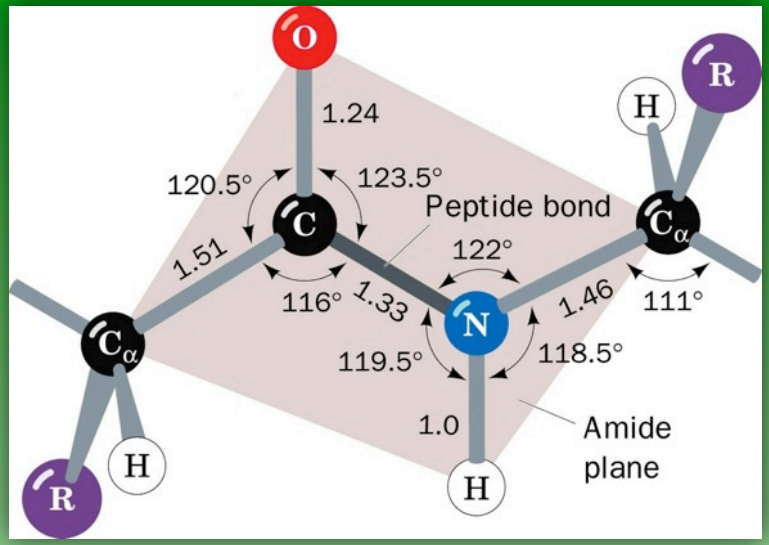
Protein Secondary, Tertiary & Quaternary Structure

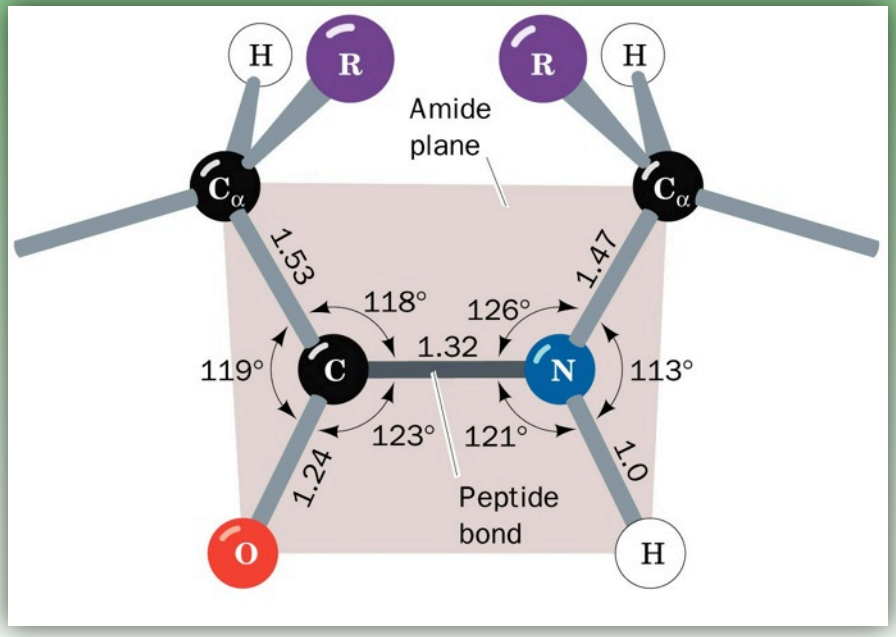
CHEM 420 – Principles of Biochemistry
Instructor – Anthony S. Serianni

Chapter 8: Voet/Voet, *Biochemistry*, 2011
Fall 2015

September 16 & 18



trans peptide (amide) configuration



cis peptide (amide) configuration: less stable for most α-amino acids

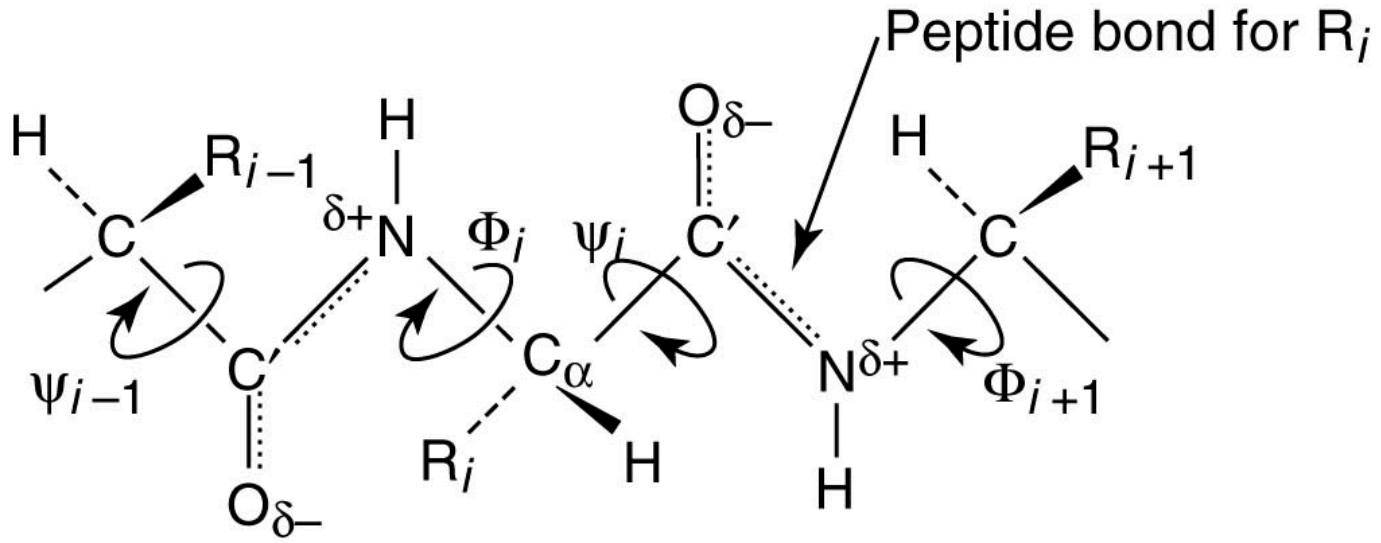
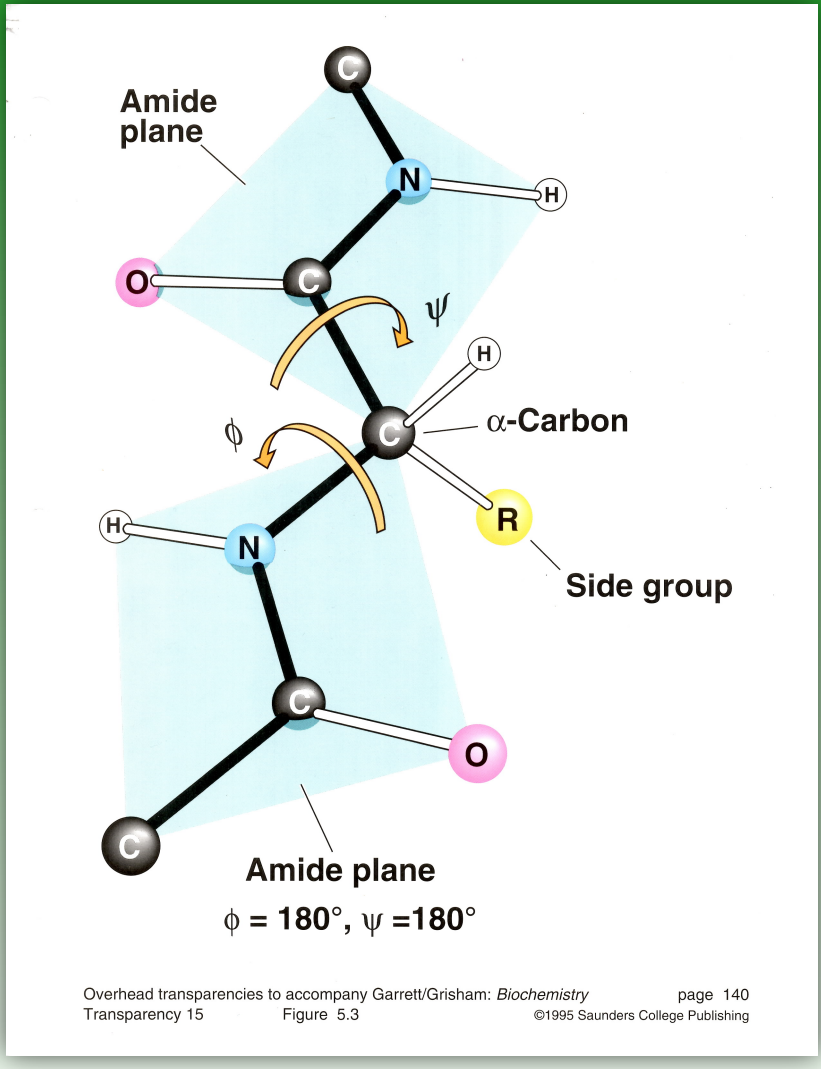


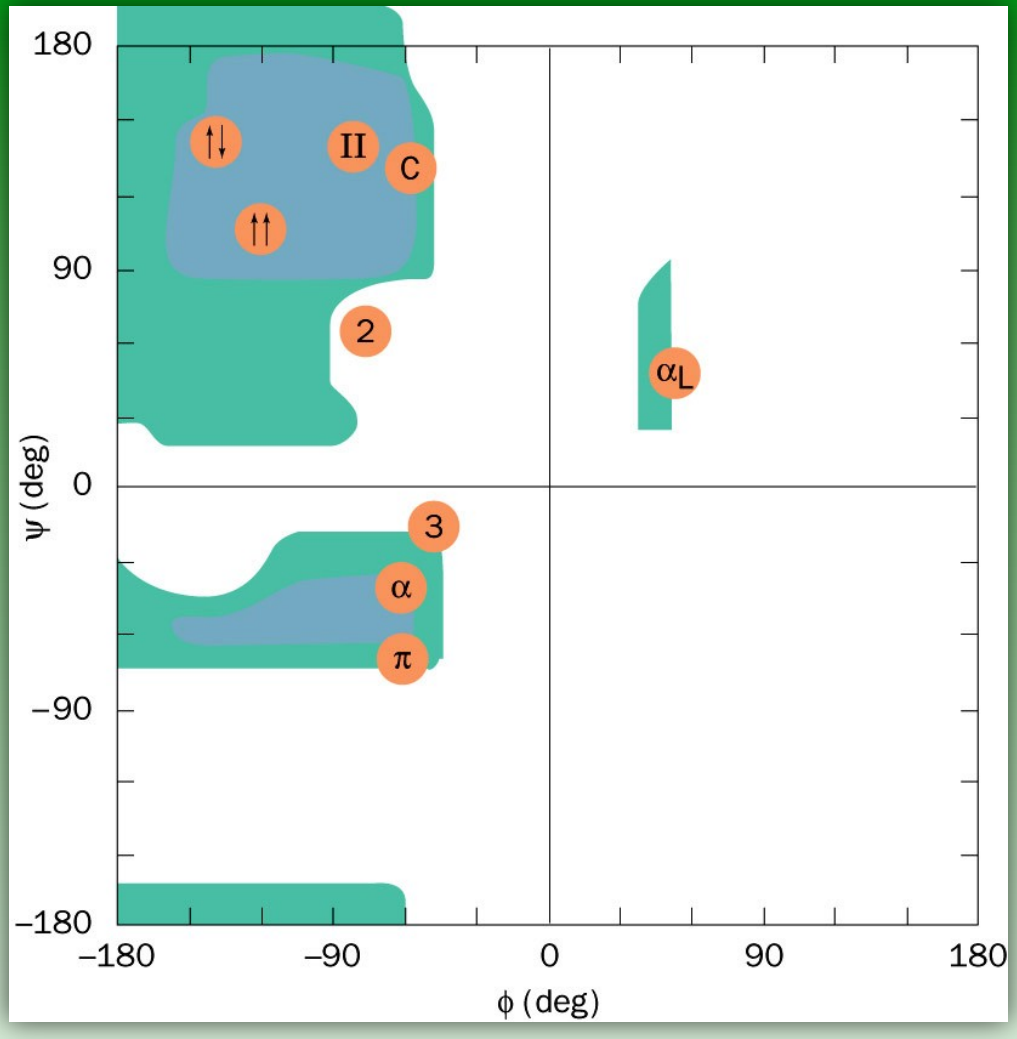
Figure 3.11. Amino acid residue within a polypeptide chain.

Three distinct bond types along the backbone of a protein:
the "rigid" peptide bond and the rotatable
phi (ϕ) and psi (ψ) bonds involving C_α.



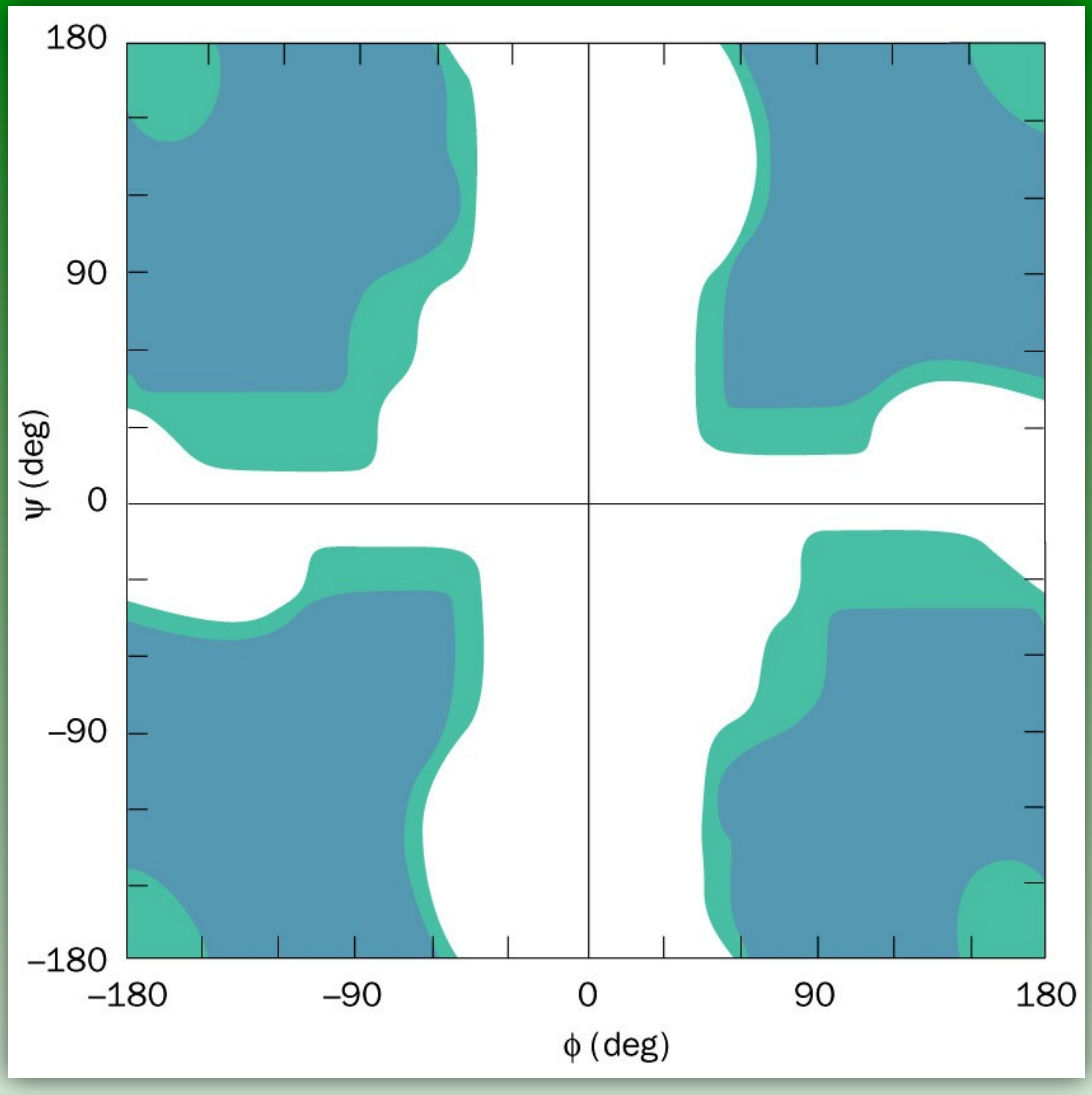
Overhead transparencies to accompany Garrett/Grisham: *Biochemistry* page 140
Transparency 15 Figure 5.3

Definitions of ϕ and ψ along the backbone of a protein



Predicting protein secondary structure

Ramachandran ϕ/ψ plot for proteins calculated from analyses of van der Waals radii in proteins



Ramachandran diagram of Gly residues
in a polypeptide chain; normally allowed areas are shown in blue.

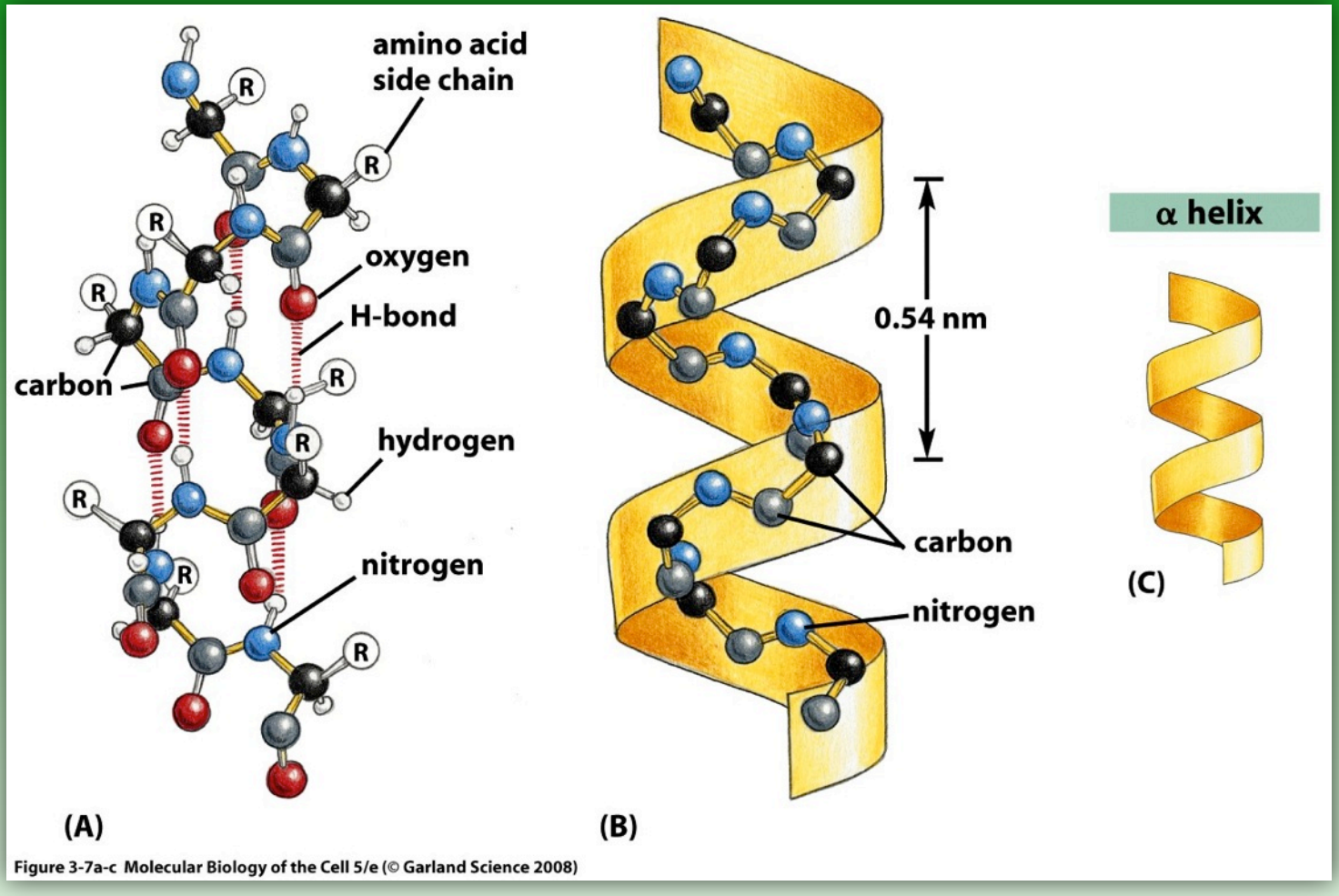


Figure 3-7a-c Molecular Biology of the Cell 5/e (© Garland Science 2008)

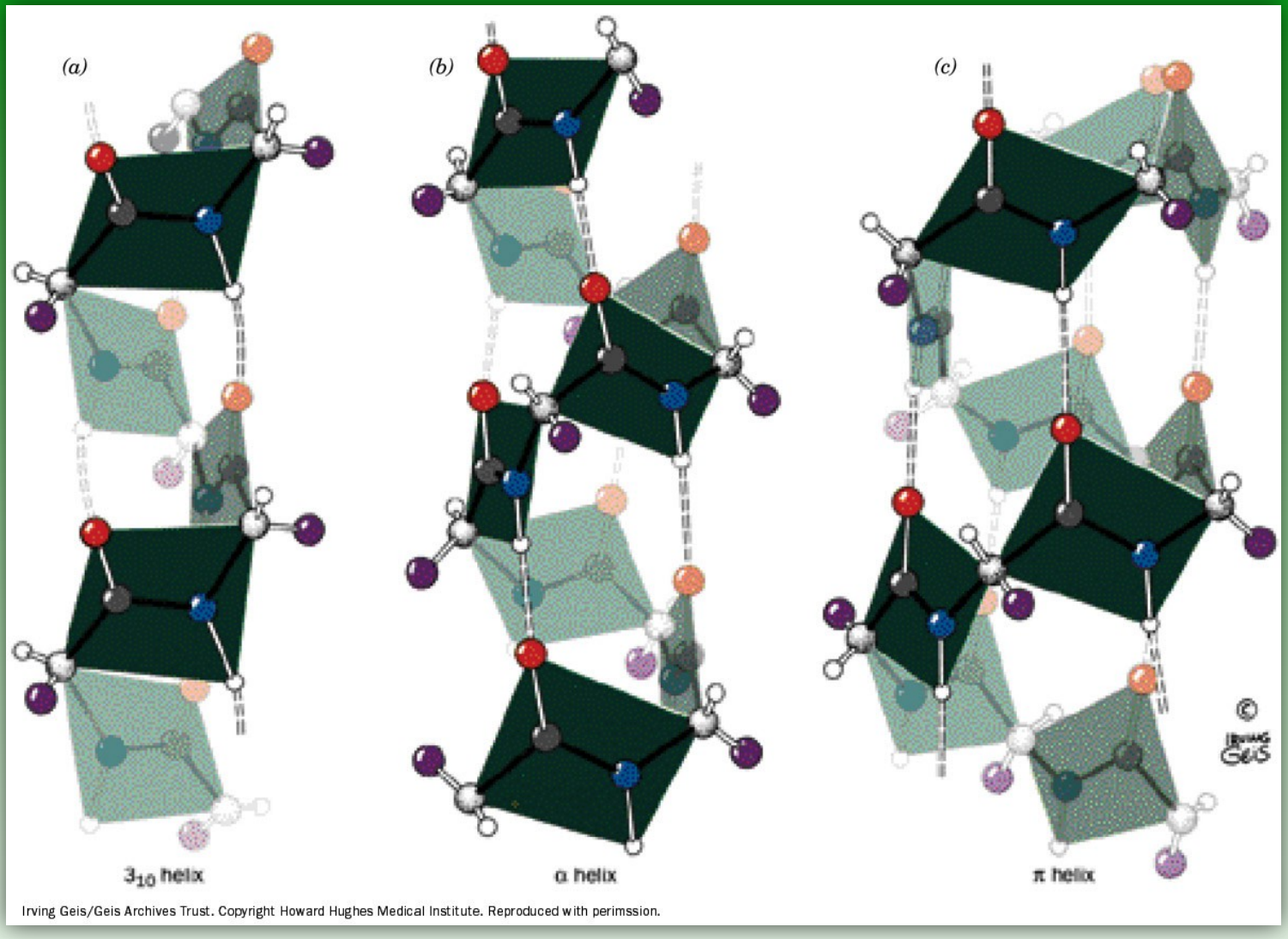
Different representations of the α-helix (3.6_{13}) secondary structure

Molecular parameters associated with the major protein secondary structures

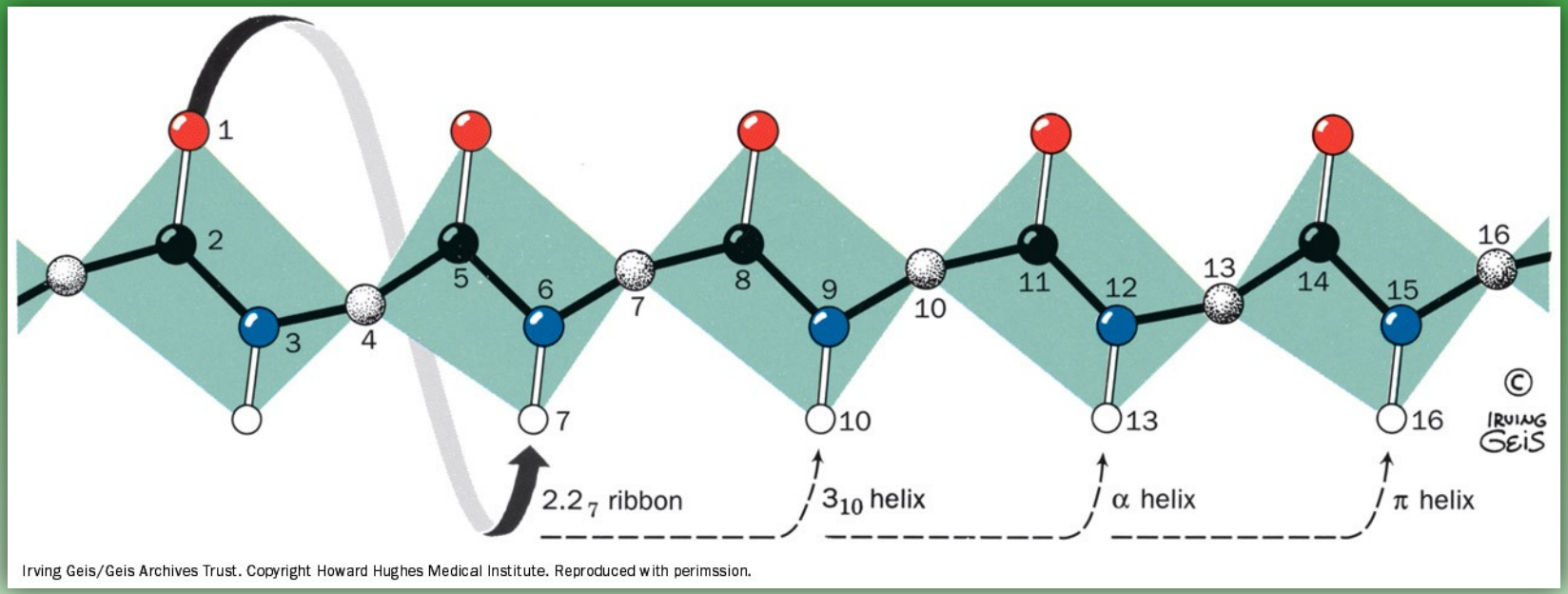
Structure Type	Residues/ Turn	Rise (nm)	Number of Atoms in H-Bonded Ring	ϕ (°)	ψ (°)
Antiparallel β sheet	2.0	0.34	—[a]	−139	+135
Parallel β sheet	2.0	0.32	—[a]	−119	+113
3_{10} helix	3.0	0.20	10	−49	−26
α helix (3.6_{13})	3.6	0.15	13	−57	−47
π helix (4.4_{16})[b]	4.4	0.12	16	−57	−70

[a]Bonding is between polypeptide chains.

