiki/Small_molecule) and ions. The membrane alone has a [hydrophobic](http://en.wikipedia.org/wiki/Hydrophobic) core through which [polar](http://en.wikipedia.org/wiki/Chemical_polarity) or charged molecules cannot [diffuse](http://en.wikipedia.org/wiki/Diffusion). Membrane proteins contain internal channels that allow such molecules to enter and exit the cell. Many [ion channel](http://en.wikipedia.org/wiki/Ion_channel) proteins are specialized to select for only a particular ion; for example, [potassium](http://en.wikipedia.org/wiki/Potassium) and [sodium](http://en.wikipedia.org/wiki/Sodium) channels often discriminate for only one of the two ions.[[35]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-35)

**Structural proteins**

Structural proteins confer stiffness and rigidity to otherwise-fluid biological components. Most structural proteins are [fibrous proteins](http://en.wikipedia.org/wiki/Fibrous_protein); for example, [collagen](http://en.wikipedia.org/wiki/Collagen) and [elastin](http://en.wikipedia.org/wiki/Elastin) are critical components of [connective tissue](http://en.wikipedia.org/wiki/Connective_tissue) such as [cartilage](http://en.wikipedia.org/wiki/Cartilage), and [keratin](http://en.wikipedia.org/wiki/Keratin) is found in hard or filamentous structures such as [hair](http://en.wikipedia.org/wiki/Hair), [nails](http://en.wikipedia.org/wiki/Nail_(anatomy)), [feathers](http://en.wikipedia.org/wiki/Feather), [hooves](http://en.wikipedia.org/wiki/Hoof), and some [animal shells](http://en.wikipedia.org/wiki/Animal_shell).[[36]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-36) Some [globular proteins](http://en.wikipedia.org/wiki/Globular_proteins) can also play structural functions, for example, [actin](http://en.wikipedia.org/wiki/Actin) and [tubulin](http://en.wikipedia.org/wiki/Tubulin) are globular and soluble as monomers, but [polymerize](http://en.wikipedia.org/wiki/Polymer) to form long, stiff fibers that make up the [cytoskeleton](http://en.wikipedia.org/wiki/Cytoskeleton), which allows the cell to maintain its shape and size.

Other proteins that serve structural functions are [motor proteins](http://en.wikipedia.org/wiki/Motor_protein) such as [myosin](http://en.wikipedia.org/wiki/Myosin), [kinesin](http://en.wikipedia.org/wiki/Kinesin), and [dynein](http://en.wikipedia.org/wiki/Dynein), which are capable of generating mechanical forces. These proteins are crucial for cellular [motility](http://en.wikipedia.org/wiki/Motility) of single celled organisms and the [sperm](http://en.wikipedia.org/wiki/Spermatozoon) of many multicellular organisms which reproduce [sexually](http://en.wikipedia.org/wiki/Sexual_reproduction). They also generate the forces exerted by contracting [muscles](http://en.wikipedia.org/wiki/Muscle)[[37]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-37) and play essential roles in intracellular transport.

**Methods of study**

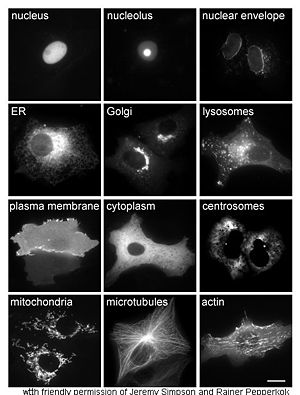
The activities and structures of proteins may be examined [*in vitro*](http://en.wikipedia.org/wiki/In_vitro)*,* [*in vivo*](http://en.wikipedia.org/wiki/In_vivo)*, and*[*in silico*](http://en.wikipedia.org/wiki/In_silico). ***In vitro*** studies of purified proteins in controlled environments are useful for learning how a protein carries out its function: for example, [enzyme kinetics](http://en.wikipedia.org/wiki/Enzyme_kinetics) studies explore the[chemical mechanism](http://en.wikipedia.org/wiki/Reaction_mechanism) of an enzyme's catalytic activity and its relative affinity for various possible substrate molecules. By contrast, ***in vivo*** experiments can provide information about the physiological role of a protein in the context of a [cell](http://en.wikipedia.org/wiki/Cell_biology) or even a whole[organism](http://en.wikipedia.org/wiki/Organism). ***In silico*** studies use computational methods to study proteins.