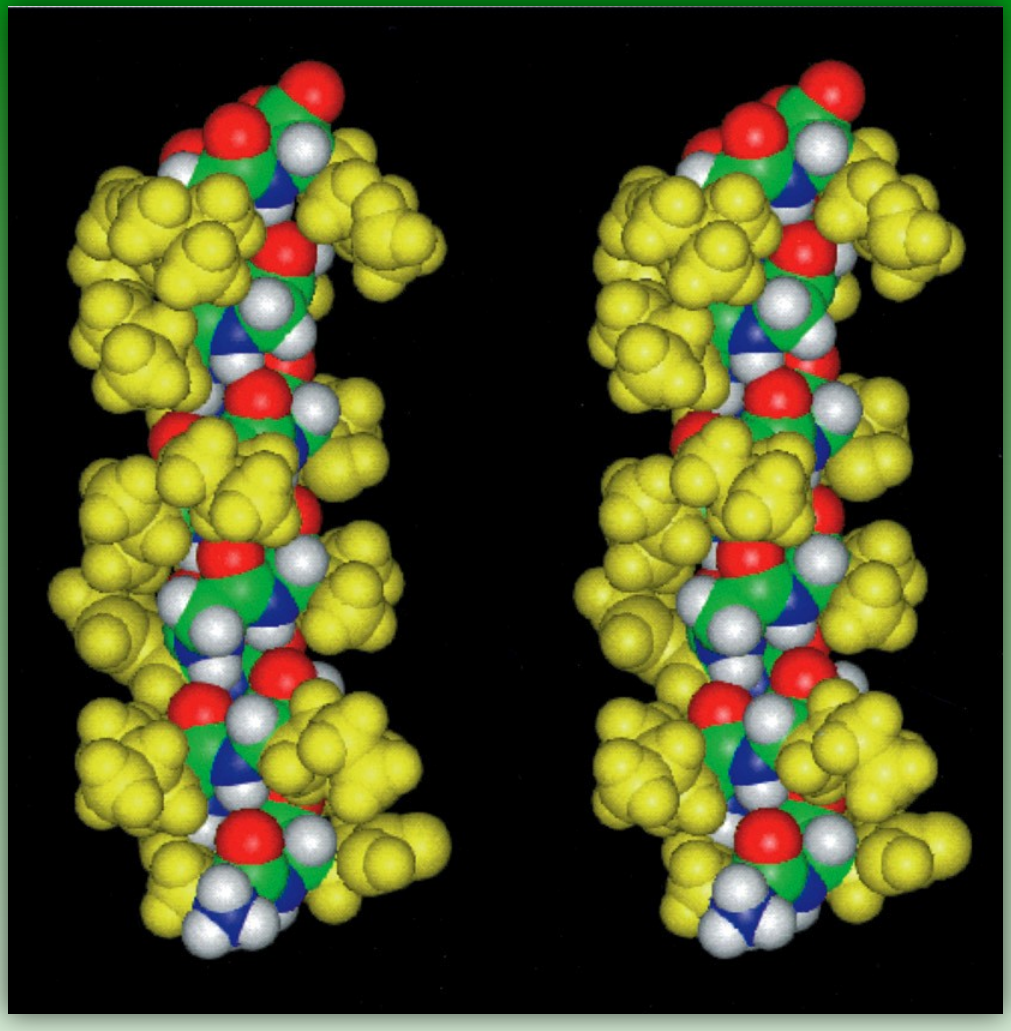
[b]Sterically permitted but not observed in protein.



Structural comparison of 3_{10}, 3.6_{13} (α) and 4.4_{16} (π) helices

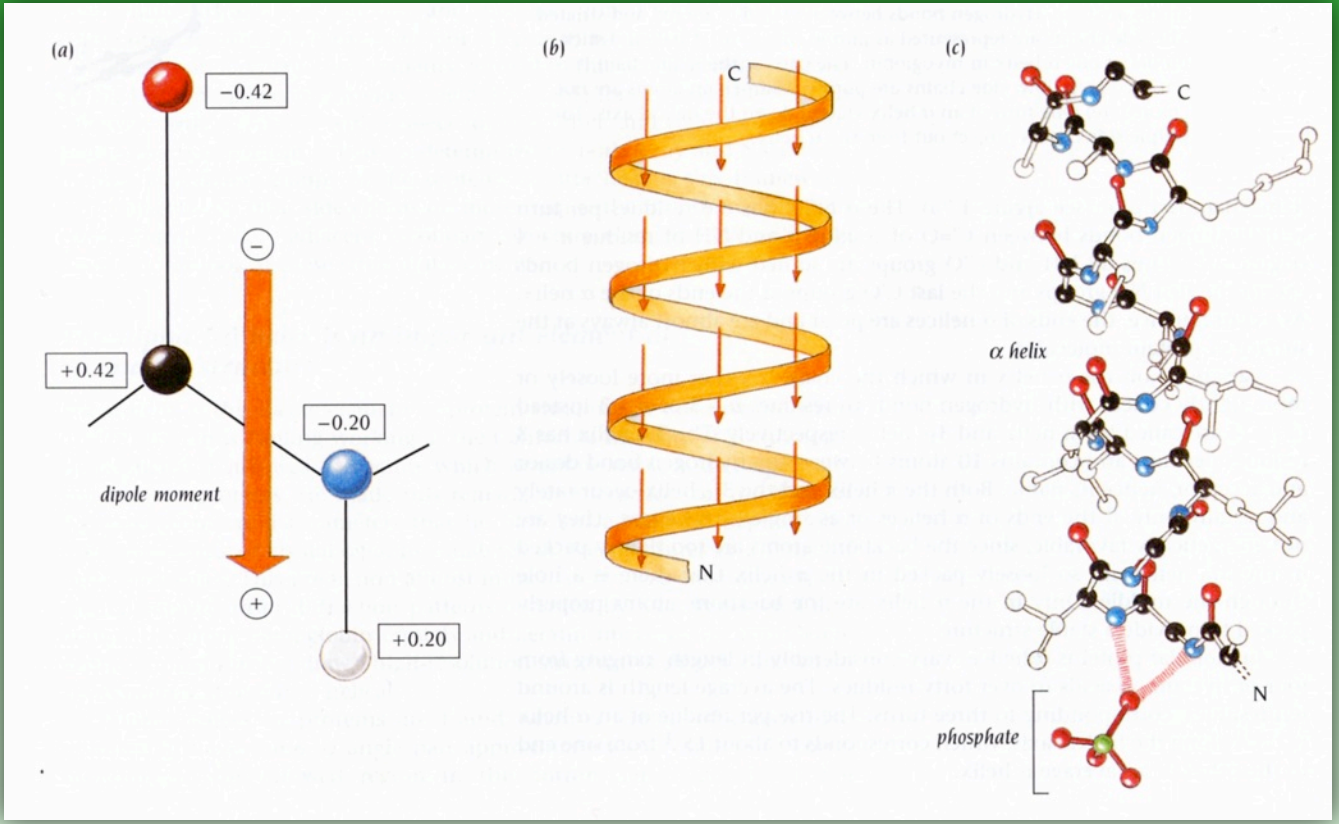


The hydrogen bonding patterns of several polypeptide helices



Stereo space-filling representation of an α-helical segment of sperm whale myoglobin (E-helix) determined by X-ray single crystal structure analysis: R-groups shown in yellow

The α-helix has a dipole moment



(a) The dipole of a peptide bond showing approximate fractional charges. **(b)** Individual peptide dipoles of the helix are aligned parallel to the helix axis, creating an overall dipole moment, positive at the amino end and negative at the carboxyl end. **(c)** Phosphate H-bonded to the NH end of the helix - binding is facilitated by the helix dipole.

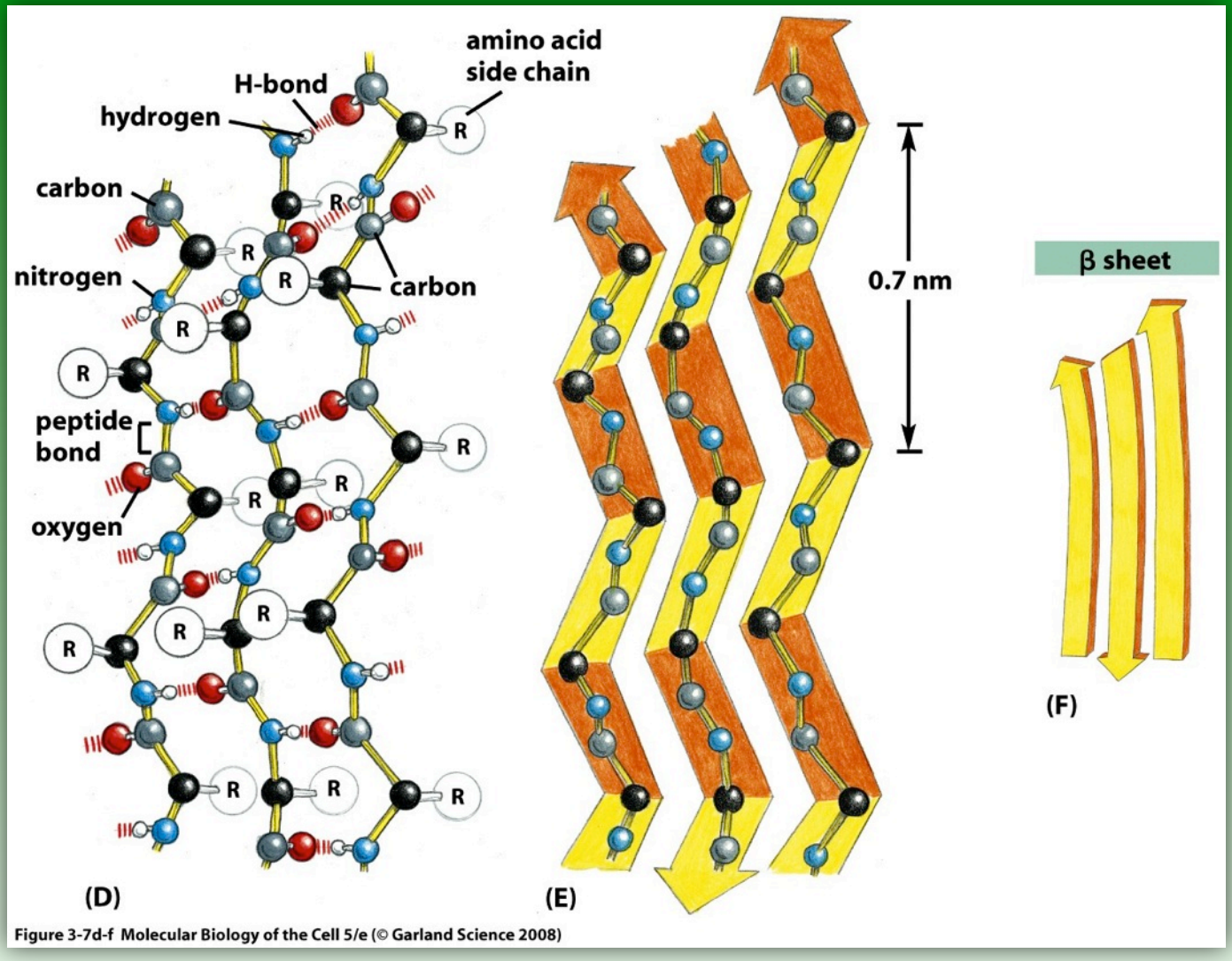
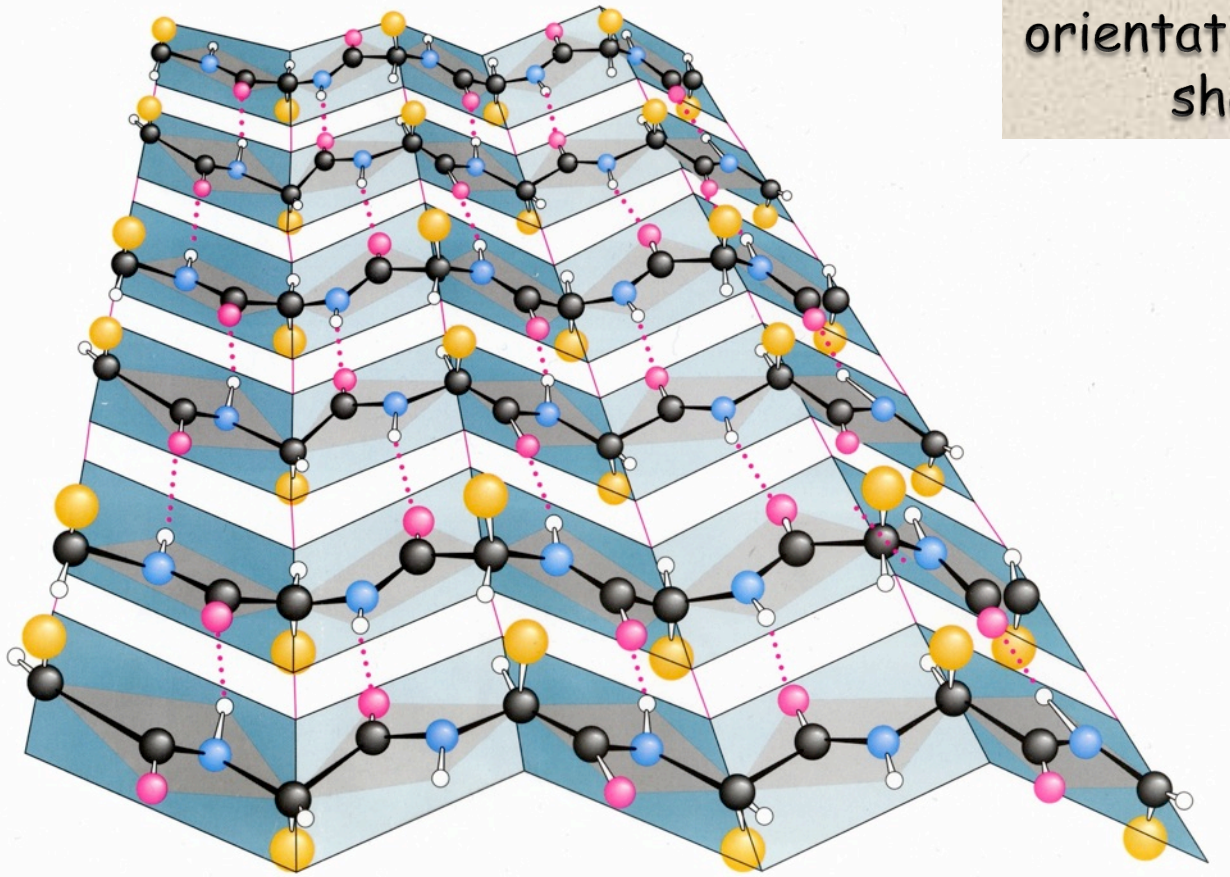


Figure 3-7d-f Molecular Biology of the Cell 5/e (© Garland Science 2008)

Different representations of the β (pleated) sheet secondary structure

Another view of the side-by-side arrangement of β-sheet secondary structure (antiparallel). Note the up/down orientation of the R-groups shown in yellow.



Overhead transparencies to accompany Garrett/Grisham: *Biochemistry*
Transparency 19 Figure 5.9