**Protein purification**

To perform [*in vitro*](http://en.wikipedia.org/wiki/In_vitro) analysis, a protein must be purified away from other cellular components. This process usually begins with [cell lysis](http://en.wikipedia.org/wiki/Cytolysis), in which a cell's membrane is disrupted and its internal contents released into a solution known as a [crude lysate](http://en.wikipedia.org/wiki/Crude_lysate). The resulting mixture can be purified using [ultracentrifugation](http://en.wikipedia.org/wiki/Ultracentrifugation), which fractionates the various cellular components into fractions containing soluble proteins; membrane [lipids](http://en.wikipedia.org/wiki/Lipid) and proteins; cellular [organelles](http://en.wikipedia.org/wiki/Organelle), and [nucleic acids](http://en.wikipedia.org/wiki/Nucleic_acid). [Precipitation](http://en.wikipedia.org/wiki/Precipitation_(chemistry)) by a method known as [salting out](http://en.wikipedia.org/wiki/Salting_out) can concentrate the proteins from this lysate. Various types of [chromatography](http://en.wikipedia.org/wiki/Chromatography) are then used to isolate the protein or proteins of interest based on properties such as molecular weight, net charge and binding affinity.[[38]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-38) The level of purification can be monitored using various types of [gel electrophoresis](http://en.wikipedia.org/wiki/Gel_electrophoresis) if the desired protein's molecular weight and [isoelectric point](http://en.wikipedia.org/wiki/Isoelectric_point) are known, by [spectroscopy](http://en.wikipedia.org/wiki/Spectroscopy) if the protein has distinguishable spectroscopic features, or by [enzyme assays](http://en.wikipedia.org/wiki/Enzyme_assay) if the protein has enzymatic activity. Additionally, proteins can be isolated according their charge using [electrofocusing](http://en.wikipedia.org/wiki/Electrofocusing).[[39]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Hey2008-39)

For natural proteins, a series of purification steps may be necessary to obtain protein sufficiently pure for laboratory applications. To simplify this process, [genetic engineering](http://en.wikipedia.org/wiki/Genetic_engineering) is often used to add chemical features to proteins that make them easier to purify without affecting their structure or activity. Here, a "tag" consisting of a specific amino acid sequence, often a series of [histidine](http://en.wikipedia.org/wiki/Histidine) residues (a "[His-tag](http://en.wikipedia.org/wiki/His-tag)"), is attached to one terminus of the protein. As a result, when the lysate is passed over a chromatography column containing [nickel](http://en.wikipedia.org/wiki/Nickel), the histidine residues ligate the nickel and attach to the column while the untagged components of the lysate pass unimpeded. A number of different tags have been developed to help researchers purify specific proteins from complex mixtures.[[40]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Terpe2003-40)

**Cellular localization**

[](http://en.wikipedia.org/wiki/File:Localisations02eng.jpg)

Proteins in different [cellular compartments](http://en.wikipedia.org/wiki/Cellular_compartment) and structures tagged with [green fluorescent protein](http://en.wikipedia.org/wiki/Green_fluorescent_protein) (here, white)

The study of proteins *in vivo* is often concerned with the synthesis and localization of the protein within the cell. Although many intracellular proteins are synthesized in the [cytoplasm](http://en.wikipedia.org/wiki/Cytoplasm) and membrane-bound or secreted proteins in the [endoplasmic reticulum](http://en.wikipedia.org/wiki/Endoplasmic_reticulum), the specifics of how proteins are [targeted](http://en.wikipedia.org/wiki/Protein_targeting) to specific organelles or cellular structures is often unclear. A useful technique for assessing cellular localization uses genetic engineering to express in a cell a [fusion protein](http://en.wikipedia.org/wiki/Fusion_protein) or [chimera](http://en.wikipedia.org/wiki/Chimera_(protein)) consisting of the natural protein of interest linked to a "[reporter](http://en.wikipedia.org/wiki/Reporter_gene)" such as [green fluorescent protein](http://en.wikipedia.org/wiki/Green_fluorescent_protein) (GFP).[[41]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Stepanenko2008-41) The fused protein's position within the cell can be cleanly and efficiently visualized using [microscopy](http://en.wikipedia.org/wiki/Microscopy),[[42]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Yuste2005-42) as shown in the figure opposite.

Other methods for elucidating the cellular location of proteins requires the use of known compartmental markers for regions such as the ER, the Golgi, lysosomes or vacuoles, mitochondria, chloroplasts, plasma membrane, etc. With the use of fluorescently tagged versions of these markers or of antibodies to known markers, it becomes much simpler to identify the localization of a protein of interest. For example, [indirect immunofluorescence](http://en.wikipedia.org/wiki/Indirect_immunofluorescence) will allow for fluorescence colocalization and demonstration of location. Fluorescent dyes are used to label cellular compartments for a similar purpose.[[43]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Margolin2000-43)

Other possibilities exist, as well. For example, [immunohistochemistry](http://en.wikipedia.org/wiki/Immunohistochemistry) usually utilizes an antibody to one or more proteins of interest that are conjugated to enzymes yielding either luminescent or chromogenic signals that can be compared between samples, allowing for localization information. Another applicable technique is cofractionation in sucrose (or other material) gradients using [isopycnic centrifugation](http://en.wikipedia.org/wiki/Isopycnic_centrifugation).[[44]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Walker2000-44) While this technique does not prove colocalization of a compartment of known density and the protein of interest, it does increase the likelihood, and is more amenable to large-scale studies.

Finally, the gold-standard method of cellular localization is [immunoelectron microscopy](http://en.wikipedia.org/wiki/Immunoelectron_microscopy). This technique also uses an antibody to the protein of interest, along with classical electron microscopy techniques. The sample is prepared for normal electron microscopic examination, and then treated with an antibody to the protein of interest that is conjugated to an extremely electro-dense material, usually gold. This allows for the localization of both ultrastructural details as well as the protein of interest.[[45]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Mayhew2008-45)

Through another genetic engineering application known as [site-directed mutagenesis](http://en.wikipedia.org/wiki/Site-directed_mutagenesis), researchers can alter the protein sequence and hence its structure, cellular localization, and susceptibility to regulation. This technique even allows the incorporation of unnatural amino acids into proteins, using modified tRNAs,[[46]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Hohsaka2002-46) and may allow the rational design of new proteins with novel properties.[[47]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Cedrone2000-47)

**Proteomics**

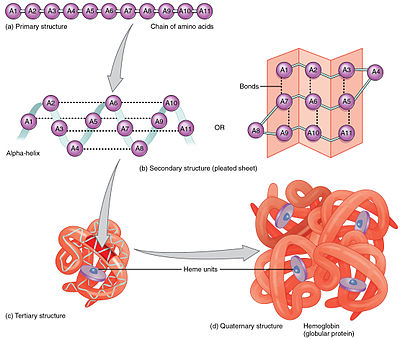
The total complement of proteins present at a time in a cell or cell type is known as its [proteome](http://en.wikipedia.org/wiki/Proteome), and the study of such large-scale data sets defines the field of [proteomics](http://en.wikipedia.org/wiki/Proteomics), named by analogy to the related field of[genomics](http://en.wikipedia.org/wiki/Genomics). Key experimental techniques in proteomics include [2D electrophoresis](http://en.wikipedia.org/wiki/Two-dimensional_gel_electrophoresis),[[48]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Gorg2008-48) which allows the separation of a large number of proteins, [mass spectrometry](http://en.wikipedia.org/wiki/Mass_spectrometry),[[49]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Conrotto2008-49) which allows rapid high-throughput identification of proteins and sequencing of peptides (most often after [in-gel digestion](http://en.wikipedia.org/wiki/In-gel_digestion)), [protein microarrays](http://en.wikipedia.org/wiki/Protein_microarray),[[50]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Joos2009-50) which allow the detection of the relative levels of a large number of proteins present in a cell, and[two-hybrid screening](http://en.wikipedia.org/wiki/Two-hybrid_screening), which allows the systematic exploration of [protein–protein interactions](http://en.wikipedia.org/wiki/Protein%E2%80%93protein_interaction).[[51]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Koegl2007-51) The total complement of biologically possible such interactions is known as the [interactome](http://en.wikipedia.org/wiki/Interactome).[[52]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Plewczynski2009-52) A systematic attempt to determine the structures of proteins representing every possible fold is known as [structural genomics](http://en.wikipedia.org/wiki/Structural_genomics).[[53]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Zhang2003-53)