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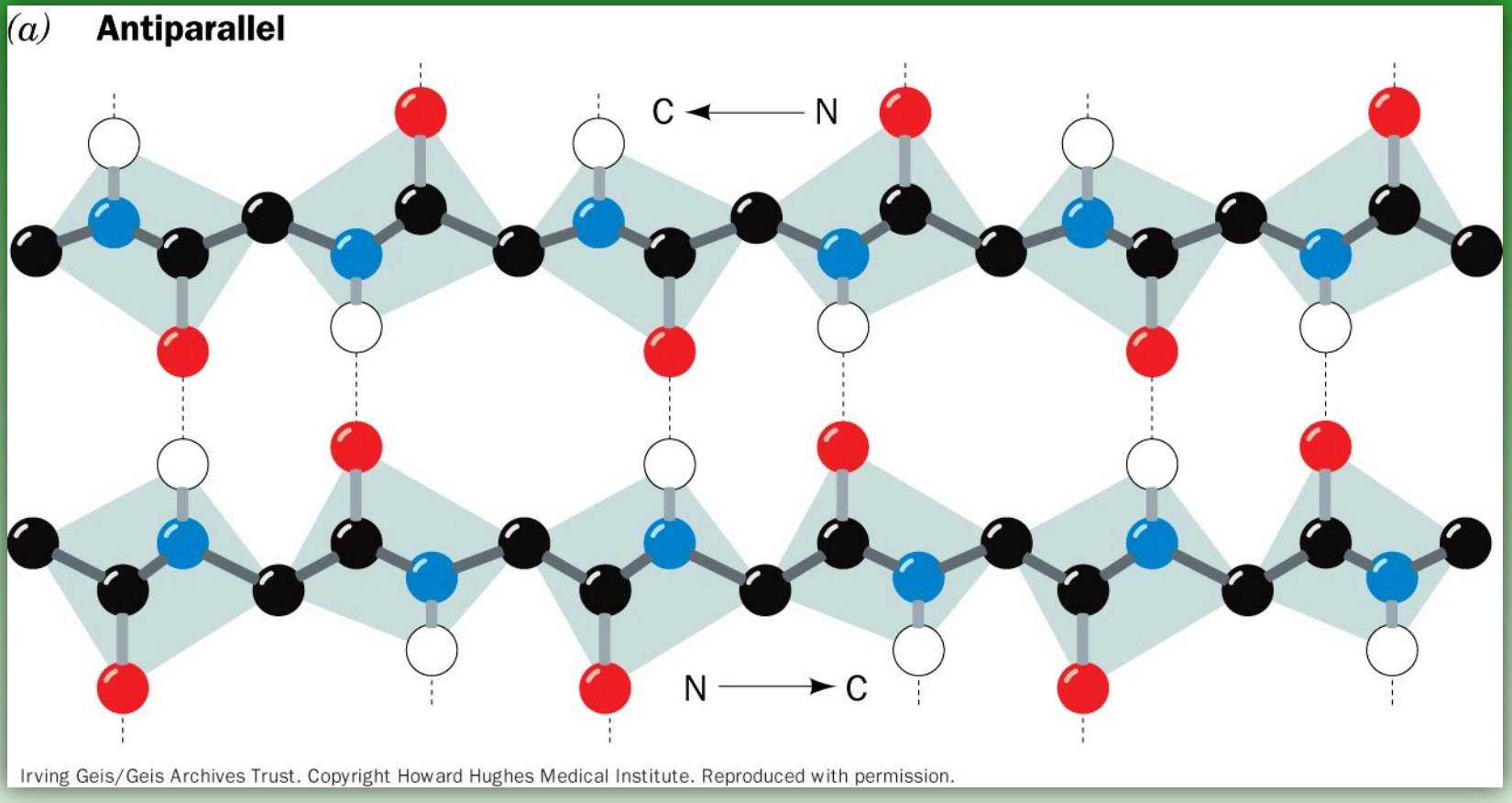
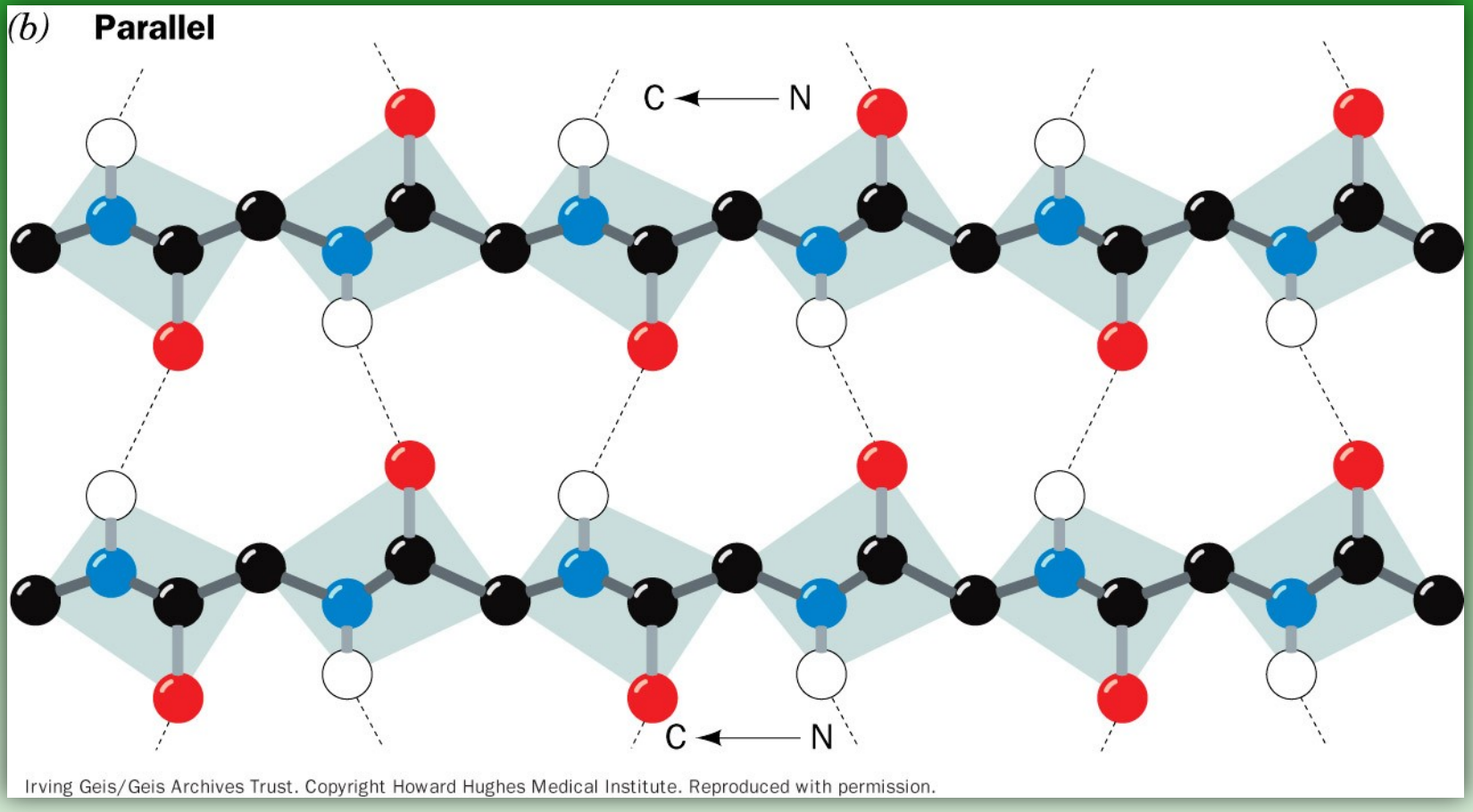
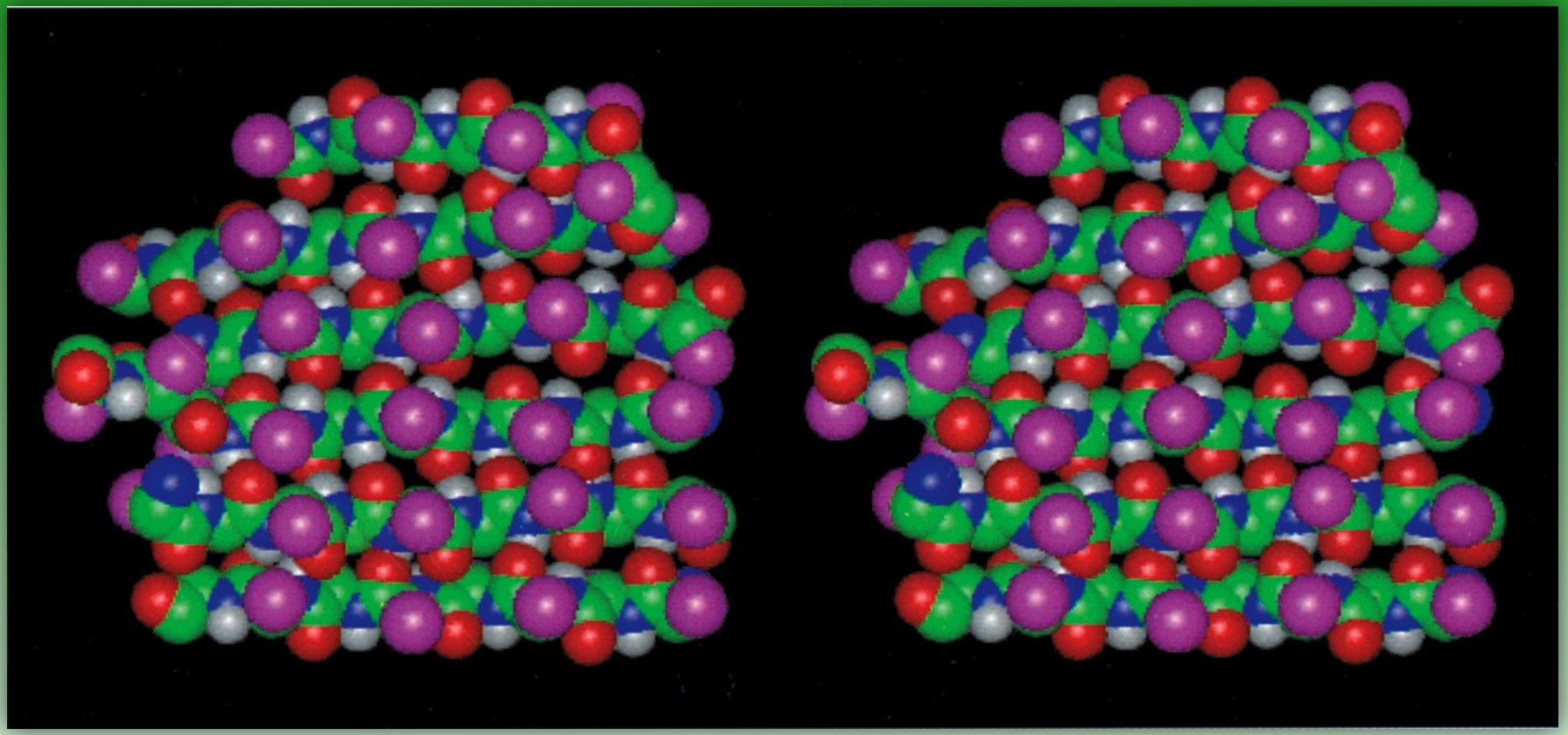


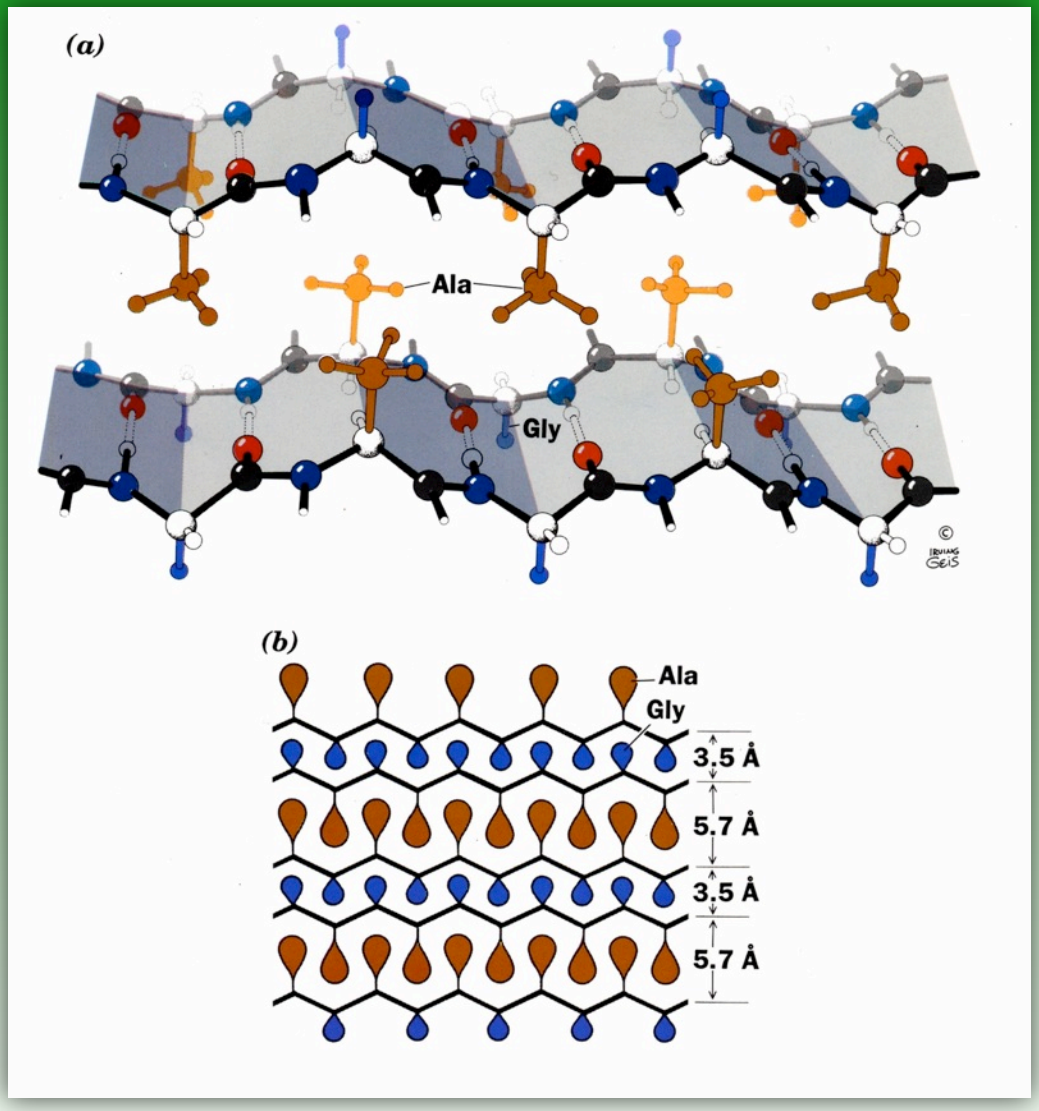
β pleated sheet: antiparallel orientation



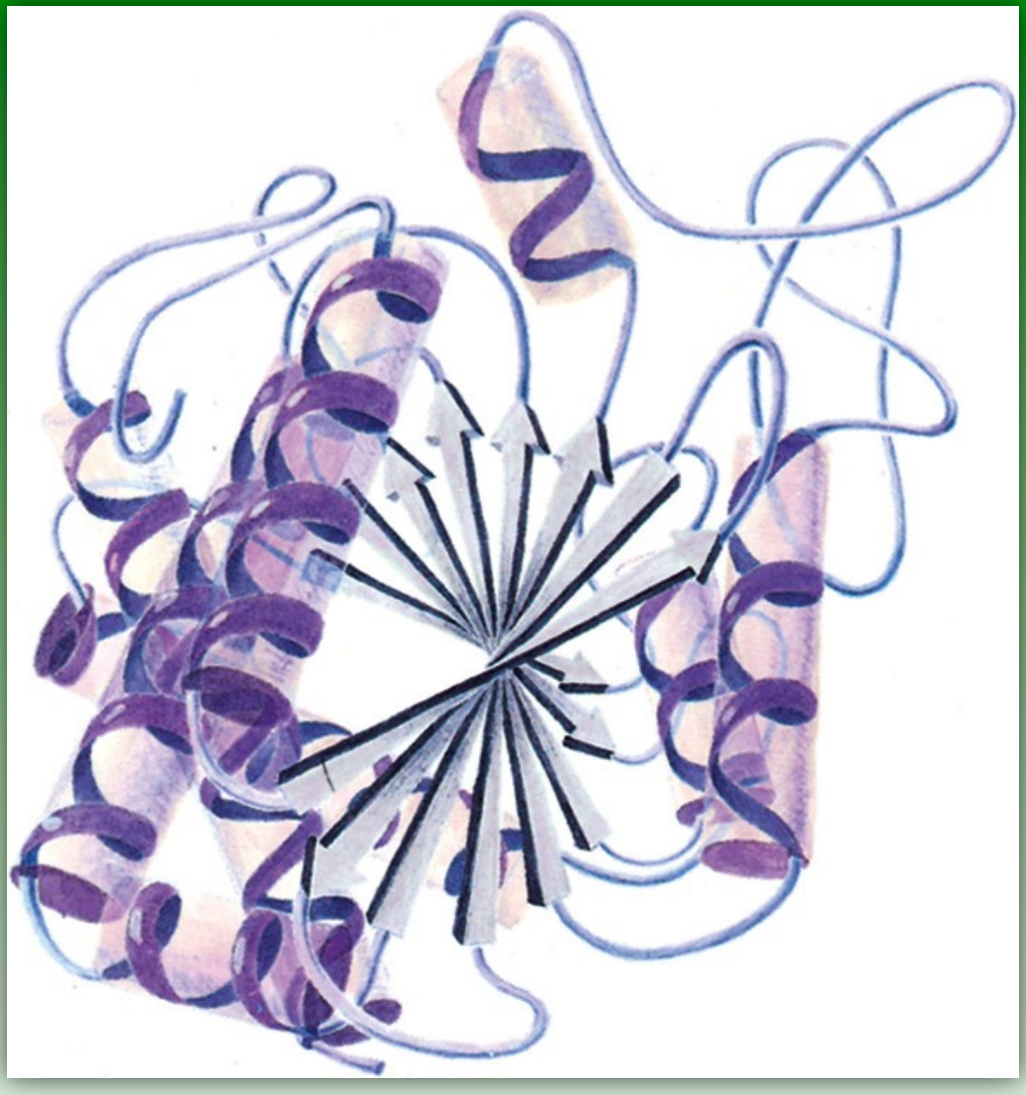
β pleated sheet: parallel orientation



Stereo space-filling representation of the 6-stranded antiparallel β pleated sheet in jack bean concanavalin A as determined by crystal X-ray analysis; β structure in a globular protein

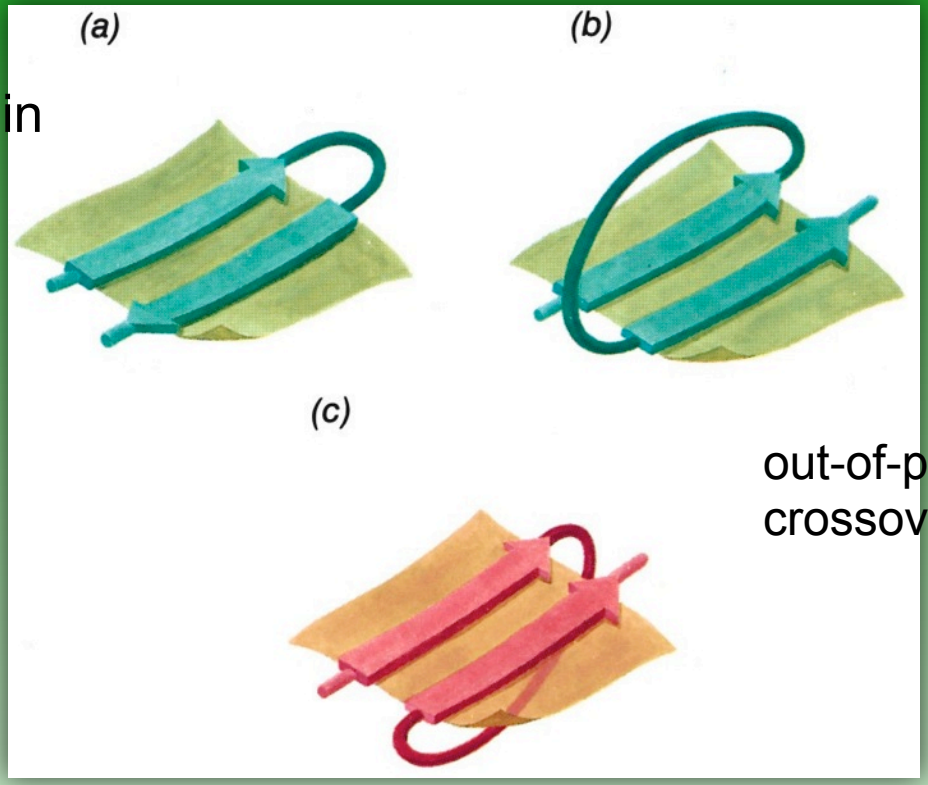


Stacking of side-by-side β-sheet structures showing "registry" of their R-groups. Spacial complementarity produces protein strength (illustrated for the silk protein)



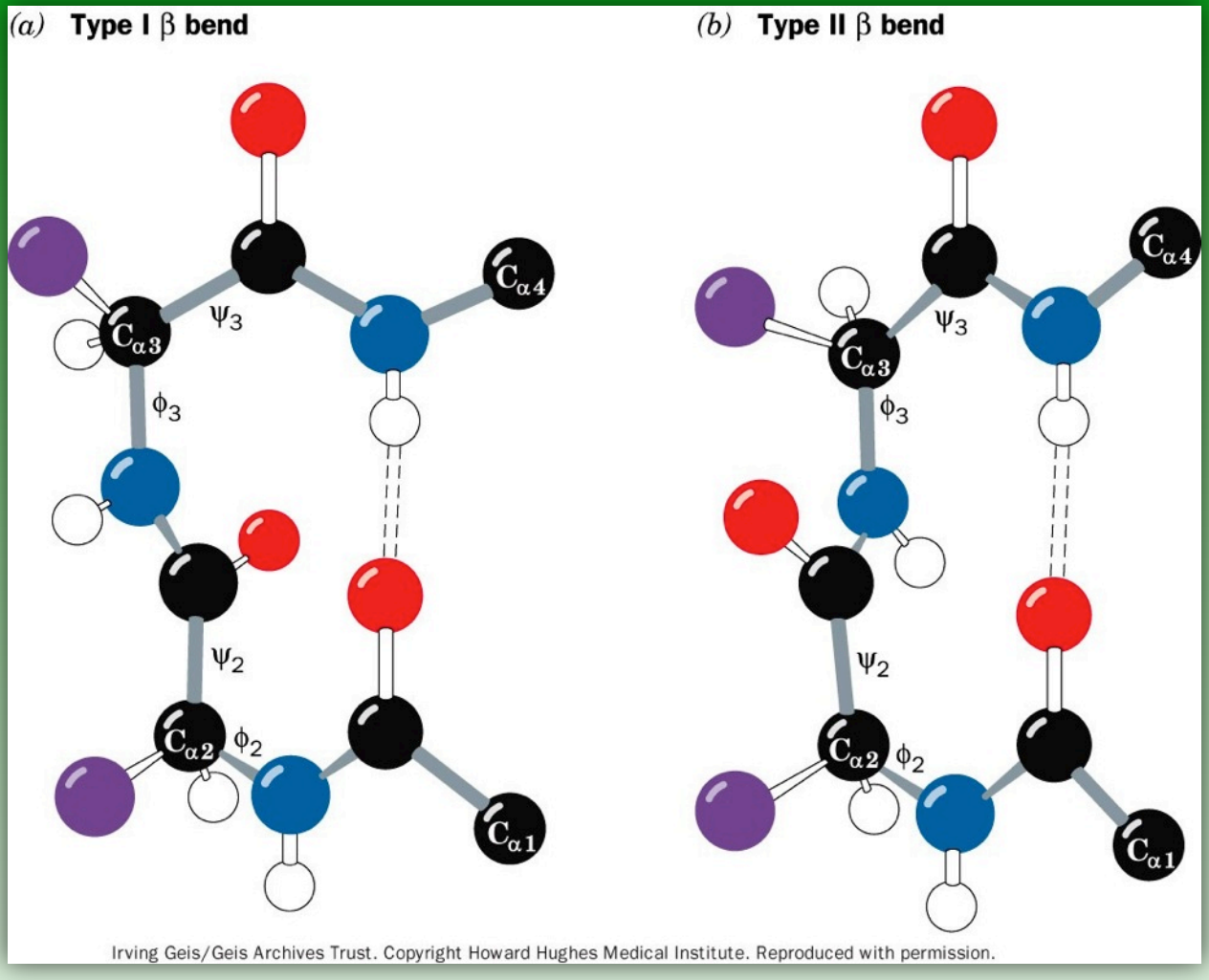
Polypeptide chain folding in a globular protein illustrating the right-handed twist of β sheets: bovine carboxypeptidase A

hairpin



out-of-plane crossovers

Connections between adjacent polypeptide segments in β-pleated sheets: hairpins are sufficient for antiparallel β-sheet formation; crossovers are minimally required for parallel β-sheet formation



Reverse turns in polypeptide chains: two (2) residues per turn for a β-bend, stabilized by a single H-bond

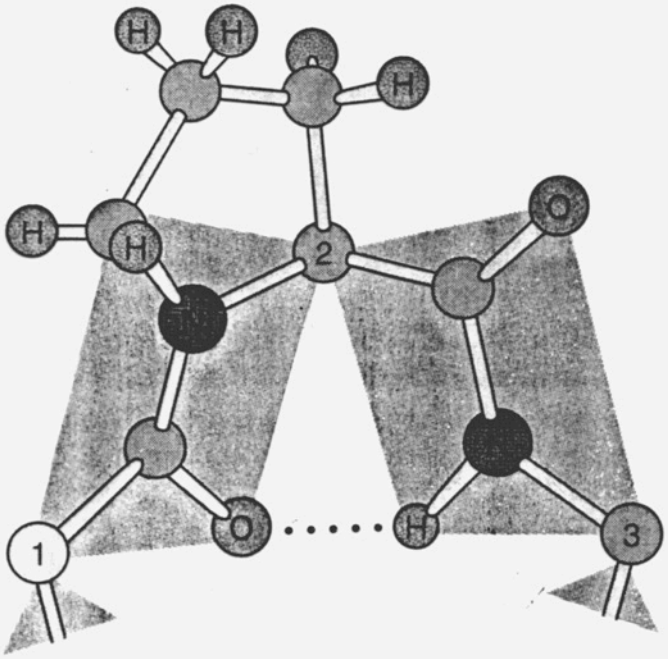
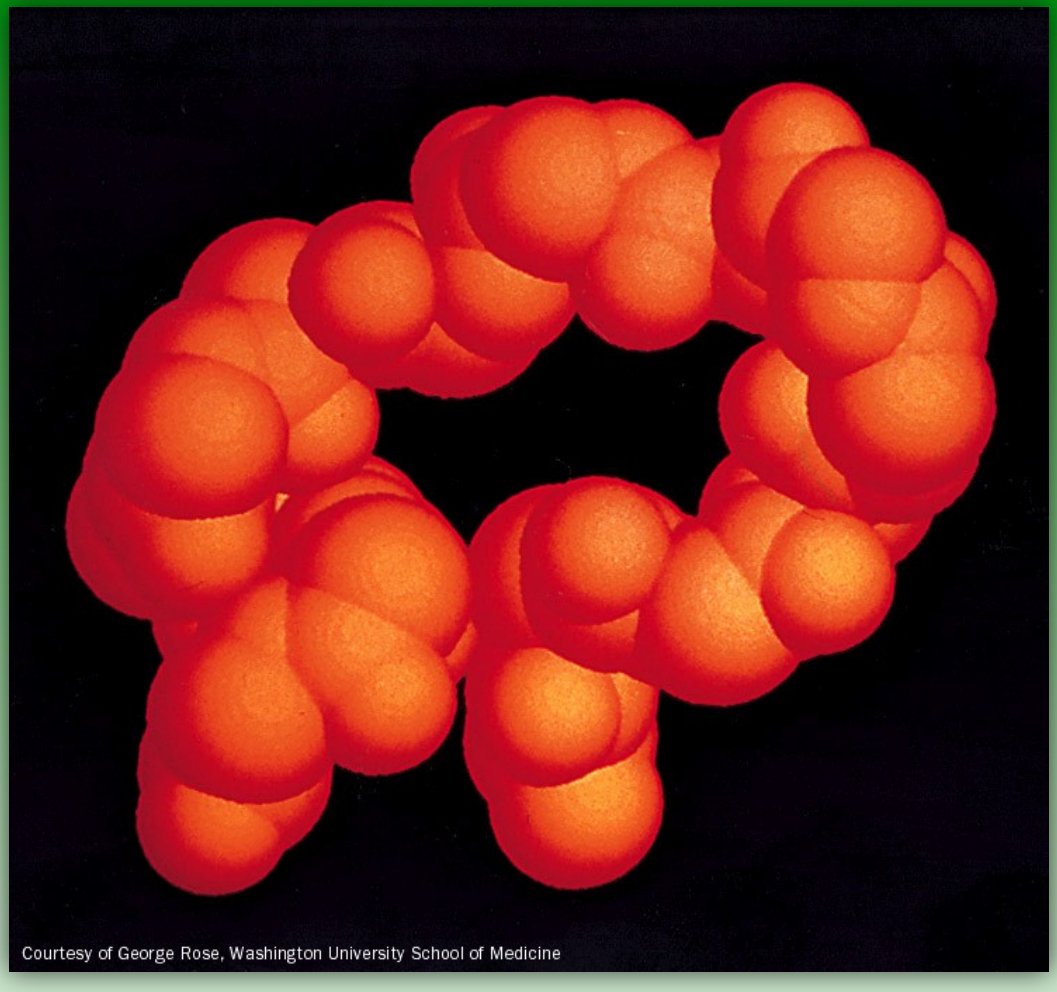


FIGURE **6.19**

A γ turn. Only one residue is out of the hydrogen bonding sequence. In this case it is a proline, which cannot make such a bond in any case.