**Bioinformatics**

A vast array of computational methods have been developed to analyze the structure, function, and evolution of proteins.

The development of such tools has been driven by the large amount of genomic and proteomic data available for a variety of organisms, including the [human genome.](http://en.wikipedia.org/wiki/Human_genome) It is simply impossible to study all proteins experimentally, hence only a few are subjected to laboratory experiments while computational tools are used to extrapolate to similar proteins. Such [homologous](http://en.wikipedia.org/wiki/Homology_(biology)) proteins can be efficiently identified in distantly related organisms by [sequence alignment](http://en.wikipedia.org/wiki/Sequence_alignment). Genome and gene sequences can be searched by a variety of tools for certain properties. [Sequence profiling tools](http://en.wikipedia.org/wiki/Sequence_profiling_tool) can find [restriction enzyme](http://en.wikipedia.org/wiki/Restriction_enzyme) sites, [open reading frames](http://en.wikipedia.org/wiki/Open_reading_frame) in [nucleotide](http://en.wikipedia.org/wiki/Nucleotide) sequences, and predict [secondary structures](http://en.wikipedia.org/wiki/Secondary_structure). P[hylogenetic trees](http://en.wikipedia.org/wiki/Phylogenetic_tree) can be constructed and [evolutionary](http://en.wikipedia.org/wiki/Evolution) hypotheses developed using special software like [ClustalW](http://en.wikipedia.org/wiki/ClustalW) regarding the ancestry of modern organisms and the genes they express. The field of [bioinformatics](http://en.wikipedia.org/wiki/Bioinformatics) is now indispensable for the analysis of genes and proteins.

**Structure prediction and simulation**

[](http://en.wikipedia.org/wiki/File:225_Peptide_Bond-01.jpg)

Constituent amino-acids can be analyzed to predict secondary, tertiary and quaternary protein structure, in this case hemoglobin containing[heme](http://en.wikipedia.org/wiki/Heme) units.

Complementary to the field of structural genomics, protein structure prediction seeks to develop efficient ways to provide plausible models for proteins whose structures have not yet been determined experimentally.[[54]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Zhang2008-54) The most successful type of structure prediction, known as [homology modeling](http://en.wikipedia.org/wiki/Homology_modeling), relies on the existence of a "template" structure with sequence similarity to the protein being modeled; structural genomics' goal is to provide sufficient representation in solved structures to model most of those that remain.[[55]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Xiang2006-55) Although producing accurate models remains a challenge when only distantly related template structures are available, it has been suggested that [sequence alignment](http://en.wikipedia.org/wiki/Sequence_alignment) is the bottleneck in this process, as quite accurate models can be produced if a "perfect" sequence alignment is known.[[56]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Zhang2005-56) Many structure prediction methods have served to inform the emerging field of [protein engineering](http://en.wikipedia.org/wiki/Protein_engineering), in which novel protein folds have already been designed.[[57]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kuhlman2003-57) A more complex computational problem is the prediction of intermolecular interactions, such as in [molecular docking](http://en.wikipedia.org/wiki/Docking_(molecular)) and [protein–protein interaction prediction](http://en.wikipedia.org/wiki/Protein%E2%80%93protein_interaction_prediction).[[58]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Ritchie2008-58)

The processes of [protein folding](http://en.wikipedia.org/wiki/Protein_folding) and binding can be simulated using such technique as [molecular mechanics](http://en.wikipedia.org/wiki/Molecular_mechanics), in particular, [molecular dynamics](http://en.wikipedia.org/wiki/Molecular_dynamics) and [Monte Carlo](http://en.wikipedia.org/wiki/Monte_Carlo_method), which increasingly take advantage of parallel and [distributed computing](http://en.wikipedia.org/wiki/Distributed_computing) ([Folding@home](http://en.wikipedia.org/wiki/Folding@home) project;[[59]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Scheraga2007-59) [molecular modeling on GPU](http://en.wikipedia.org/wiki/Molecular_modeling_on_GPU)). The folding of small alpha-helical protein domains such as the [villin](http://en.wikipedia.org/wiki/Villin) headpiece[[60]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Zagrovic2002-60) and the [HIV](http://en.wikipedia.org/wiki/HIV) accessory protein[[61]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Herges2005-61) have been successfully simulated *in silico*, and hybrid methods that combine standard molecular dynamics with [quantum mechanics](http://en.wikipedia.org/wiki/Quantum_mechanics) calculations have allowed exploration of the electronic states of [rhodopsins](http://en.wikipedia.org/wiki/Rhodopsin).[[62]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Hoffman2006-62)

**Nutrition**

Most [microorganisms](http://en.wikipedia.org/wiki/Microorganism) and plants can biosynthesize all 20 standard [amino acids](http://en.wikipedia.org/wiki/Amino_acids), while animals (including humans) must obtain some of the amino acids from the [diet](http://en.wikipedia.org/wiki/Diet_(nutrition)).[[23]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Voet-23) The amino acids that an organism cannot synthesize on its own are referred to as [essential amino acids](http://en.wikipedia.org/wiki/Essential_amino_acids). Key enzymes that synthesize certain amino acids are not present in animals — such as [aspartokinase](http://en.wikipedia.org/wiki/Aspartokinase), which catalyzes the first step in the synthesis of [lysine](http://en.wikipedia.org/wiki/Lysine), [methionine](http://en.wikipedia.org/wiki/Methionine), and [threonine](http://en.wikipedia.org/wiki/Threonine) from [aspartate](http://en.wikipedia.org/wiki/Aspartate). If amino acids are present in the environment, microorganisms can conserve energy by taking up the amino acids from their surroundings and [downregulating](http://en.wikipedia.org/wiki/Downregulation_and_upregulation) their biosynthetic pathways.

In animals, amino acids are obtained through the consumption of foods containing protein. Ingested proteins are then broken down into amino acids through [digestion](http://en.wikipedia.org/wiki/Digestion), which typically involves[denaturation](http://en.wikipedia.org/wiki/Denaturation_(biochemistry)) of the protein through exposure to [acid](http://en.wikipedia.org/wiki/Acid) and [hydrolysis](http://en.wikipedia.org/wiki/Hydrolysis) by enzymes called [proteases](http://en.wikipedia.org/wiki/Protease). Some ingested amino acids are used for protein biosynthesis, while others are converted to [glucose](http://en.wikipedia.org/wiki/Glucose)through [gluconeogenesis](http://en.wikipedia.org/wiki/Gluconeogenesis), or fed into the [citric acid cycle](http://en.wikipedia.org/wiki/Citric_acid_cycle). This use of protein as a fuel is particularly important under [starvation](http://en.wikipedia.org/wiki/Starvation) conditions as it allows the body's own proteins to be used to support life, particularly those found in [muscle](http://en.wikipedia.org/wiki/Muscle).[[63]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-BrosnanJ-63) Amino acids are also an important dietary source of [nitrogen](http://en.wikipedia.org/wiki/Nitrogen).

**History and etymology**

Proteins were recognized as a distinct class of biological molecules in the eighteenth century by [Antoine Fourcroy](http://en.wikipedia.org/wiki/Antoine_Fran%C3%A7ois,_comte_de_Fourcroy) and others, distinguished by the molecules' ability to [coagulate](http://en.wikipedia.org/wiki/Coagulate) or [flocculate](http://en.wikipedia.org/wiki/Flocculation) under treatments with heat or acid.[[64]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-64) Noted examples at the time included albumin from [egg whites](http://en.wikipedia.org/wiki/Egg_white), blood [serum albumin](http://en.wikipedia.org/wiki/Serum_albumin), [fibrin](http://en.wikipedia.org/wiki/Fibrin), and wheat [gluten](http://en.wikipedia.org/wiki/Gluten).