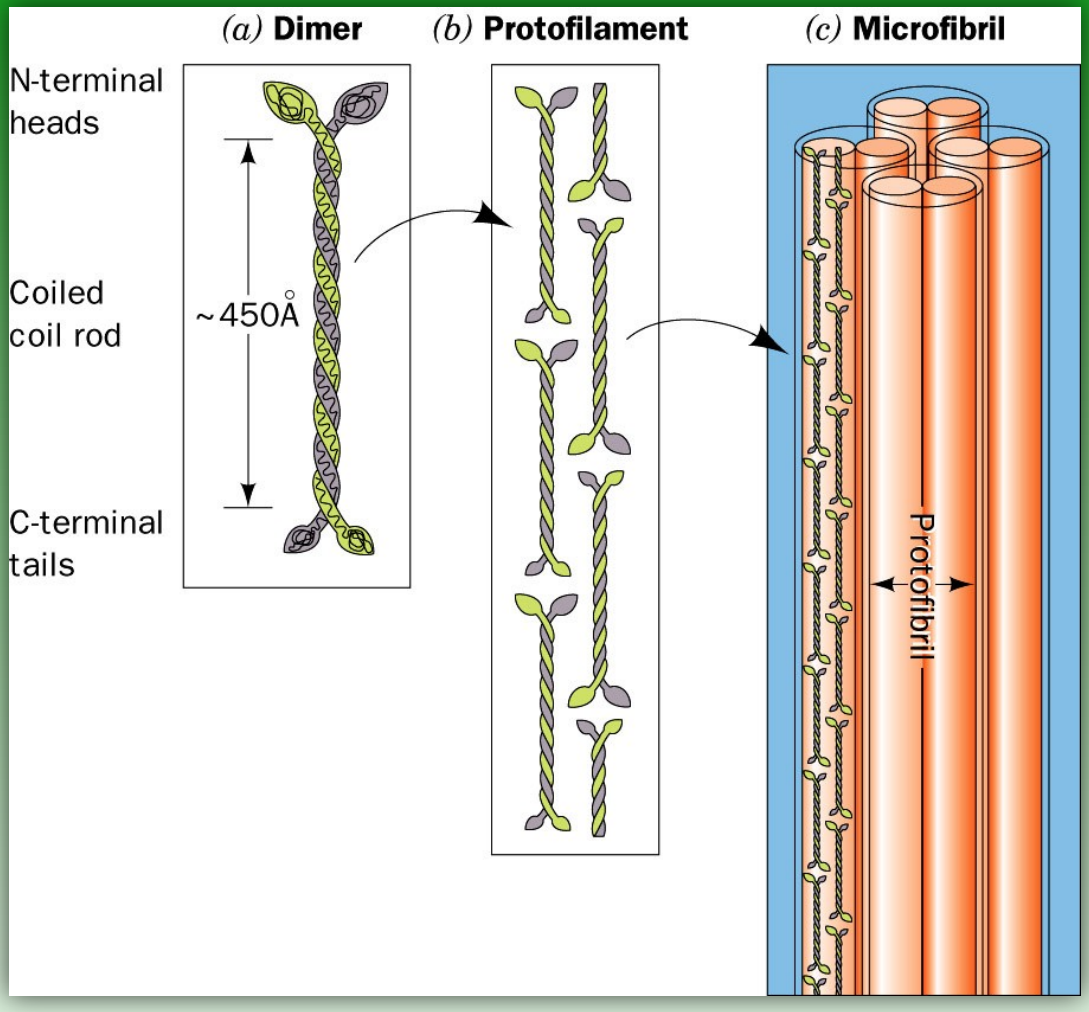
Gamma (γ) turns (tighter)



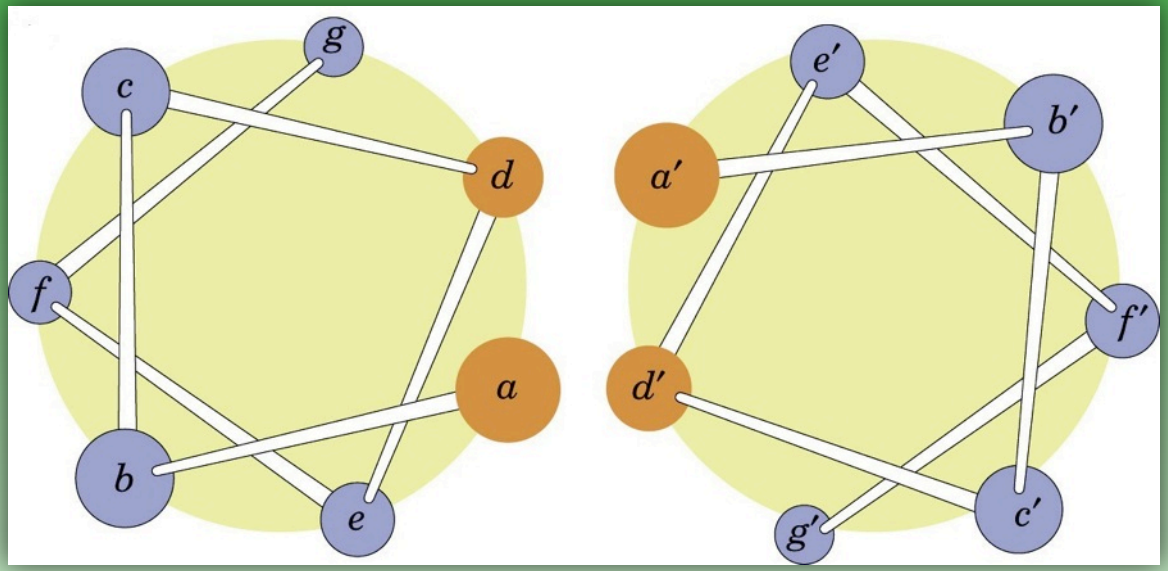
Another backbone bending motif: Space-filling representation of an Ω (omega) loop comprising residues 40 to 54 of cytochrome *c*

Fibrous proteins

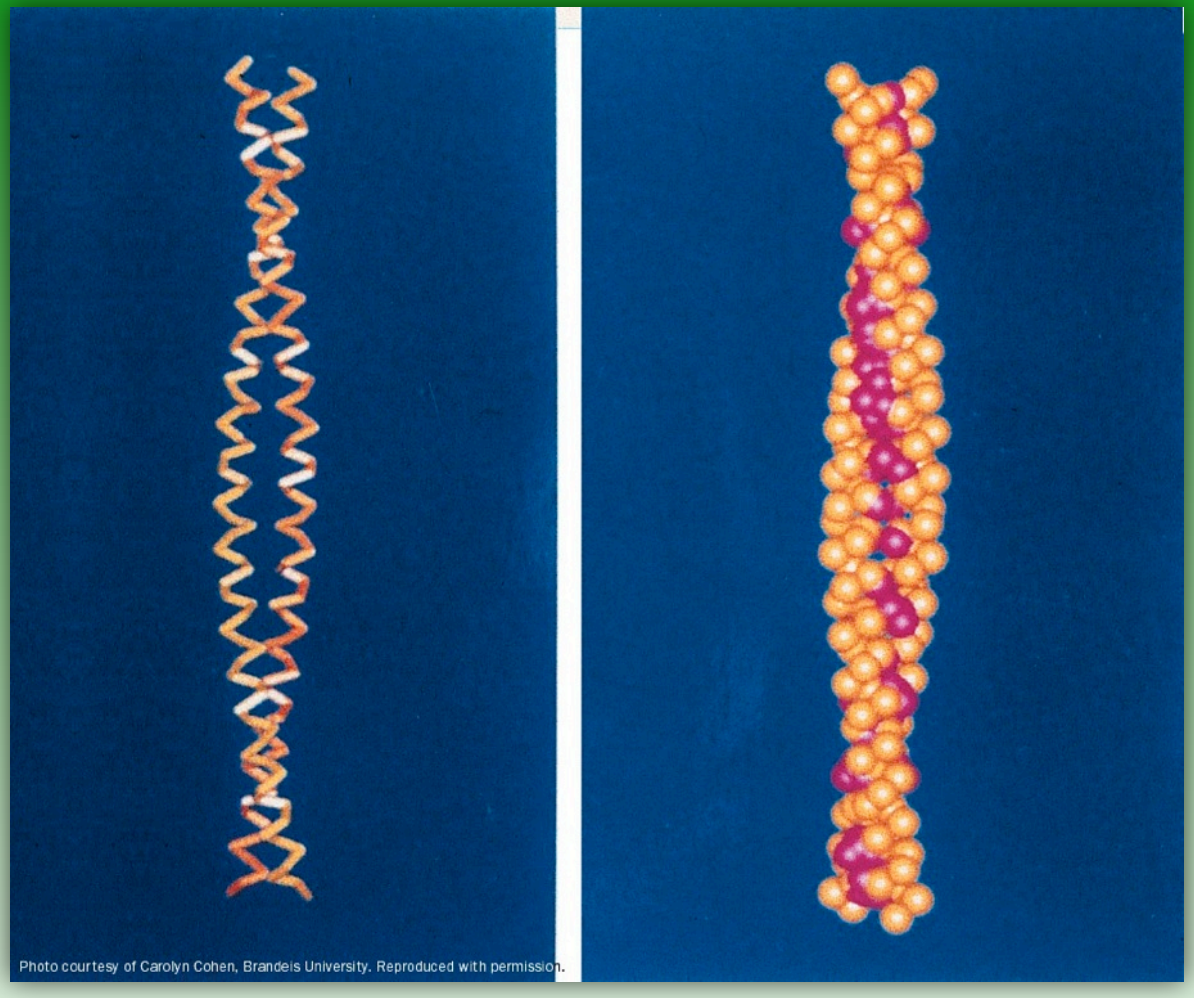
- α-keratins
- collagen



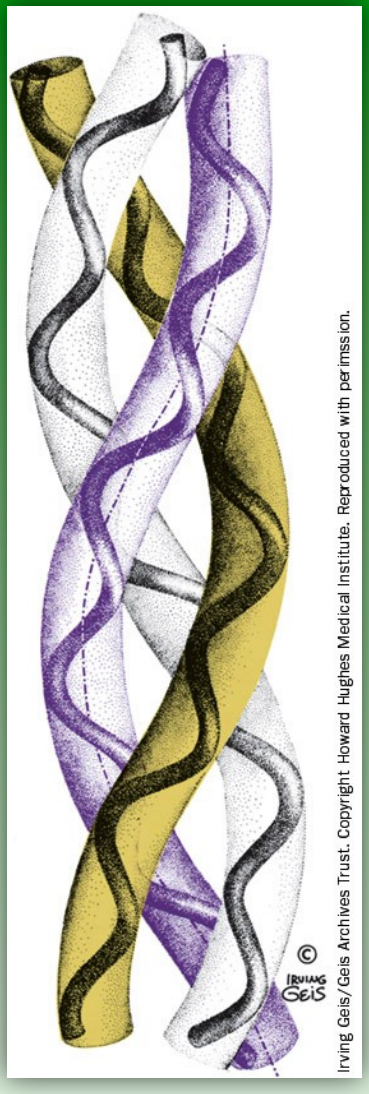
A fibrous protein: The structural organization of α-keratin
What stabilizes the formation of the coiled coil?



The two-stranded coiled coil: view down the coil axis showing the interactions between the non-polar edges of the α-helices. The α-helices have a repeating heptameric sequence *a-b-c-d-e-f-g* in which residues *a* and *d* are predominantly non-polar.



The two-stranded coiled coil: side view in which the polypeptide back bone is represented by skeletal (*left*) and space-filling (*right*) forms.



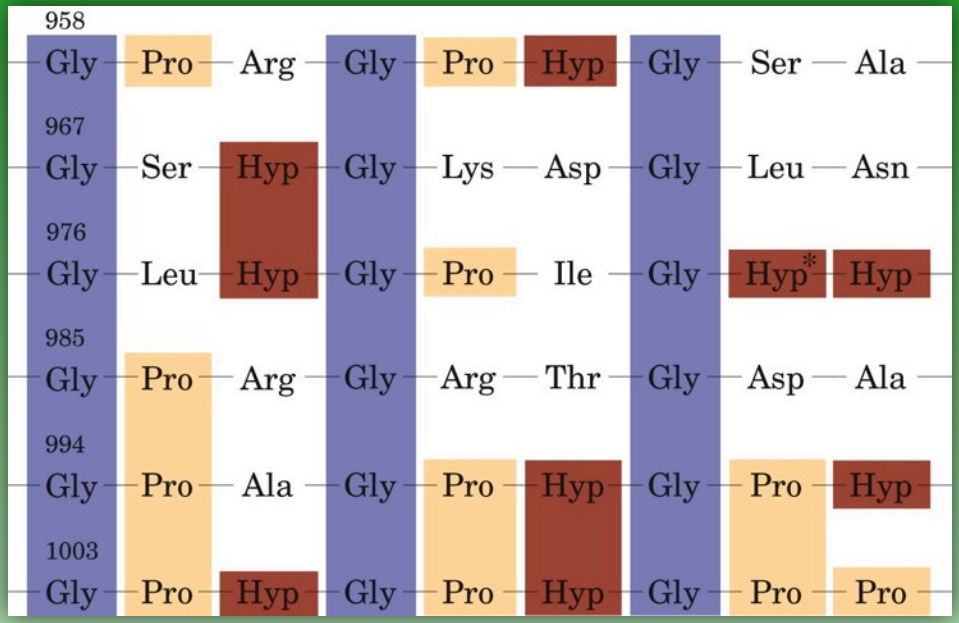
The right-handed triple helix of collagen

Another fibrous protein

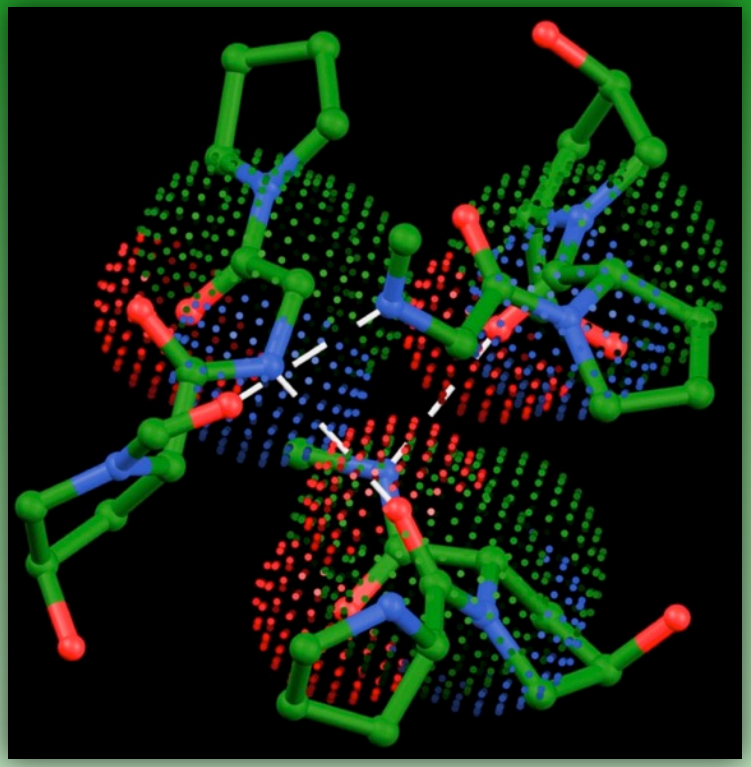
Collagen is an extracellular protein organized into insoluble fibers having great strength; a major component of connective tissue.

Its amino acid composition is distinctive: ~33% Gly and 15-30% Pro and 4-hydroxyproline (Hyp). 3-Hydroxyproline and 5-hydroxylysine (Hyl) are also present.

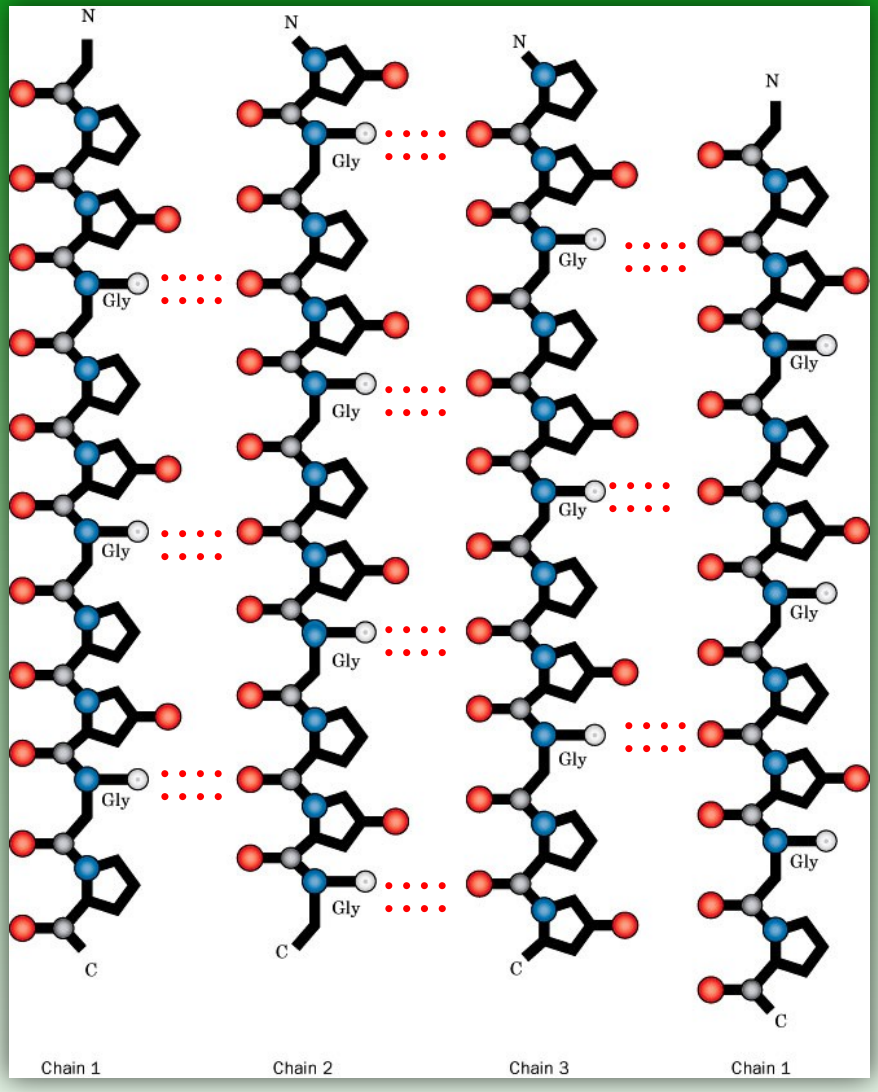
Collagen has a triple helical structure. The individual polypeptide chains (polyproline-like helices - left-handed) are parallel and wound around each other with a right-handed rope-like twist to form the triple helical structure.



The amino acid sequence at the C-terminal end of the triple helical region of the bovine α1(I) collagen chain. Note repeating triplets Gly-X-Y where X is often Pro and Y is Hyp.



View along helix axis showing inter-chain H-bonding that stabilizes the triple helix structure (Gly N atoms and Pro O atoms in adjacent chains).

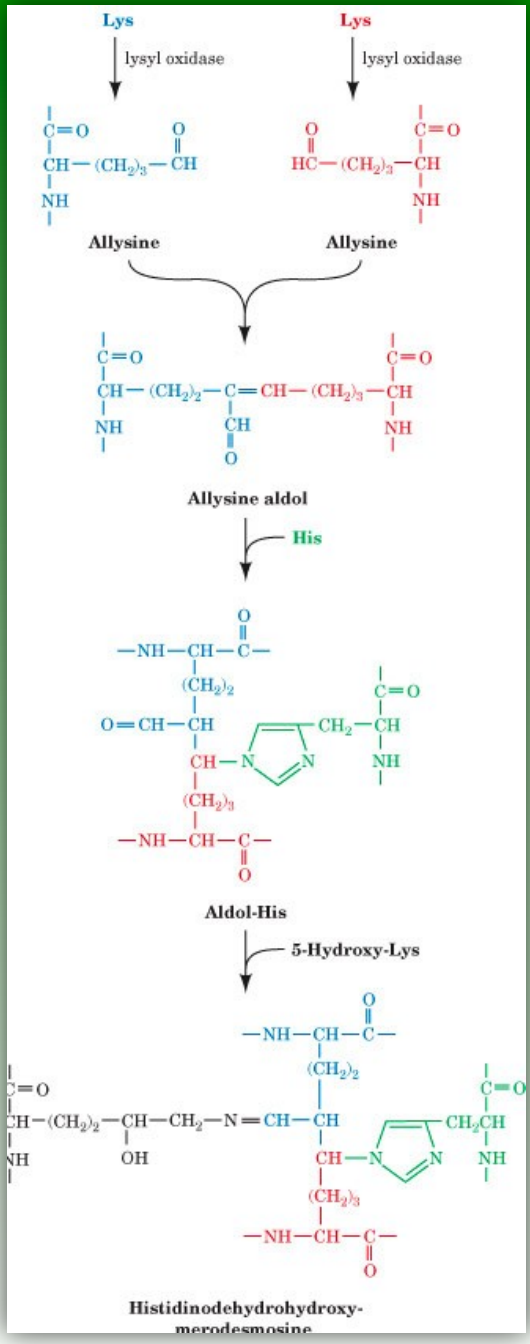


A schematic diagram showing inter-chain H-bonding in the Gly-containing regions of the triple helix of collagen.

Collagen is also glycosylated at Hyl residues with a Glc-Gal disaccharide (a post-translational modification / *O*-glycosylation).

Collagen (tropocollagen units)
is organized into fibrils;
the fibrils are covalently crosslinked.

A biosynthetic pathway for cross-linking Lys, Hyl, and His side-chains in collagen; crosslinking is enzyme-catalyzed.



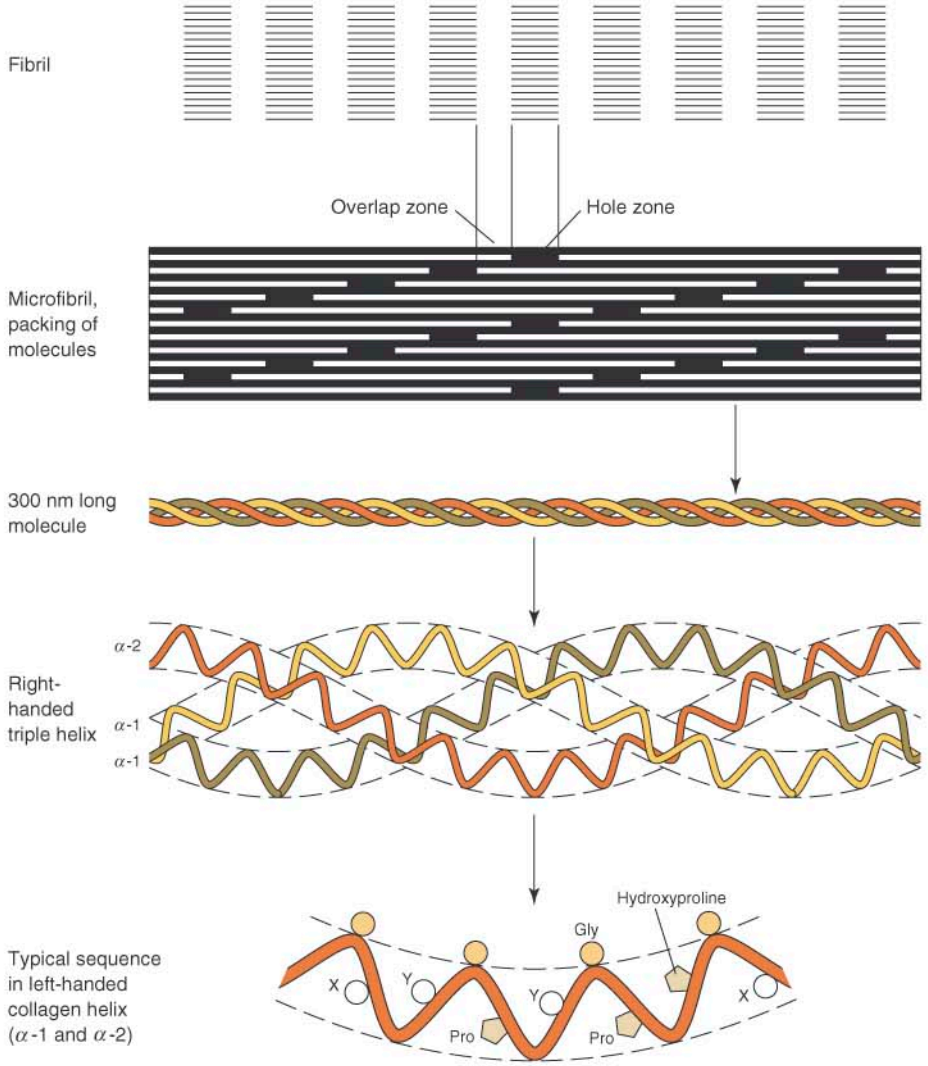
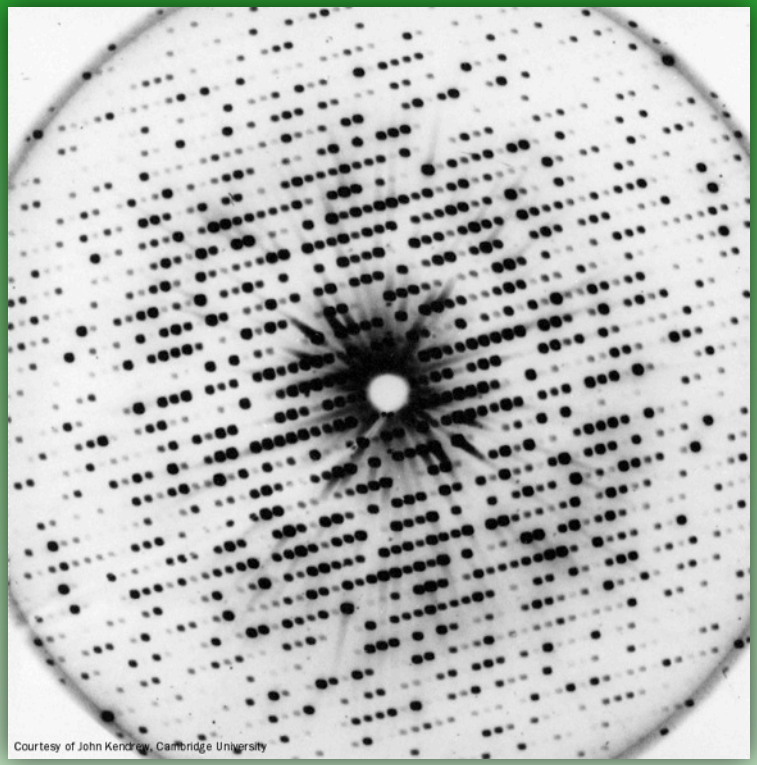
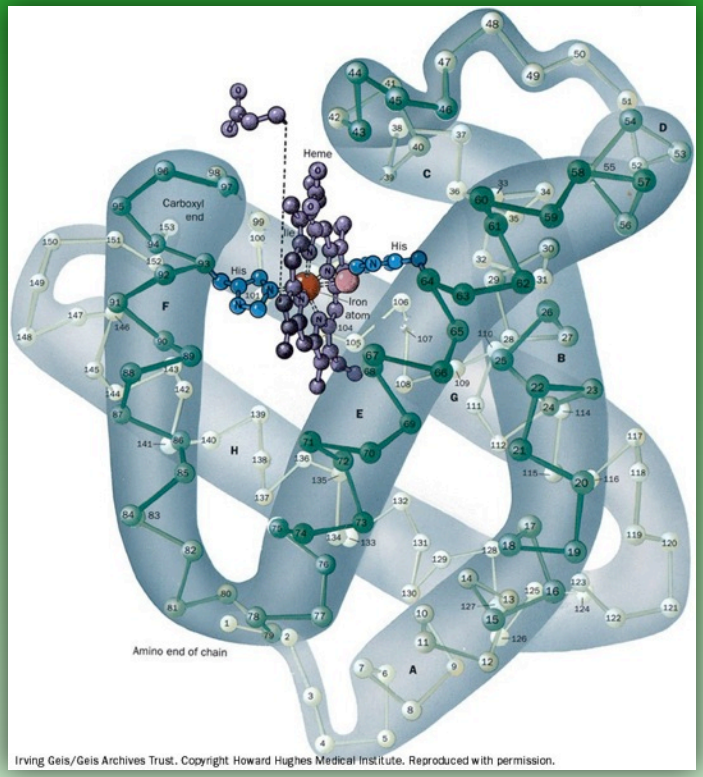


Figure 6.21. Collagen structure, illustrating (bottom to top) the regularity of primary sequence in a left-handed polyproline type II helix; the right-handed triple helix; the 300-nm molecule; and the organization of molecules in a typical fibril, within which collagen molecules are cross-linked.

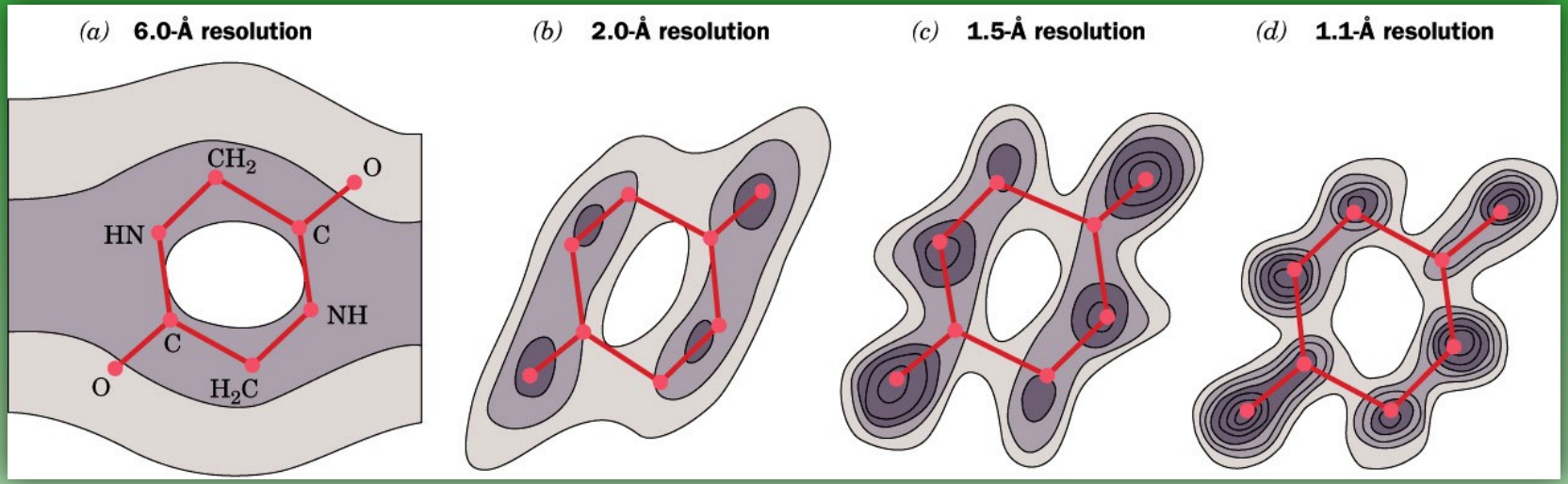
Determination of protein 3D structure (globular): Single crystal X-ray crystallography and NMR



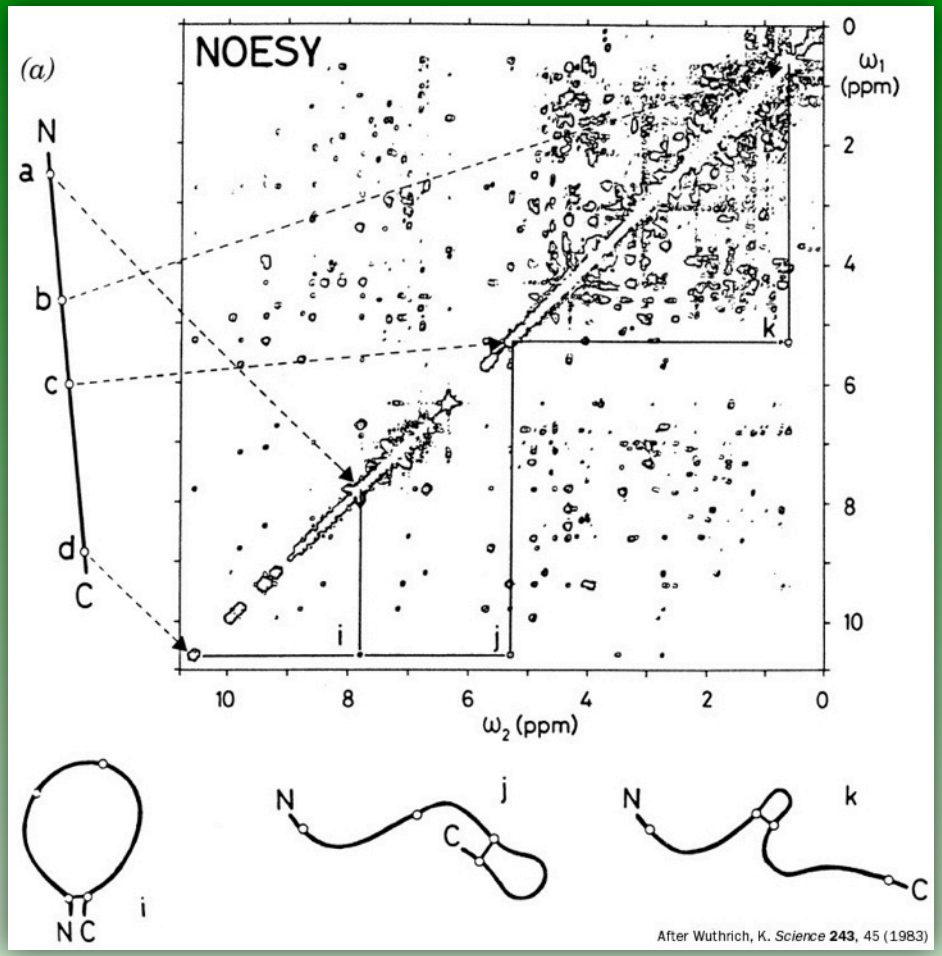
X-Ray diffraction photograph of a single crystal of sperm whale myoglobin



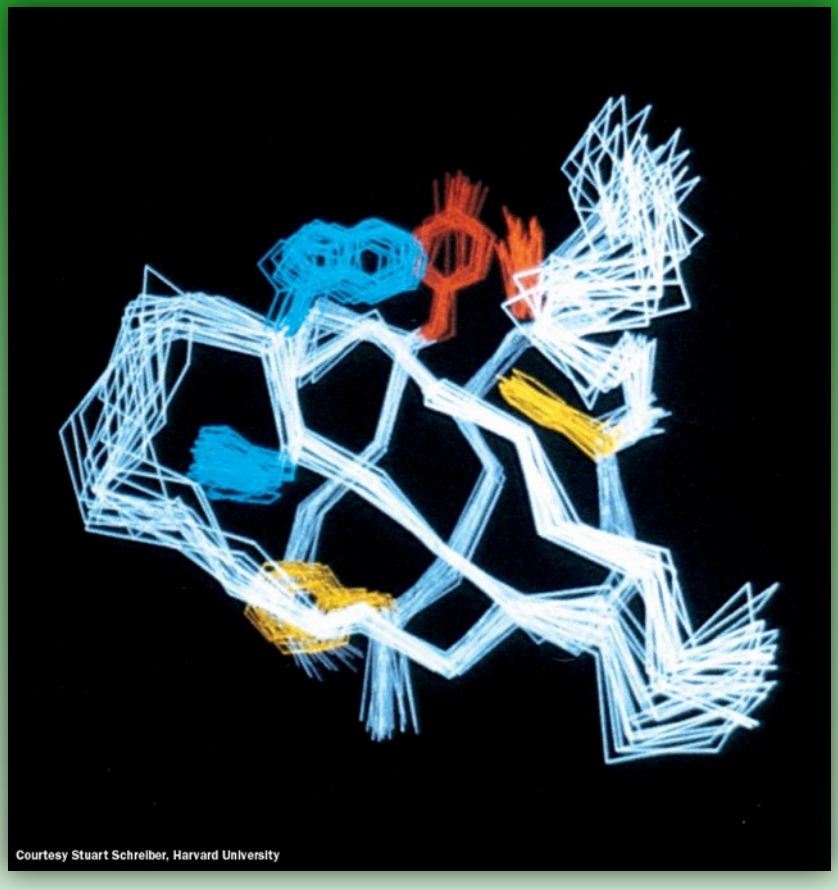
98-residue globular protein



Sections through the electron density map of a small organic molecule, diketopiperazine, calculated at the indicated resolution. As atomic resolution decreases, the ability to measure accurate bond lengths, angles and torsions also decreases (implications for structure/ mechanism work, determination of substrate structure/conformation in a co-crystal).



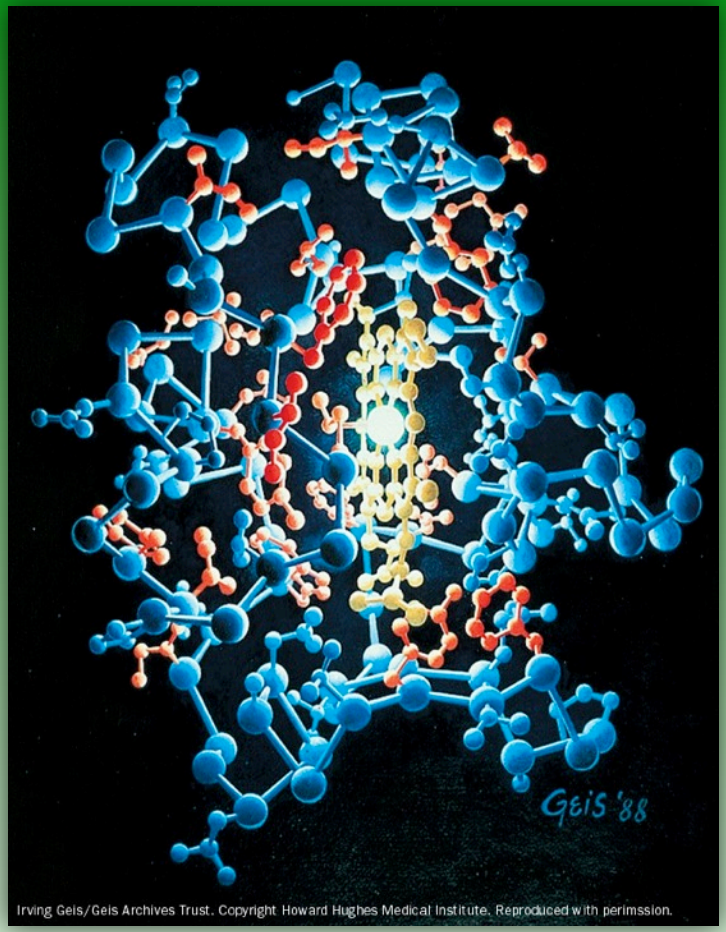
2D ^{1}H NMR spectra of proteins: a 2D NOESY spectrum of a protein presented as a contour plot with two frequency axes ω_1 and ω_2.
NOESY provides information about the relative internuclear distances between specific proton pairs in a molecule



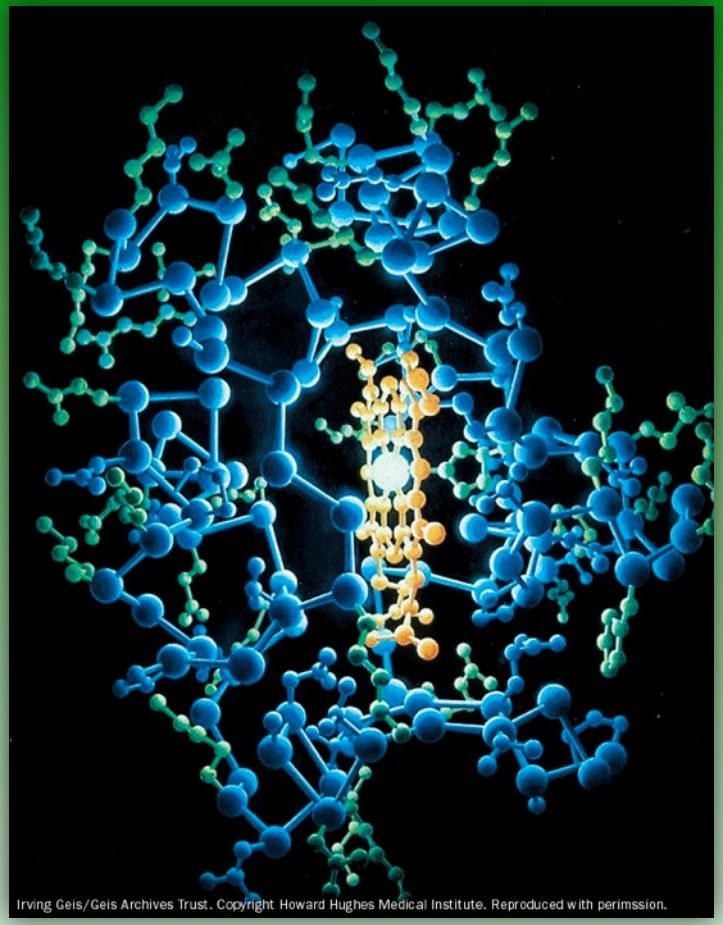
2D NMR structure of a 64-residue polypeptide comprising the Src protein SH3 domain.

NMR data can be collected in 3D and 4D dimensions using isotopically labeled protein. These multidimensional NMR datasets allow signal assignments in, and 3D structure determinations of, larger proteins.

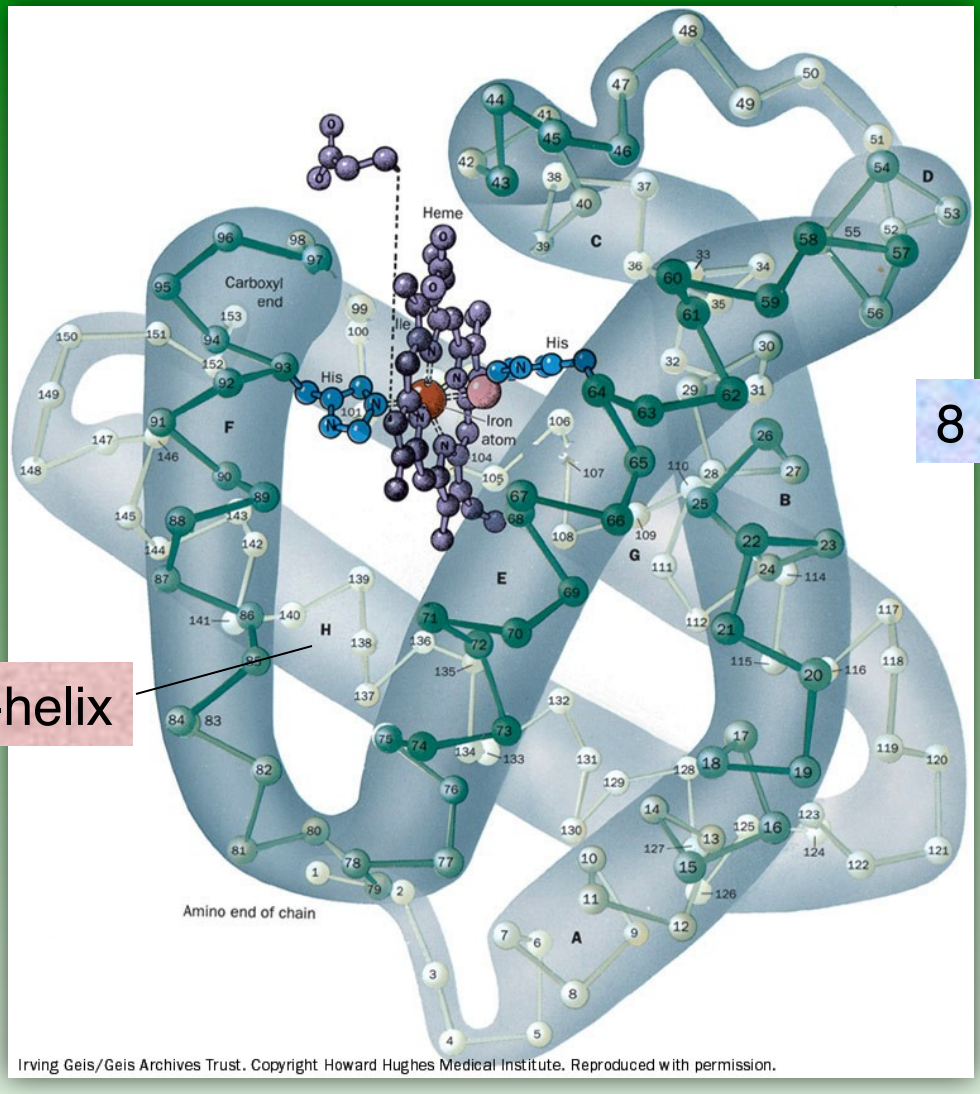
Some generalities about globular protein structure



X-ray structure of horse heart cytochrome *c*: hydrophobic residues (red) are largely buried



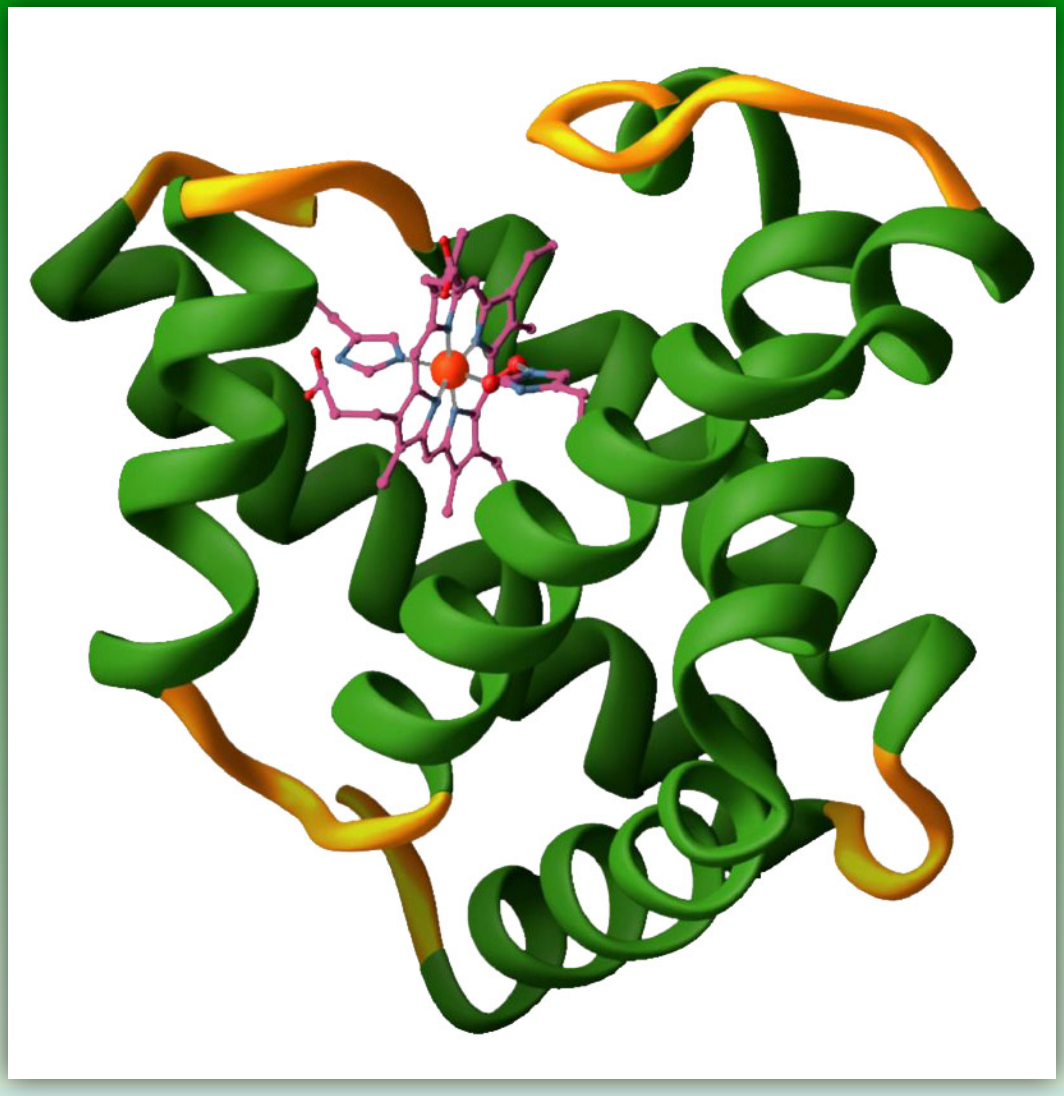
X-ray structure of horse heart cytochrome *c*: hydrophilic residues (green) are largely solvent exposed (on surface)