Proteins were first described by the [Dutch](http://en.wikipedia.org/wiki/Dutch_people) chemist [Gerardus Johannes Mulder](http://en.wikipedia.org/wiki/Gerardus_Johannes_Mulder) and named by the Swedish chemist [Jöns Jacob Berzelius](http://en.wikipedia.org/wiki/J%C3%B6ns_Jacob_Berzelius) in 1838. Mulder carried out [elemental analysis](http://en.wikipedia.org/wiki/Elemental_analysis) of common proteins and found that nearly all proteins had the same [empirical formula](http://en.wikipedia.org/wiki/Empirical_formula), C400H620N100O120P1S1.[[65]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Perrett2007-65) He came to the erroneous conclusion that they might be composed of a single type of (very large) molecule. The term "protein" to describe these molecules was proposed by Mulder's associate Berzelius; protein is derived from the [Greek](http://en.wikipedia.org/wiki/Greek_language) word πρώτειος (*proteios*), meaning "primary",[[66]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-66) "in the lead", or "standing in front".[[67]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Reynolds2003-67) Mulder went on to identify the products of protein degradation such as the [amino acid](http://en.wikipedia.org/wiki/Amino_acid) [leucine](http://en.wikipedia.org/wiki/Leucine) for which he found a (nearly correct) molecular weight of 131 [Da](http://en.wikipedia.org/wiki/Atomic_mass_unit).[[65]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Perrett2007-65)

Early nutritional scientists such as the German [Carl von Voit](http://en.wikipedia.org/wiki/Carl_von_Voit) believed that protein was the most important nutrient for maintaining the structure of the body, because it was generally believed that "flesh makes flesh."[[68]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Bischoff1860-68) [Karl Heinrich Ritthausen](http://en.wikipedia.org/wiki/Karl_Heinrich_Ritthausen) extended known protein forms with the identification of [glutamic acid](http://en.wikipedia.org/wiki/Glutamic_acid). At the [Connecticut Agricultural Experiment Station](http://en.wikipedia.org/wiki/Connecticut_Agricultural_Experiment_Station) a detailed review of the vegetable proteins was compiled by [Thomas Burr Osborne](http://en.wikipedia.org/wiki/Thomas_Burr_Osborne_(chemist)). Working with [Lafayette Mendel](http://en.wikipedia.org/wiki/Lafayette_Mendel) and applying [Liebig's law of the minimum](http://en.wikipedia.org/wiki/Liebig%27s_law_of_the_minimum)in feeding [laboratory rats](http://en.wikipedia.org/wiki/Laboratory_rat), the nutritionally [essential amino acids](http://en.wikipedia.org/wiki/Essential_amino_acid) were established. The work was continued and communicated by [William Cumming Rose](http://en.wikipedia.org/wiki/William_Cumming_Rose). The understanding of proteins as [polypeptides](http://en.wikipedia.org/wiki/Polypeptide) came through the work of [Franz Hofmeister](http://en.wikipedia.org/wiki/Franz_Hofmeister) and [Hermann Emil Fischer](http://en.wikipedia.org/wiki/Hermann_Emil_Fischer). The central role of proteins as [enzymes](http://en.wikipedia.org/wiki/Enzyme) in living organisms was not fully appreciated until 1926, when [James B. Sumner](http://en.wikipedia.org/wiki/James_B._Sumner) showed that the enzyme [urease](http://en.wikipedia.org/wiki/Urease) was in fact a protein.[[69]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Sumner1926-69)

The difficulty in purifying proteins in large quantities made them very difficult for early protein biochemists to study. Hence, early studies focused on proteins that could be purified in large quantities, e.g., those of [blood](http://en.wikipedia.org/wiki/Blood), [egg white](http://en.wikipedia.org/wiki/Egg_white), various [toxins](http://en.wikipedia.org/wiki/Toxin), and digestive/metabolic enzymes obtained from [slaughterhouses](http://en.wikipedia.org/wiki/Slaughterhouse). In the 1950s, the [Armour Hot Dog Co.](http://en.wikipedia.org/wiki/Armour_and_Company) purified 1 kg of pure bovine pancreatic [ribonuclease A](http://en.wikipedia.org/wiki/Ribonuclease_A) and made it freely available to scientists; this gesture helped ribonuclease A become a major target for biochemical study for the following decades.[[65]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Perrett2007-65)

[](http://en.wikipedia.org/wiki/File:KendrewMyoglobin.jpg)

John Kendrew with model of myoglobin in progress.