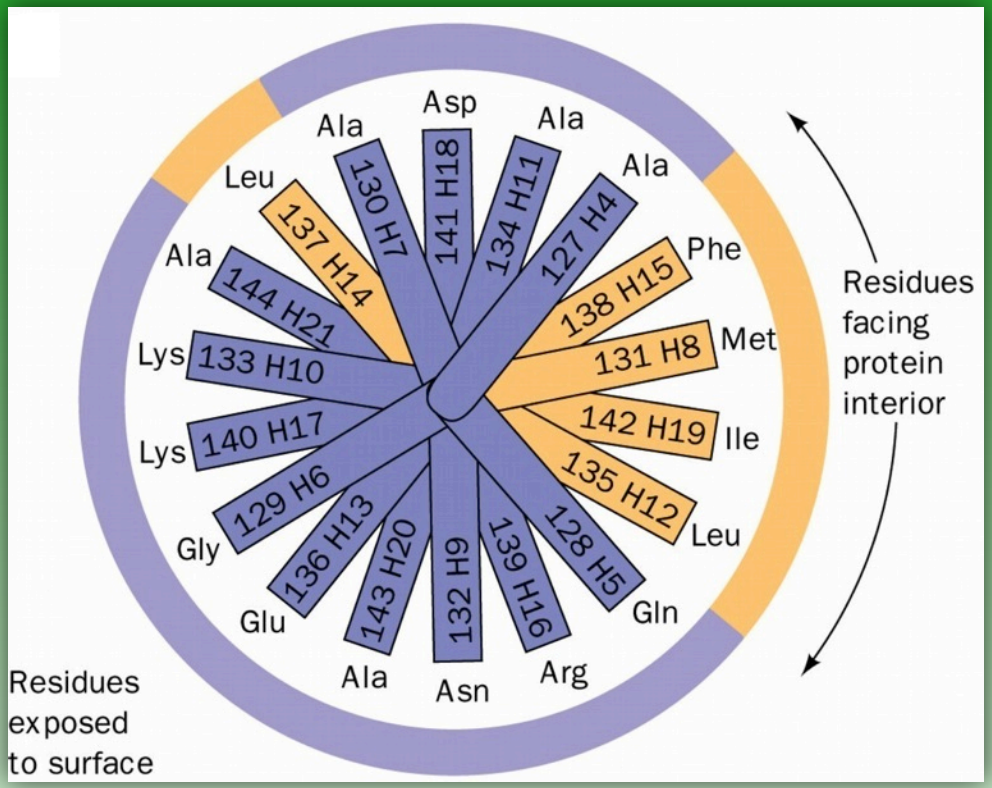
8 helices: A-H

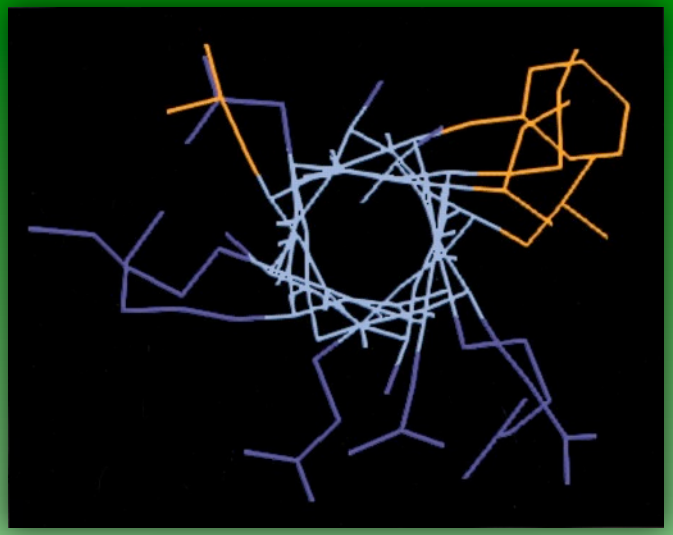
H-helix

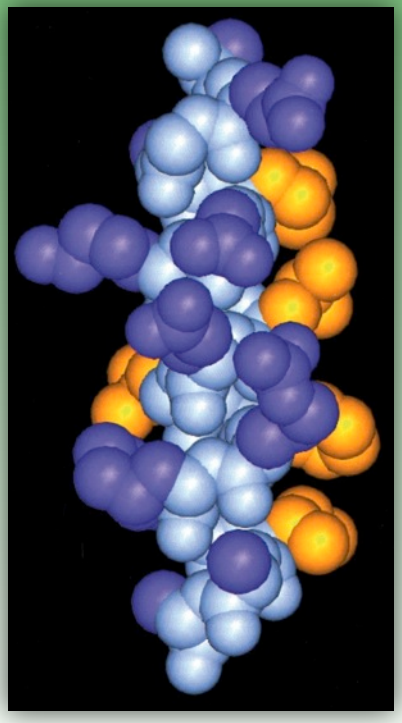
X-ray structure of sperm whale myoglobin identifying the H-helix



X-ray structure of sperm whale myoglobin: a computer-generated ribbon drawing

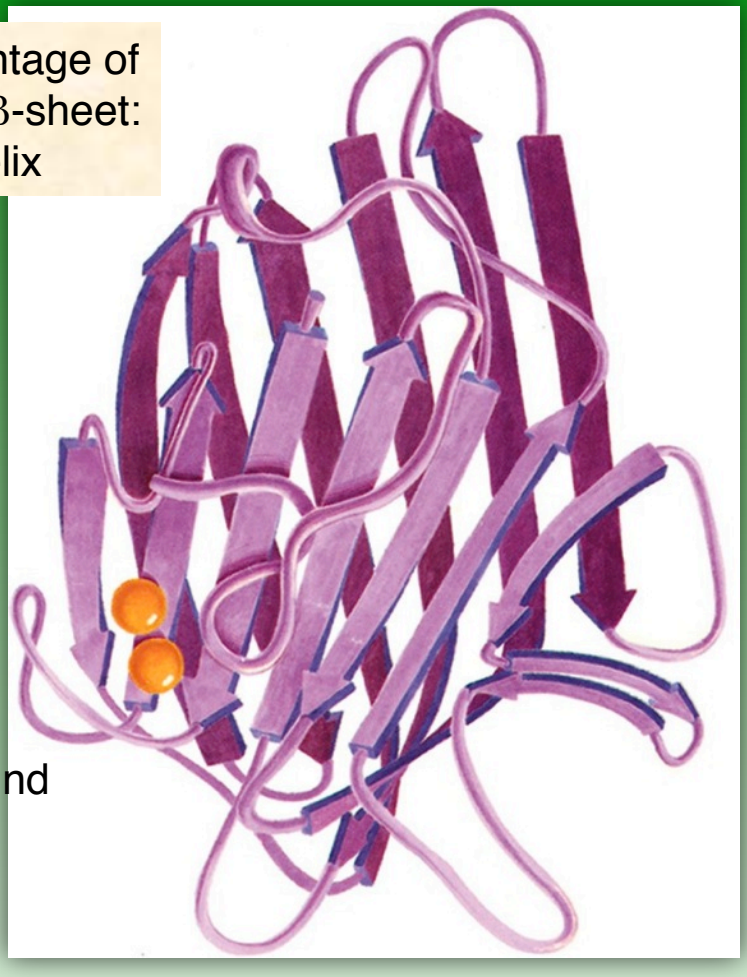






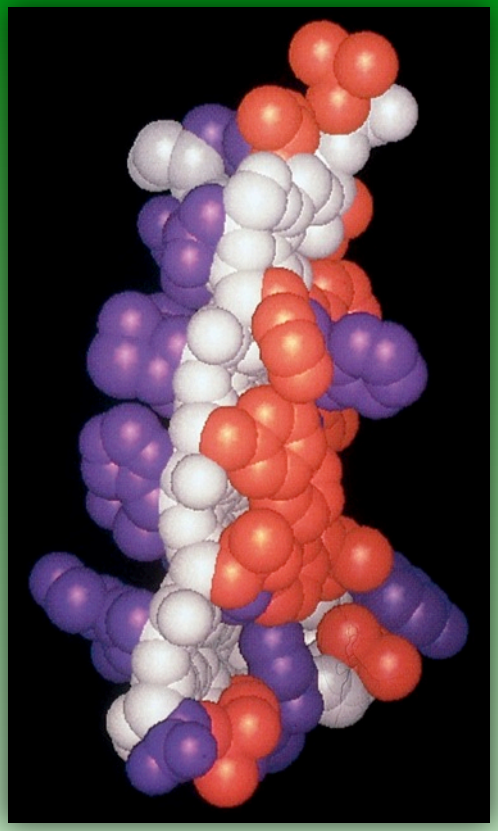
The H helix of sperm whale myoglobin. A **helical wheel** representation in which the side chain positions about the α helix are projected down the helix axis onto a plane.

Large percentage of anti-parallel β-sheet: no α-helix



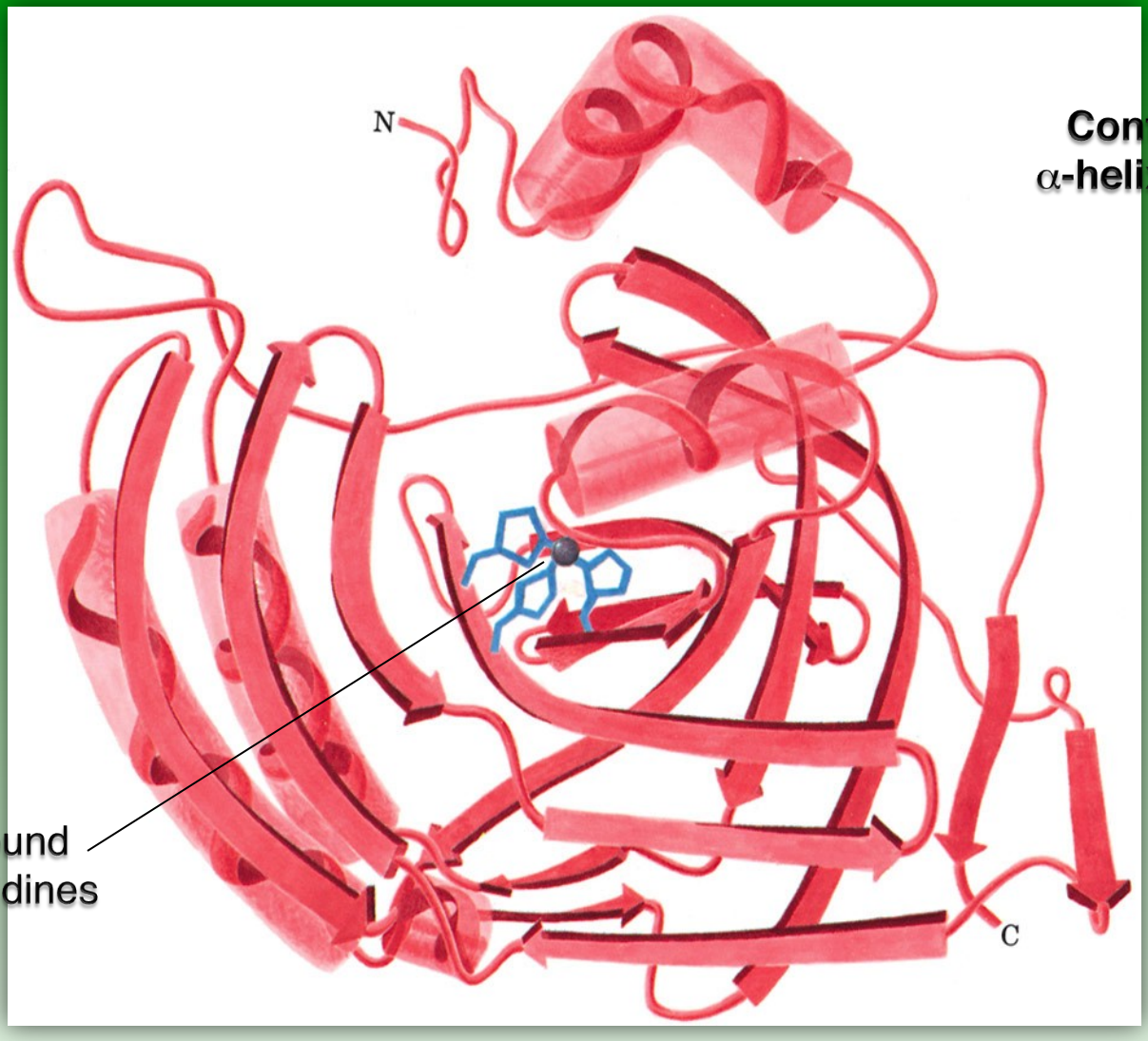
contains bound metal

The X-ray structure of jack bean protein concanavalin A



red = nonpolar
purple = polar

A space-filling model of an antiparallel β sheet from concanavalin A

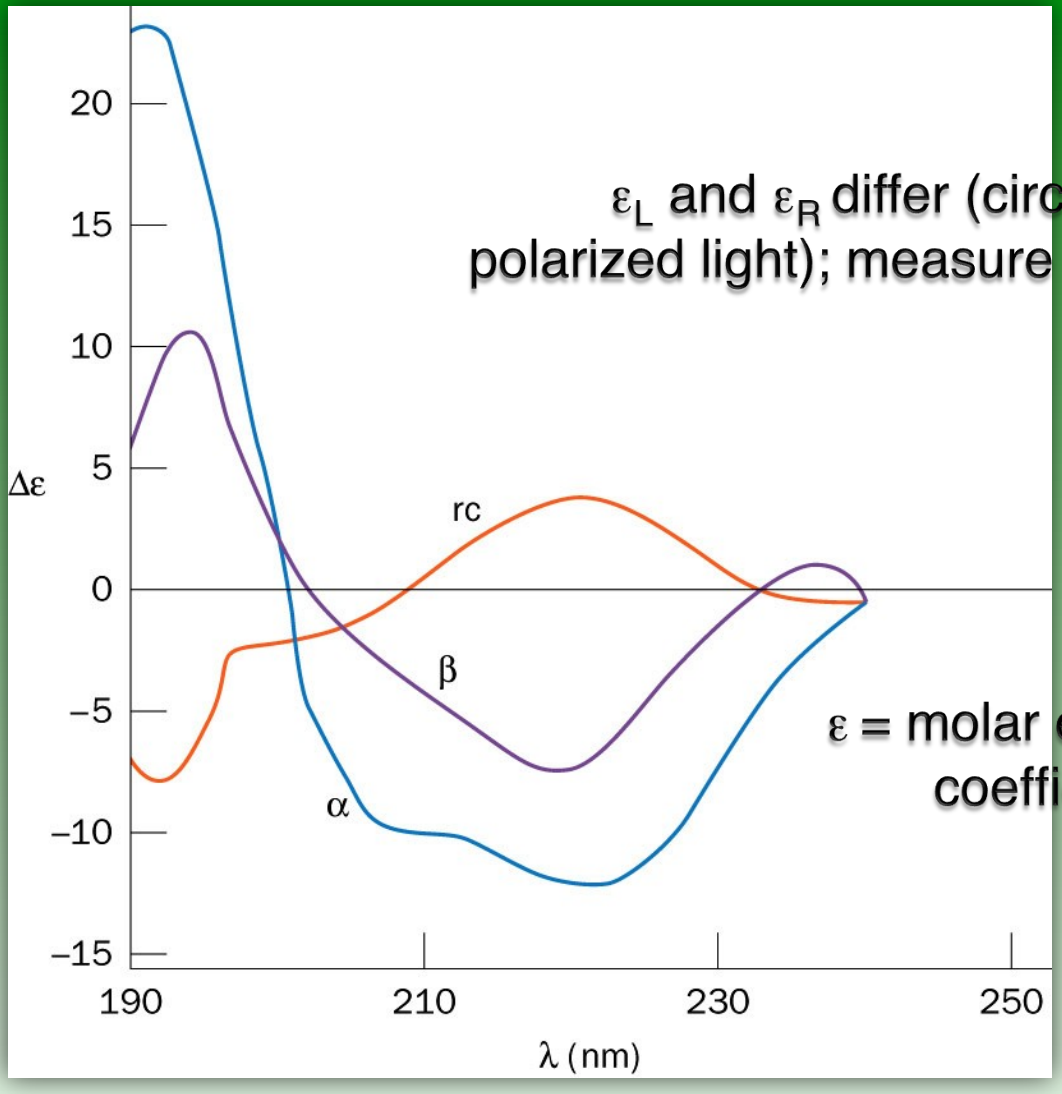


Contains mix of
α-helix and β-sheet

Zn^{2+} ion bound
by three histidines

Human carbonic anhydrase

Only chiral molecules give a CD spectrum.

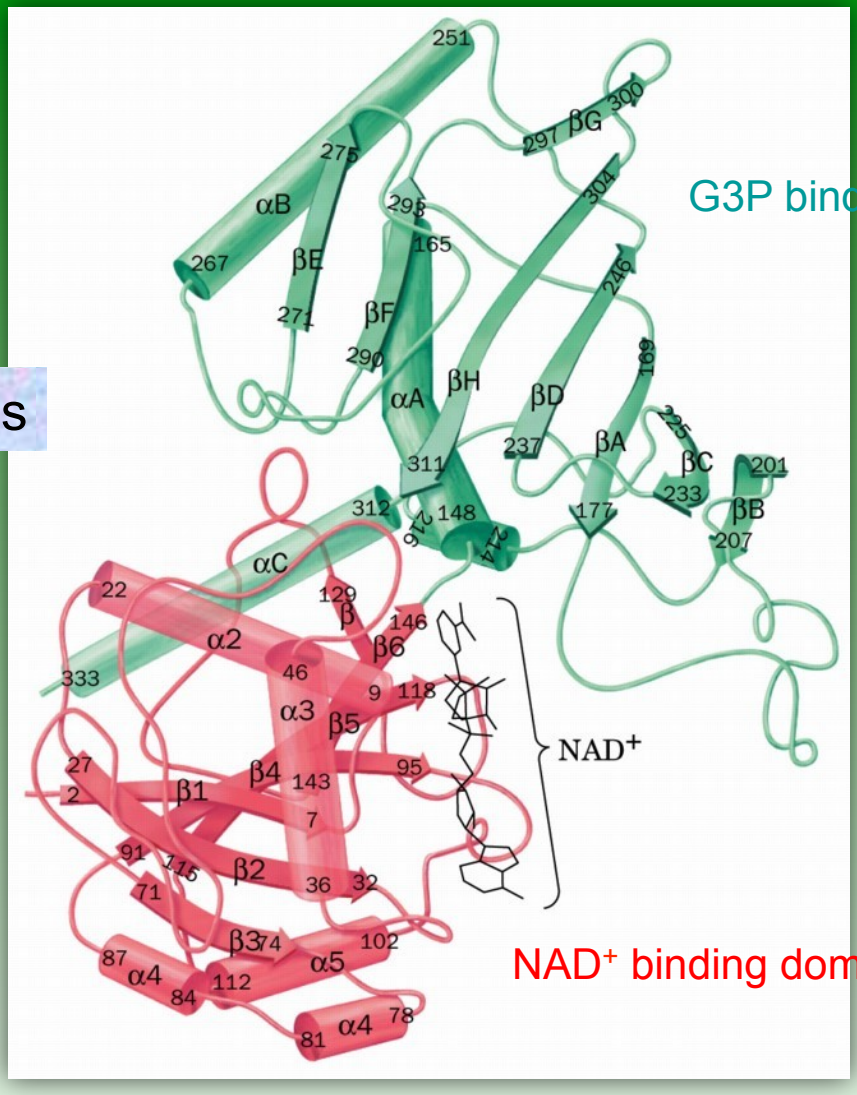


ε_L and ε_R differ (circularly polarized light); measure $\Delta\varepsilon = \varepsilon_L - \varepsilon_R$

ε = molar extinction coefficient

Circular dichroism (CD) spectra of polypeptides: α = α-helix; β = β-sheet; rc = random coil

two domains



One subunit of the enzyme, glyceraldehyde-3-phosphate dehydrogenase, from *Bacillus stearothermophilus*

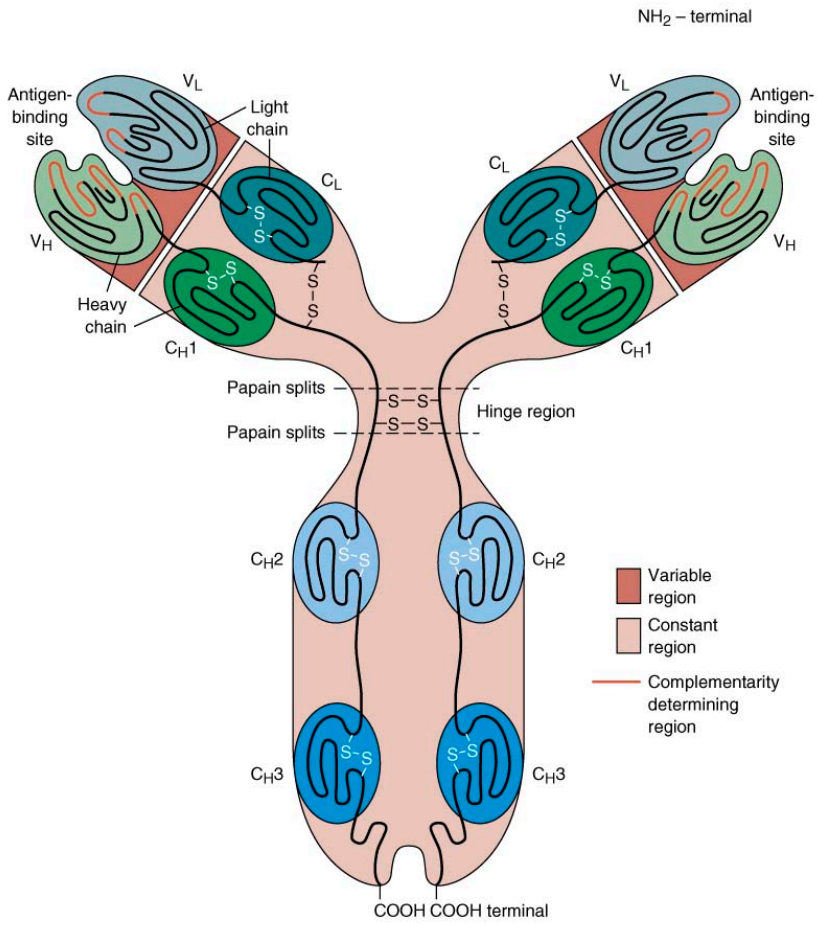
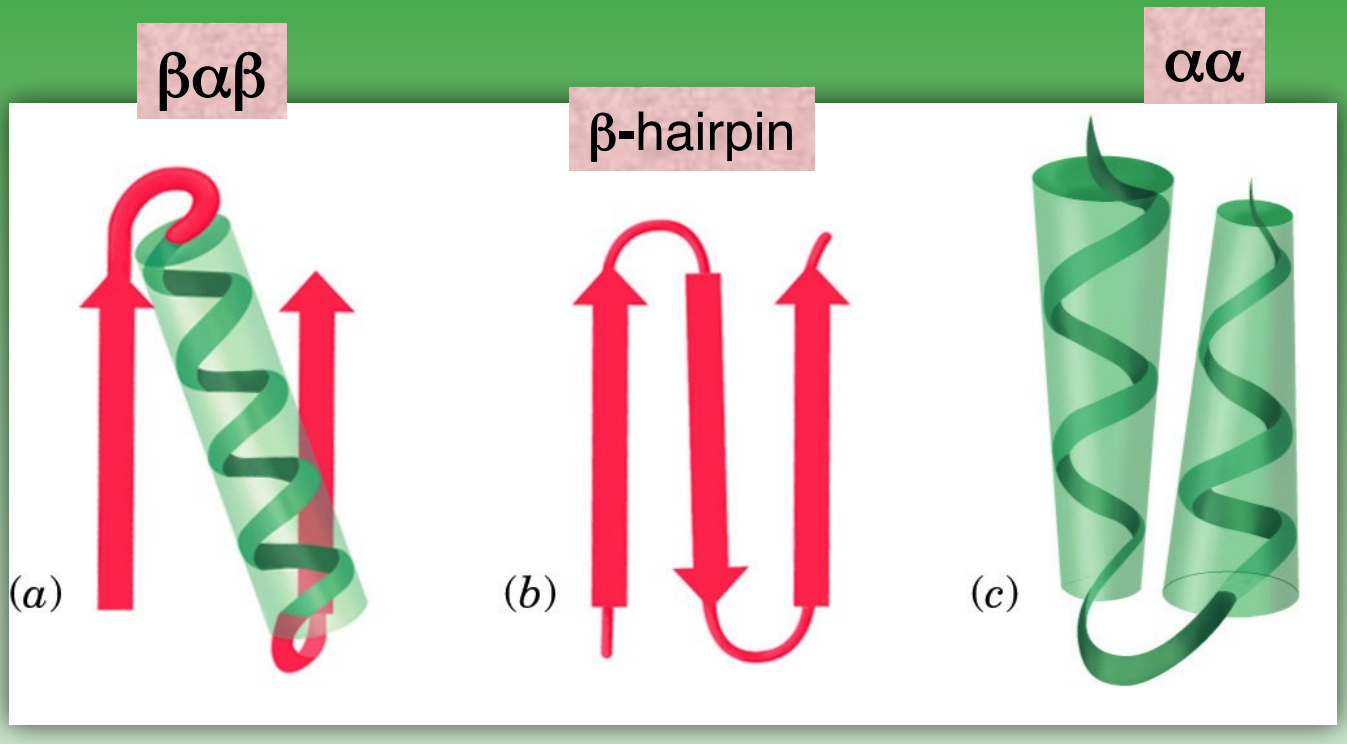
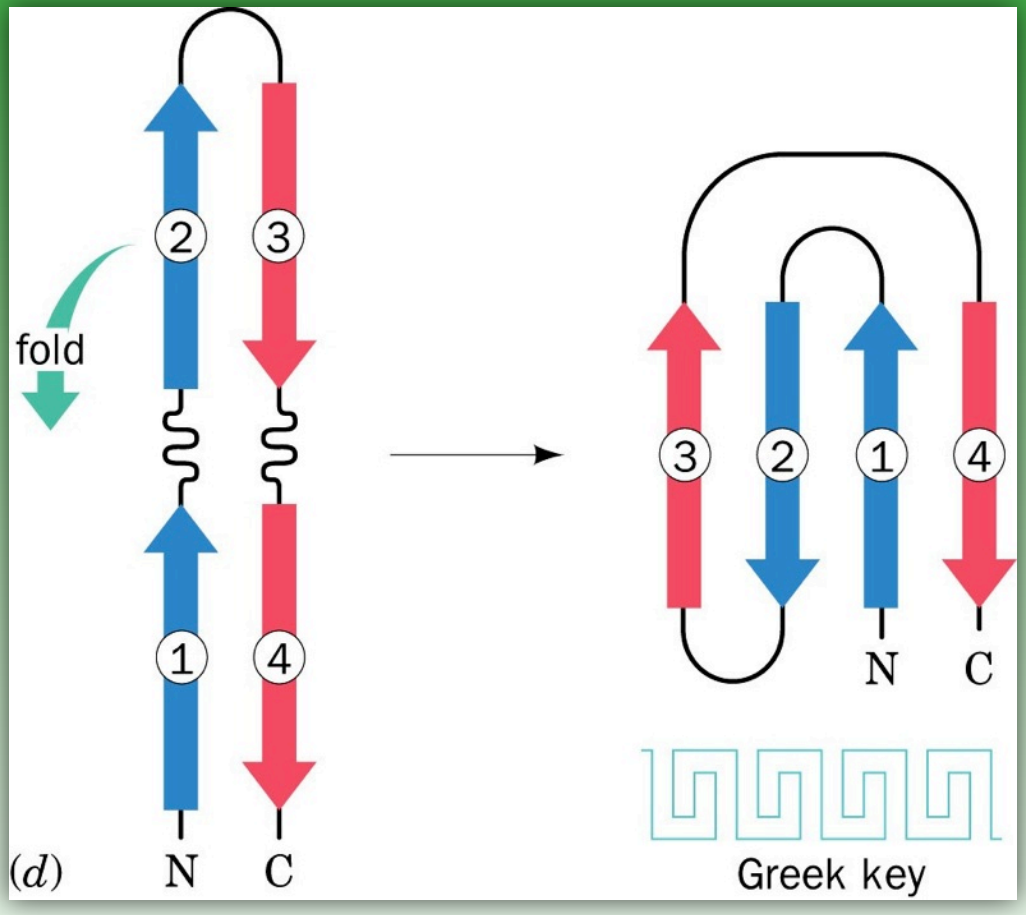


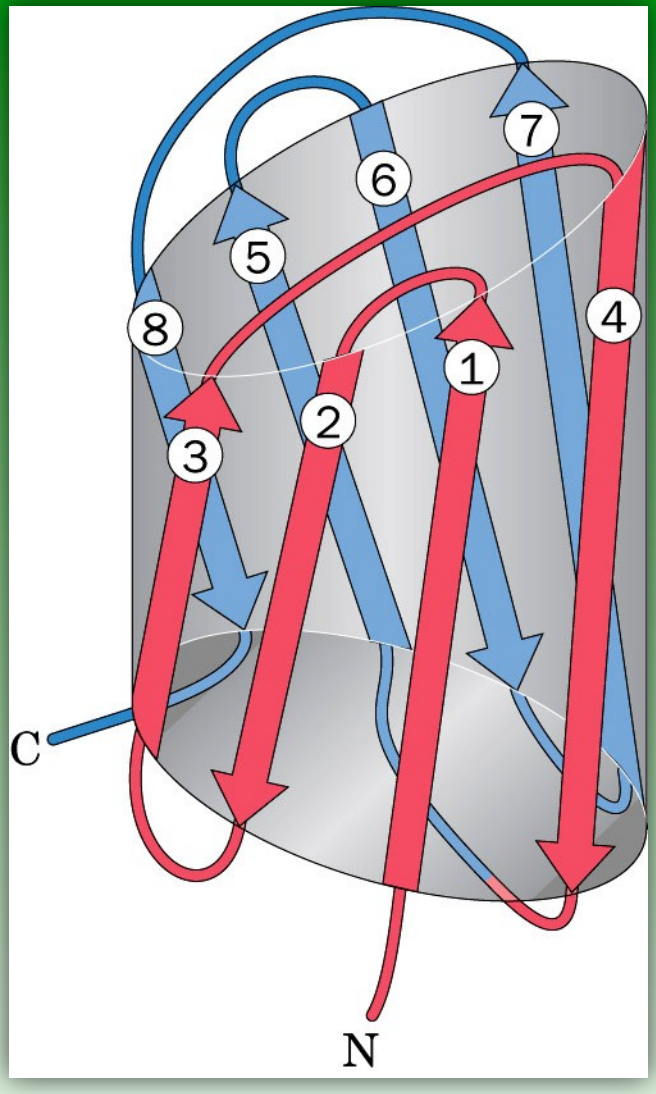
Figure 9.2. Diagrammatic structure of IgG. From Cantor, C. R. and Schimmel, P. R. *Biophysical Chemistry*, Part I, San Francisco: Freeman, 1980. Reprinted with permission of Mr. Irving Geis, New York.

Schematic diagrams of some supersecondary structures


βαβ
β-hairpin
αα
(a)
(b)
(c)

Greek key motif





ribbon form

X-ray structure of the C-terminal domain (83 residues) of bovine γ-β crystallin: a topological diagram showing how its two Greek key motifs are arranged in a β barrel.

Protein-DNA binding motifs

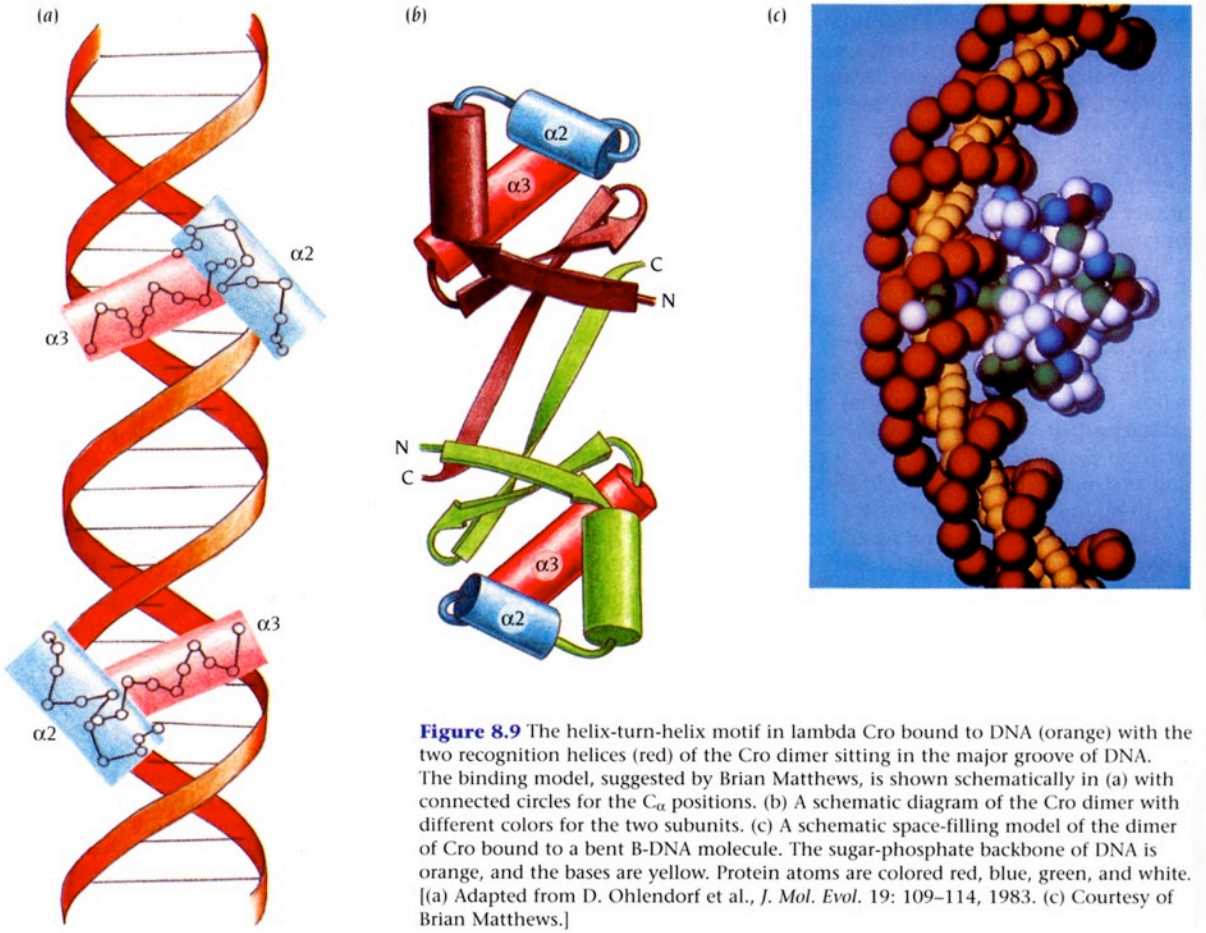


Figure 8.9 The helix-turn-helix motif in lambda Cro bound to DNA (orange) with the two recognition helices (red) of the Cro dimer sitting in the major groove of DNA. The binding model, suggested by Brian Matthews, is shown schematically in (a) with connected circles for the C_α positions. (b) A schematic diagram of the Cro dimer with different colors for the two subunits. (c) A schematic space-filling model of the dimer of Cro bound to a bent B-DNA molecule. The sugar-phosphate backbone of DNA is orange, and the bases are yellow. Protein atoms are colored red, blue, green, and white. [(a) Adapted from D. Ohlendorf et al., *J. Mol. Evol.* 19: 109–114, 1983. (c) Courtesy of Brian Matthews.]

A structure-function correlation:
Role of α-helices in the binding of Cro dimer To DNA

β-Structure at a protein dimer interface:
The stretch of sequence at the C-terminus of each Cro monomer participates in a β-sheet secondary structure, which promotes dimerization

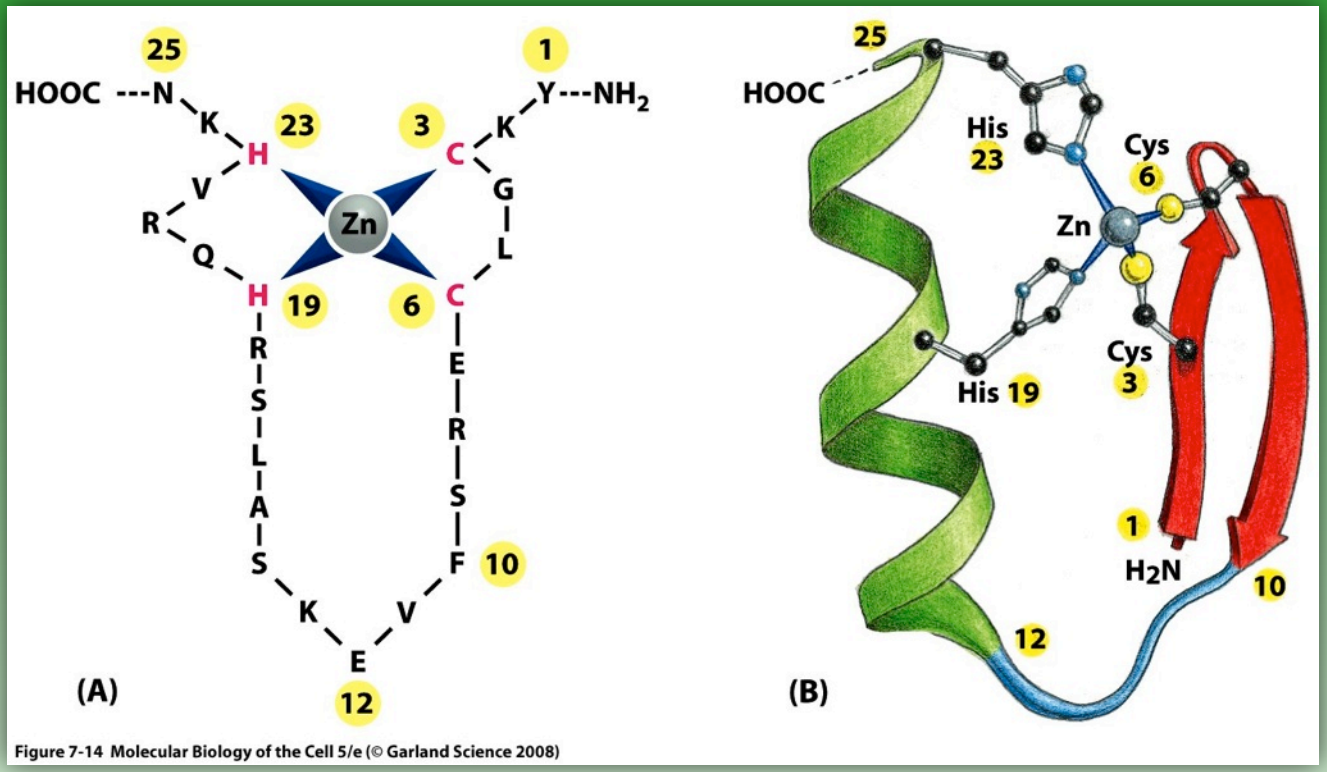


Figure 7-14 Molecular Biology of the Cell 5/e (© Garland Science 2008)

A zinc finger protein: Cys-Cys-His-His family

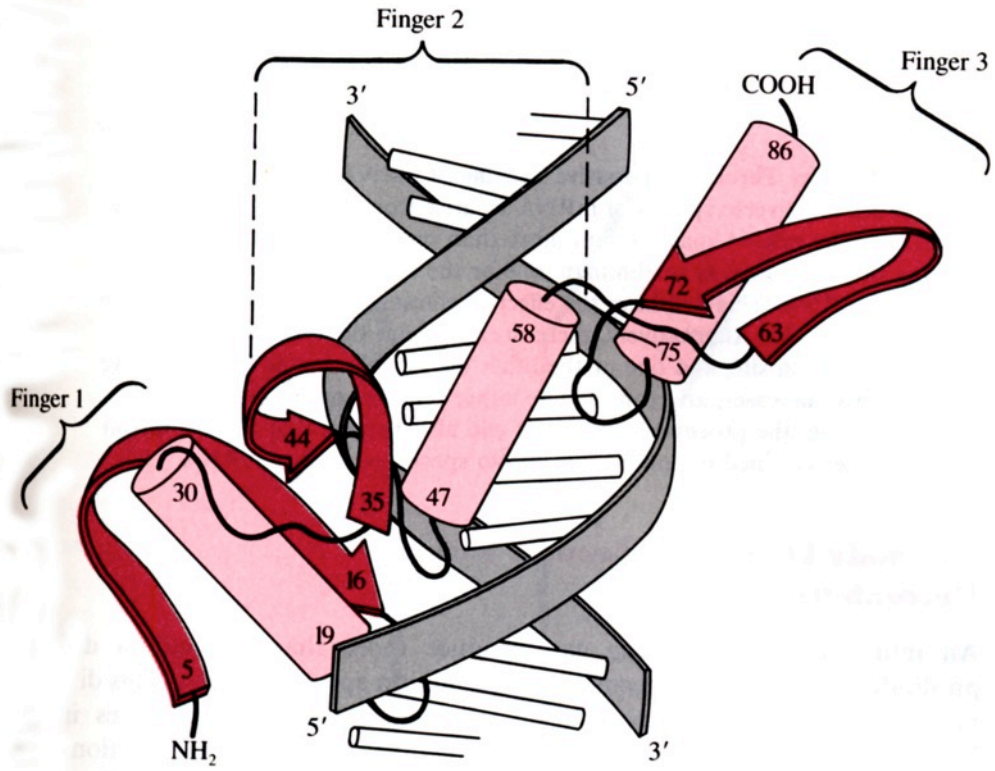


Figure 13-17

A Graphic Illustration of the X-ray Crystal Structure of the Zinc Finger Protein Zif268 Bound to DNA. Each zinc finger consists of an α-helix, shown as a cylinder, and a β-strand, shown as an arrow ribbon, held together through coordination to zinc. [After N. P. Pavletich and C. Pabo, *Science (Washington, D.C.)* 252 (1991): 809–817, Fig. 2.]

Figure 7-19 Molecular Biology of the Cell 5/e (© Garland Science 2008)

A leucine zipper dimer bound to DNA

Protein fold classification

The columns of the table are based on domain architectures as defined by the CATH hierarchical classification. Each cell provides information on an interesting fold group within that architecture and highlights a particular structural domain from that group. The first row of each column typically contains the most basic fold group for that architecture followed by fold groups with more complex structures. The population given as a percentage for each architecture is calculated from the 527 genomes present in Gene3D version 6.0.

Known functions have been automatically assigned to one of eight categories in the Gene Ontology (GO) molecular function classification (see legend). These categories are represented as a coloured octagon around the structure and are based on a classification scheme devised by Christos Ouzounis. For each fold group, the GO categories are those identified for all structures within that fold group, excluding electronically inferred annotations, as well as all annotated sequence homologues to those structures (at 60% sequence identity, 80% overlap of the larger domain) in Gene3D. Functions are assigned based on the whole structure to which the domain belongs and may therefore not always represent a specific functional attribute of that domain.

A white octagon tile means that no proteins in that fold group have that function. The incremental filling of the tile (by 1/4, 1/2, 3/4, 1/1) indicates the presence of the respective functions in the fold group and their relative importance (i.e. up to 25 / 50 / 75 / 100% of all proteins in that fold group have that function). For the fibrous proteins the functional mapping is simply that of the particular structure shown and its 60% sequence identity homologues. A completely blank octagon reflects the fact that currently no function can be automatically mapped to that fold, but not necessarily that no known function exists.

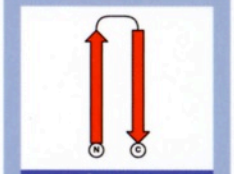
α-Proteins

Orthogonal Bundle 12.98%	Up-down Bundle 3.63%	α Horseshoe 2.03%	α Solenoid <0.01%	α/α Barrel 0.17%
1ois 001 73 (19)	1u5p A01 106 (16)	1bd8 000 207 (80)	1ppr M01 156 (1)	1fce 001 369 (58)
1.10.10 Arc repressor	1.20.58 3-Helix bundle	1.25.40 α_5 Horseshoe Ankyrin-like repeat	1.40.10 α Solenoid	1.50.10 $(\alpha/\alpha)_8$ Barrel
1ckk A01 93 (34)	1e85 A00 125 (24)	1lrv 000 481 (145)		
1.10.238 EF-hand	1.20.120 4-Helix bundle	1.25.10 α_9 Horseshoe Leucine rich repeat variant		
1mbn 000 147 (9)	1ap9 000 236 (46)	1lsh A02 481 (145)		
1.10.490 Globin	1.20.1070 7 TM bundle	1.25.10 α_{10} Horseshoe		
1a28 A00 238 (16)	1wpg B02 418 (8)	1qsa A01 363 (47)		
1.10.565 α_8 Orthogonal	1.20.1110 α_{10} Bundle	1.25.20 α_{12} Horseshoe		
1s4b P02 375	1jb0 A00 739	1u6g C00 481 (145)		
1.10.1370 α_{13} Orthogonal	1.20.1130 α_{12} Bundle	1.25.10 Superhelical horseshoe		

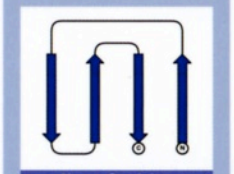
β-Proteins

β-Ribbon/Sheet/Roll 3.16%	β-Barrel 3.68%	β-Sandwich 4.90%
1www V00 101 (13)	1khi A02 91 (27)	1k5n A02 112 (24)
2.10.90 Cystine knot	2.40.50 OB fold (β_n)	2.60.40 Immunoglobulin-like
2bml A00 115 (18)	1gm6 A00 139 (25)	1g6e A00 87 (4)
2.10.270 Left-handed $(\beta\beta)_3$ solenoid	2.40.128 Lipocalin-like (β_n)	2.60.20 γβ-Crystallin Greek key
1lsh A03 98	1emg A00 223 (5)	2stv 000 194 (49)
2.20.50 Single open sheet	2.40.155 Green fluorescent protein (β_{11})	2.60.120 Jelly roll
1h64 A00 74 (19)	2fgq X00 282 (75)	3enr B00 194 (49)
2.30.30 $\beta_5\alpha_1$ roll (SH3-like)	2.40.160 Porin (β_{16})	2.60.120 Concanavalin A-like
1t77 A01 119 (24)	1kmo A02 461 (57)	
2.30.29 PH domain	2.40.170 Maltoporin (β_{22})	

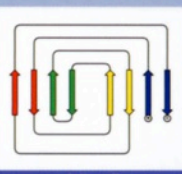
Basic topologies of secondary structure

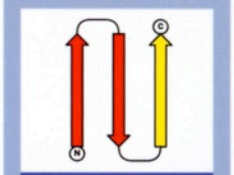


β-Hairpin

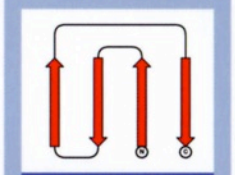


N-type Greek key

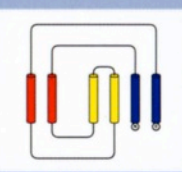

Jelly roll

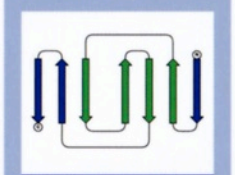


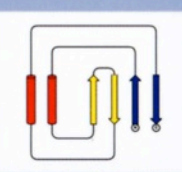
β-Meander



C-type Greek key


α-Solenoid

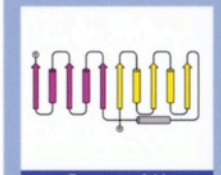

Ig domain


αβ-Plait

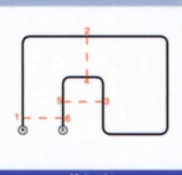
The **β-hairpin** and the **β-meander** are examples of the simplest type of up-and-down antiparallel β-sheet topologies. The latter has an additional strand (yellow) with respect to the former. They can be observed in innumerable examples of β-structures shown in the main table.