[Linus Pauling](http://en.wikipedia.org/wiki/Linus_Pauling) is credited with the successful prediction of regular protein [secondary structures](http://en.wikipedia.org/wiki/Secondary_structure) based on [hydrogen bonding](http://en.wikipedia.org/wiki/Hydrogen_bonding), an idea first put forth by [William Astbury](http://en.wikipedia.org/wiki/William_Astbury) in 1933.[[70]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Pauling1951-70) Later work by [Walter Kauzmann](http://en.wikipedia.org/wiki/Walter_Kauzmann) on[denaturation](http://en.wikipedia.org/wiki/Denaturation_(biochemistry)),[[71]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kauzmann1956-71)[[72]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kauzmann1959-72) based partly on previous studies by [Kaj Linderstrøm-Lang](http://en.wikipedia.org/wiki/Kaj_Ulrik_Linderstr%C3%B8m-Lang),[[73]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kalman1955-73) contributed an understanding of [protein folding](http://en.wikipedia.org/wiki/Protein_folding) and structure mediated by [hydrophobic interactions](http://en.wikipedia.org/wiki/Hydrophobic_core).

The first protein to be [sequenced](http://en.wikipedia.org/wiki/Protein_sequencing) was [insulin](http://en.wikipedia.org/wiki/Insulin), by [Frederick Sanger](http://en.wikipedia.org/wiki/Frederick_Sanger), in 1949. Sanger correctly determined the amino acid sequence of [insulin](http://en.wikipedia.org/wiki/Insulin), thus conclusively demonstrating that proteins consisted of linear polymers of amino acids rather than branched chains, [colloids](http://en.wikipedia.org/wiki/Colloid), or [cyclols](http://en.wikipedia.org/wiki/Cyclol).[[74]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Sanger1949-74) He won the Nobel Prize for this achievement in 1958.

The first [protein structures](http://en.wikipedia.org/wiki/Protein_structure) to be solved were [hemoglobin](http://en.wikipedia.org/wiki/Hemoglobin) and [myoglobin](http://en.wikipedia.org/wiki/Myoglobin), by [Max Perutz](http://en.wikipedia.org/wiki/Max_Perutz) and [Sir John Cowdery Kendrew](http://en.wikipedia.org/wiki/John_Kendrew), respectively, in 1958.[[75]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Muirhead1963-75)[[76]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Kendrew1958-76) As of 2014, the [Protein Data Bank](http://en.wikipedia.org/wiki/Protein_Data_Bank) has over 90,000 atomic-resolution structures of proteins.[[77]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-urlRCSB_Protein_Data_Bank-77) In more recent times, [cryo-electron microscopy](http://en.wikipedia.org/wiki/Cryo-electron_microscopy) of large [macromolecular assemblies](http://en.wikipedia.org/wiki/Macromolecular_Assembly)[[78]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Zhou2008-78) and computational [protein structure prediction](http://en.wikipedia.org/wiki/Protein_structure_prediction) of small protein [domains](http://en.wikipedia.org/wiki/Structural_domain)[[79]](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_note-Keskin2008-79) are two methods approaching atomic resolution.

**See also**

* [DNA-binding protein](http://en.wikipedia.org/wiki/DNA-binding_protein)
* [DNA, RNA and proteins: The three essential macromolecules of life](http://en.wikipedia.org/wiki/DNA,_RNA_and_proteins:_The_three_essential_macromolecules_of_life)
* [Intein](http://en.wikipedia.org/wiki/Intein)
* [List of proteins](http://en.wikipedia.org/wiki/List_of_proteins)
* [Protein design](http://en.wikipedia.org/wiki/Protein_design)
* [Proteopathy](http://en.wikipedia.org/wiki/Proteopathy)
* [Proteopedia](http://en.wikipedia.org/wiki/Proteopedia)
* [Proteolysis](http://en.wikipedia.org/wiki/Proteolysis)
* [Intrinsically disordered proteins](http://en.wikipedia.org/wiki/Intrinsically_disordered_proteins)

**Footnotes**

* 1. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-Nelson2005_1-0) Nelson DL, Cox MM (2005). *Lehninger's Principles of Biochemistry* (4th ed.). New York, New York: W. H. Freeman and Company.
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  3. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-3) Murray *et al*., p. 19.
  4. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-4) Murray *et al*., p. 31.
  5. ^ [Jump up to:***a***](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-Lodish2004_5-0) [***b***](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-Lodish2004_5-1) [***c***](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-Lodish2004_5-2) Lodish H, Berk A, Matsudaira P, Kaiser CA, Krieger M, Scott MP, Zipurksy SL, Darnell J (2004). *Molecular Cell Biology* (5th ed.). New York, New York: WH Freeman and Company.
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  11. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-Kent2009_11-0) Kent SB (2009). "Total chemical synthesis of proteins". *Chemical Society Reviews* **38** (2): 338–51. [doi](http://en.wikipedia.org/wiki/Digital_object_identifier):[10.1039/b700141j](http://dx.doi.org/10.1039%2Fb700141j). [PMID](http://en.wikipedia.org/wiki/PubMed_Identifier) [19169452](http://www.ncbi.nlm.nih.gov/pubmed/19169452).
  12. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-12) Murray *et al*., p. 36.
  13. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-13) Murray *et al*., p. 37.
  14. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-14) Murray *et al*., pp. 30–34.
  15. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-15) van Holde and Mathews, pp. 368–75.
  16. [**Jump up^**](http://en.wikipedia.org/w/index.php?title=Protein&printable=yes#cite_ref-16) van Holde and Mathews, pp. 165–85.
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**Databases and projects**

* [The Protein Naming Utility](http://www.jcvi.org/pn-utility)
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* [NCBI Protein Structure database](http://www.ncbi.nlm.nih.gov/sites/entrez?db=structure)
* [Human Protein Reference Database](http://www.hprd.org/)
* [Human Proteinpedia](http://www.humanproteinpedia.org/)
* [Folding@Home (Stanford University)](http://folding.stanford.edu/)
* [Comparative Toxicogenomics Database](http://ctd.mdibl.org/) curates protein–chemical interactions, as well as gene/protein–disease relationships and chemical-disease relationships.
* [Bioinformatic Harvester](http://harvester.fzk.de/) A Meta search engine (29 databases) for gene and protein information.
* [Protein Databank in Europe](http://www.pdbe.org/) (see also [PDBeQuips](http://www.pdbe.org/quips), short articles and tutorials on interesting PDB structures)
* [Research Collaboratory for Structural Bioinformatics](http://www.rcsb.org/) (see also [Molecule of the Month](http://www.rcsb.org/pdb/static.do?p=education_discussion/molecule_of_the_month/index.html), presenting short accounts on selected proteins from the PDB)
* [Proteopedia – Life in 3D](http://www.proteopedia.org/): rotatable, zoomable 3D model with wiki annotations for every known protein molecular structure.
* [UniProt the Universal Protein Resource](http://www.expasy.uniprot.org/)
* [neXtProt – Exploring the universe of human proteins](http://www.nextprot.org/): human-centric protein knowledge resource
* [Multi-Omics Profiling Expression Database: MOPED](https://www.proteinspire.org/MOPED/mopedviews/mopedAbout.jsf/) human and model organism protein/gene knowledge and expression data

**Tutorials and educational websites**

* ["An Introduction to Proteins"](http://hopes.stanford.edu/basics/proteins/p0.html) from [HOPES](http://en.wikipedia.org/wiki/HOPES) (Huntington's Disease Outreach Project for Education at Stanford)
* [Proteins: Biogenesis to Degradation – The Virtual Library of Biochemistry and Cell Biology](http://www.biochemweb.org/proteins.shtml)

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