The **Ig fold** is one of the most well-known of all protein structures. An Ig constant domain, as shown here, has an **N-type Greek key** embedded within it (shown in green).

The **jelly roll**, **α-solenoid** and **αβ-plait** topologies are surprisingly similar despite their different secondary structures. All are based on a giant hairpin which is subsequently rolled up to form a compact domain in which the secondary structures form two layers (the β-sheets in the case of the jelly roll). The latter is probably the most well-known of the three folds and takes its name from the topology diagram of its β-strands, which resembles a slice of a jelly roll (Swiss roll).


Rossmann fold

The **Rossmann fold** was first described by Michael Rossmann as a motif observed in lactate dehydrogenase. It is common in α/β proteins with open β-sheets and particularly in nucleotide binding proteins. It is composed of two topologically identical and pseudo-symmetrically related substructures, which are shown in different colours. The term Rossmann fold is also occasionally used to refer to such substructures. Several examples can be seen in the main table.

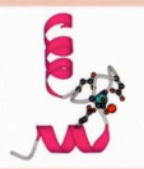


Kringle

The **kringle** takes its name from the topology imposed by its three disulphide bridges, which in two dimensions resembles a Danish pastry of the same name. It is a common modular element in proteins of the coagulation pathways.

Important structural motifs


HTH motif

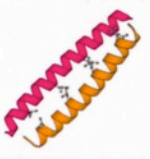

EF hand

The **helix-turn-helix** and **EF-hand** motifs are both characterized by two orthogonal α-helices. The former is a specific example of an α/α corner and is found in DNA binding proteins, where the second (recognition) helix inserts into the major groove. The EF-hand is observed in Ca^{2+} binding proteins, where the Ca^{2+} is bound by a loop between the two helices.


Greek key


2 β-Arches

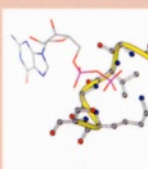
The **Greek key** and the interdigitated **β-arches** are two of the most commonly observed motifs (or substructures) in β-proteins. The former is predominantly observed at the edges of antiparallel β-sheets where the motif is often divided between two such sheets. The latter has been described as the most common sub-structure observed in β-sandwiches.


Leucine zipper


HLH motif

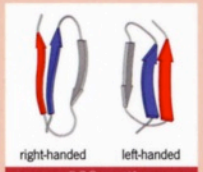
Both the **leucine zipper** and the **helix-loop-helix** are dimerization motifs. In the former case this occurs via the formation of a classical left-handed coiled coil, with leucines at every 7th position (the d position of the coiled coil). In the case of the HLH, the two helices of the motif come together with those of the second monomer to form a 4-helix bundle.


Zinc finger

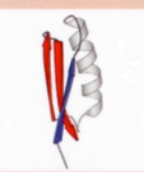

P-loop

Zinc fingers are metal binding motifs involved in DNA recognition. They differ in their Zn^{2+} ligands, 3D structures and DNA binding modes. The example shown is a 'classical' Zinc finger involving two His and two Cys ligands. The **P-loop** is a glycine rich motif involved in nucleotide binding, where it interacts directly with the α and β phosphate moieties.


Right handed βαβ



βββ motif


βαββ motif

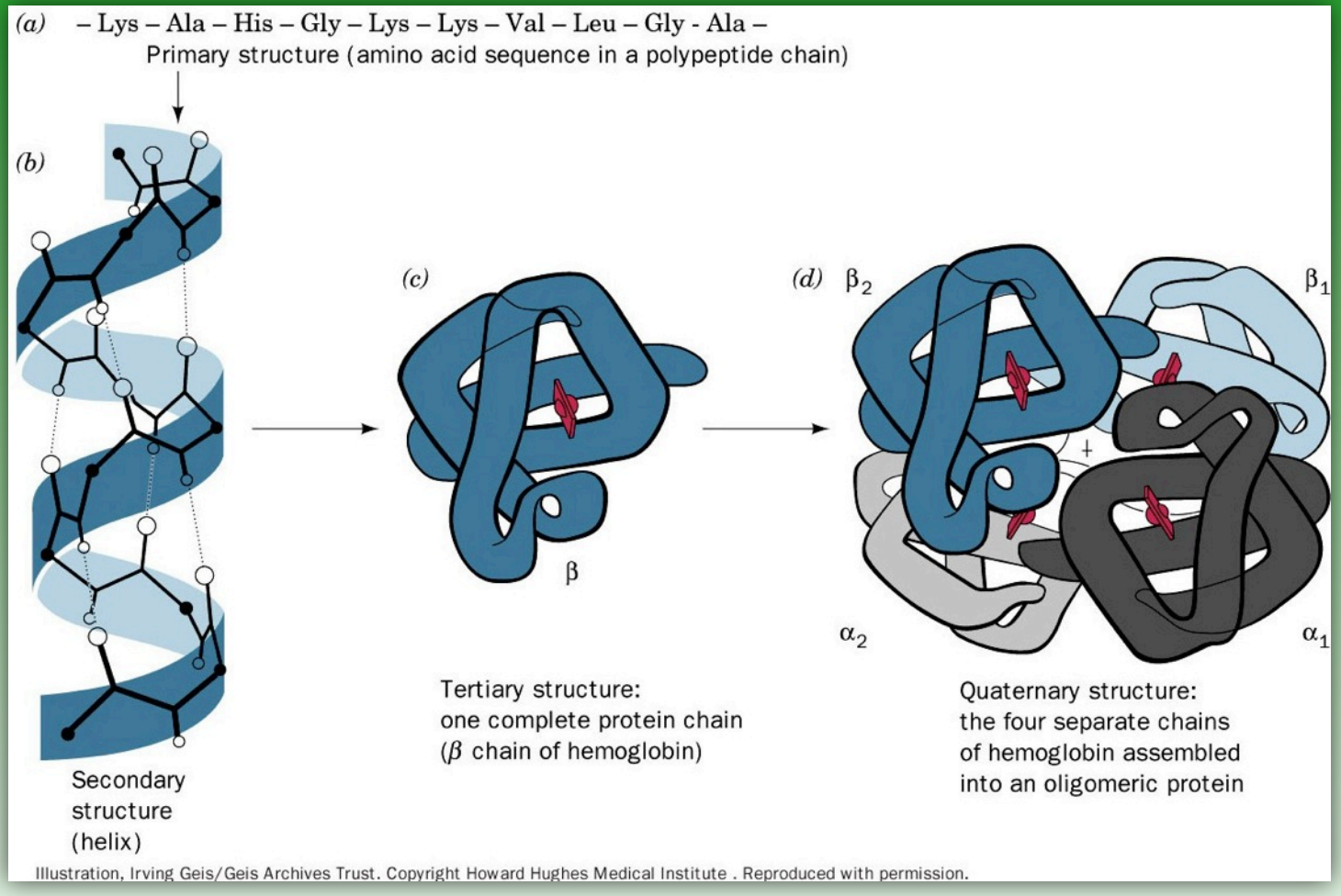
Most connections between parallel β-strands are right-handed, but exceptions are to be seen in the left-handed β-helices of the main table. The **βαββ motif** includes an additional intervening antiparallel strand.


Leucine rich repeat

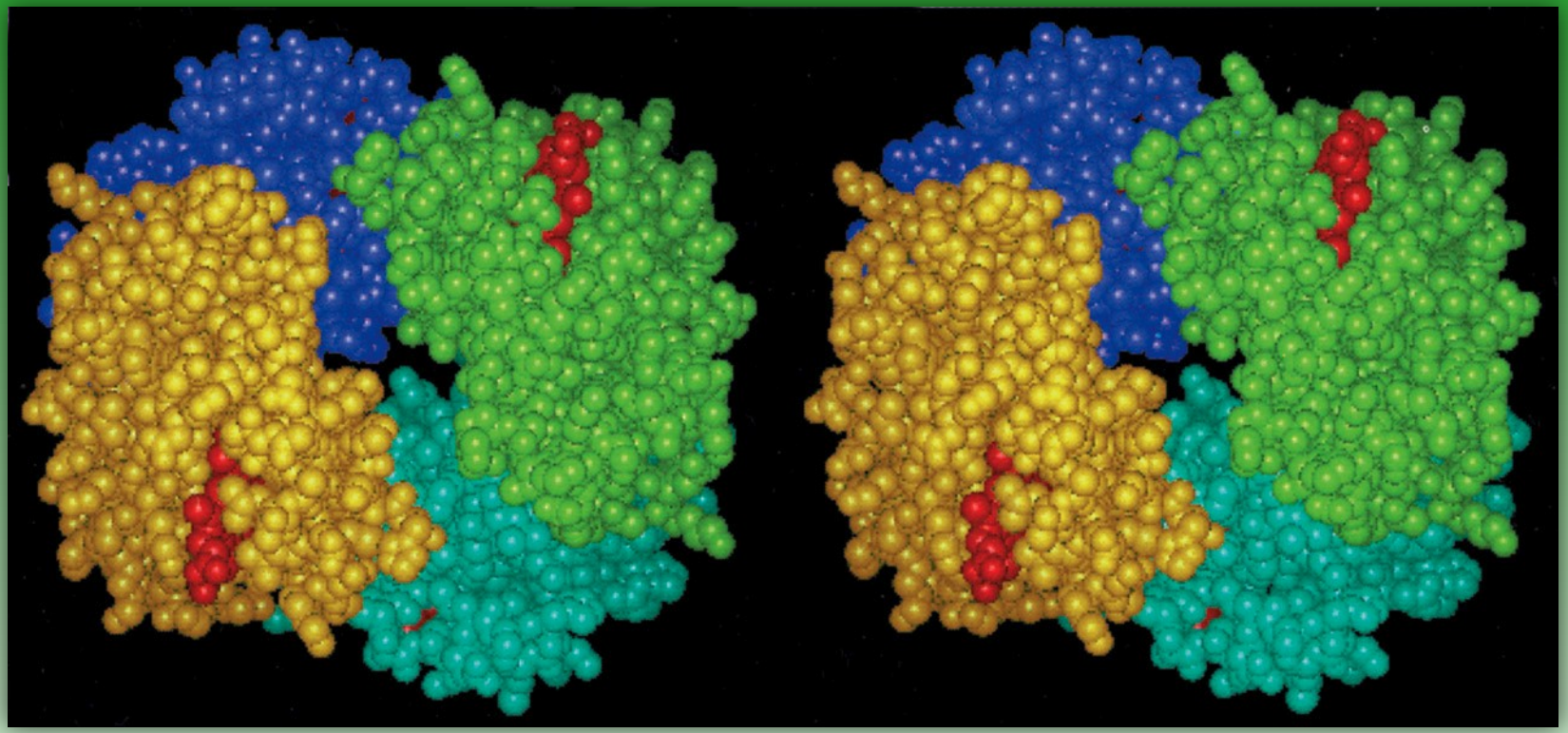
The **Leucine rich repeat** (LRR) is characterized by a sequence motif which typically contains 6 leucines. They form a structural motif of a β-strand, α-helix and connecting loop. Several examples of proteins, containing different numbers of repeats, can be seen in the αβ-horseshoes of the main table.

Multi-subunit (oligomeric) proteins

4° structure (quaternary structure)



The structural hierarchy in proteins: 4º structure



The quaternary structure of hemoglobin (tetramer; two α and two β polypeptides; four O_2 binding sites/hemoglobin tetramer); a binding protein (no catalytic activity)

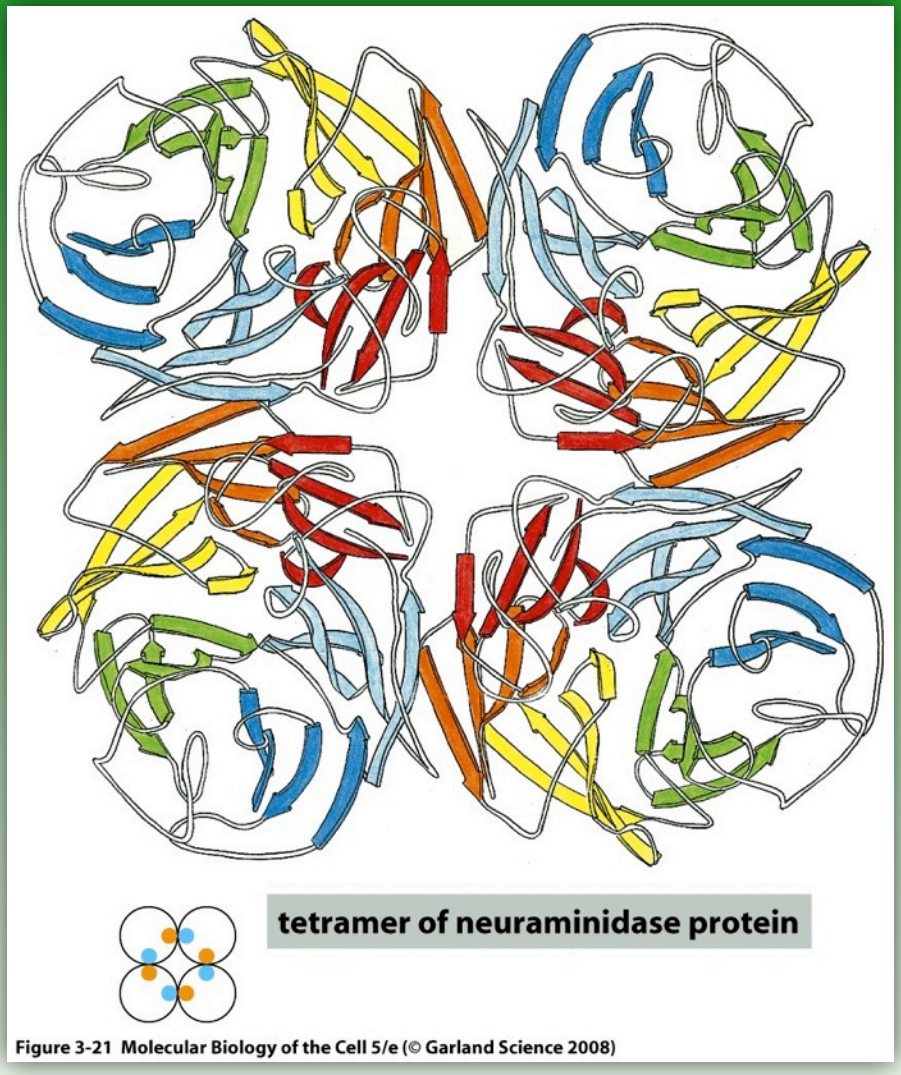
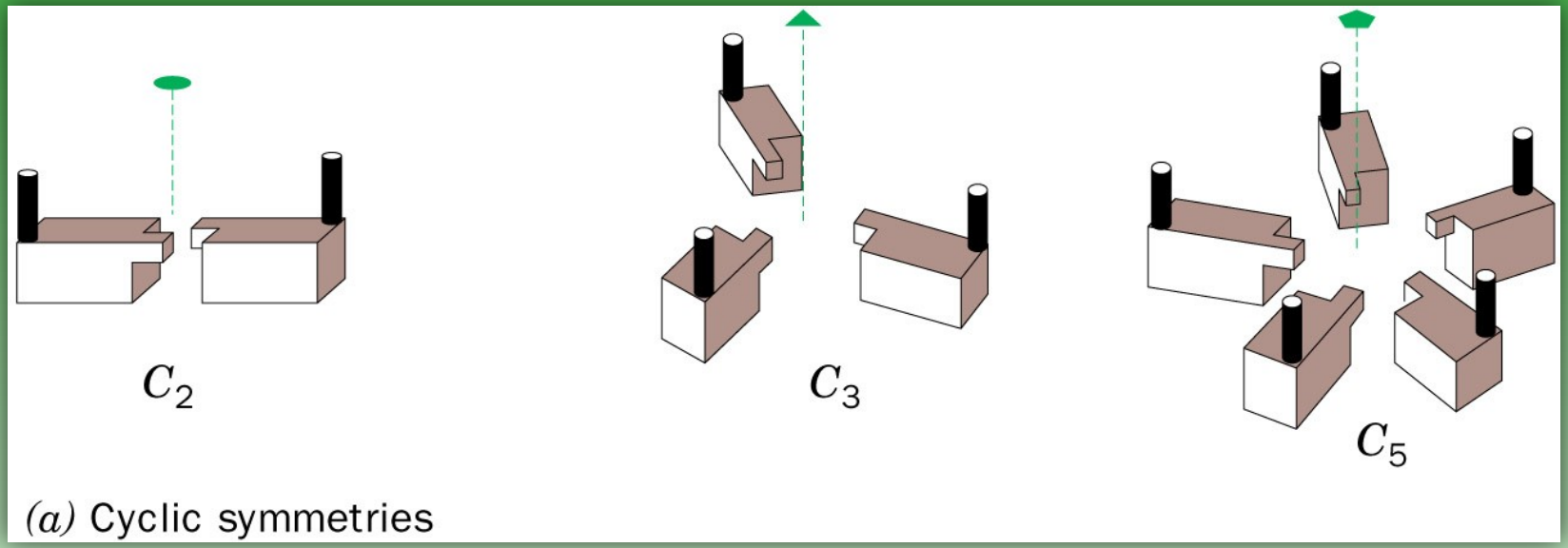
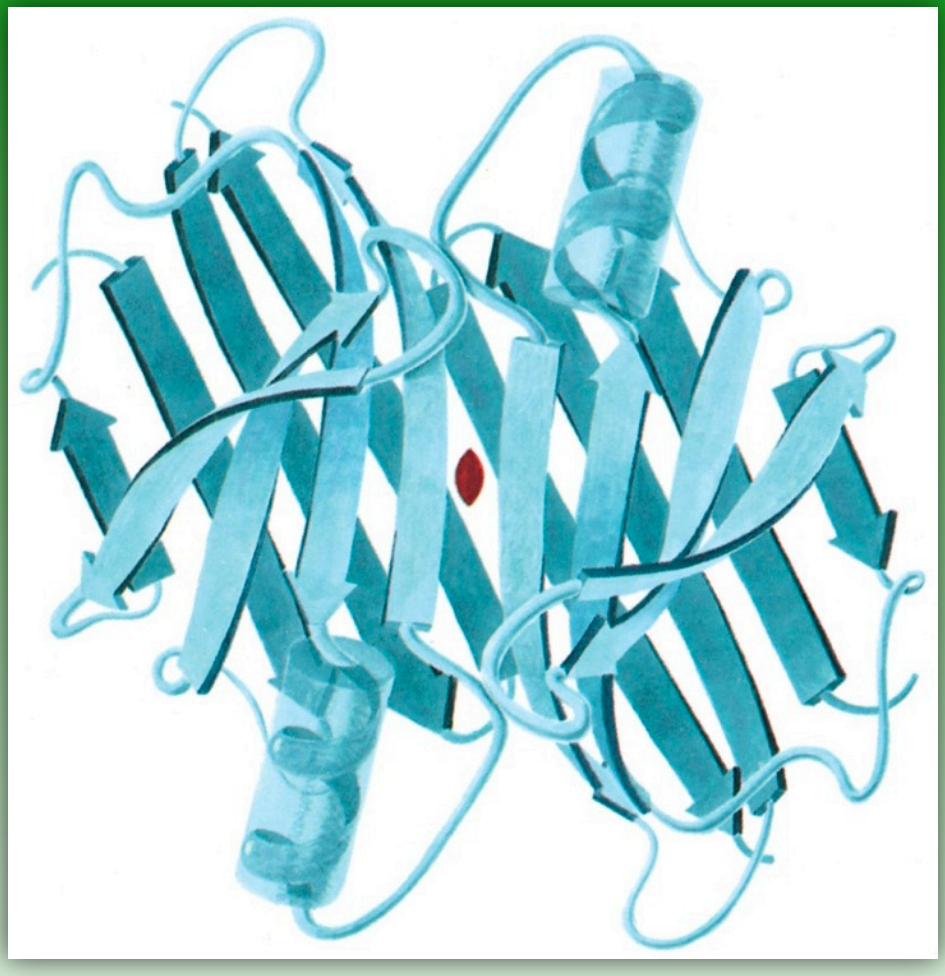


Figure 3-21 Molecular Biology of the Cell 5/e (© Garland Science 2008)

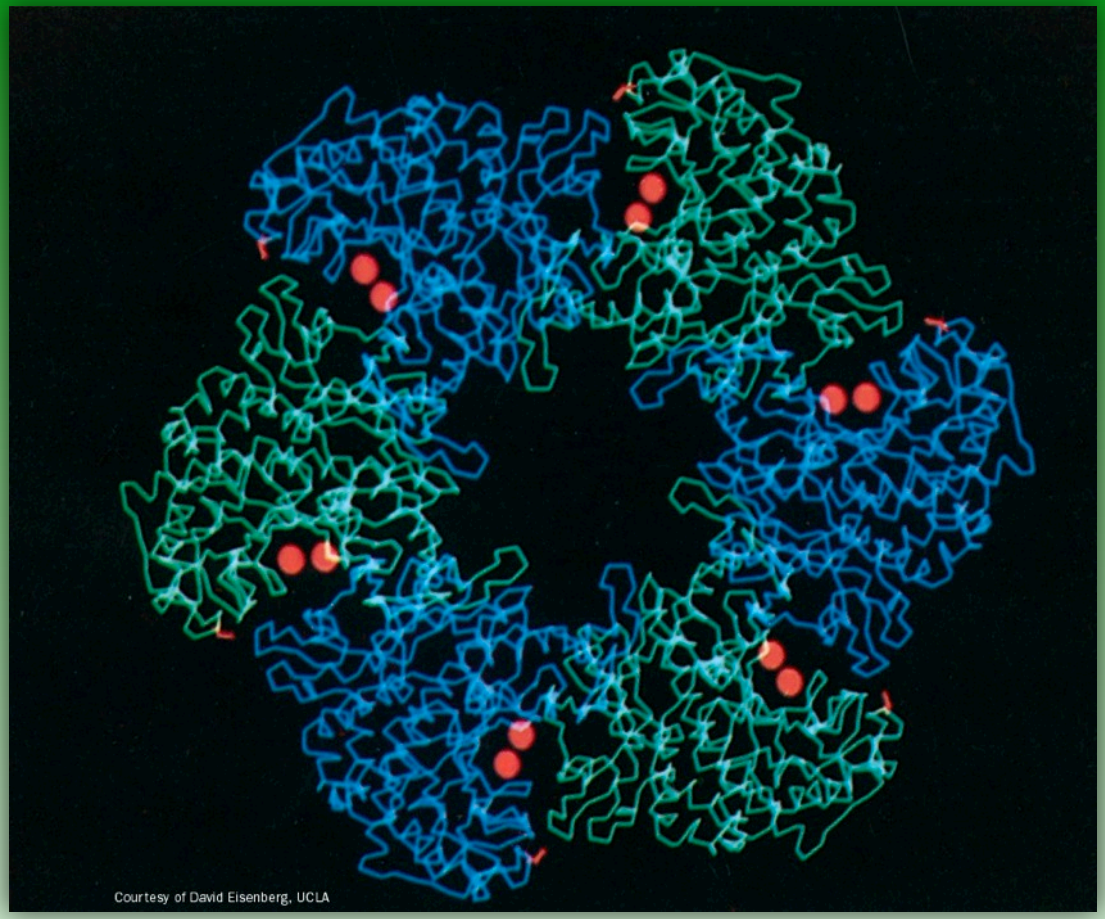
Neuraminidase:
A tetrameric enzyme comprised of four identical subunits



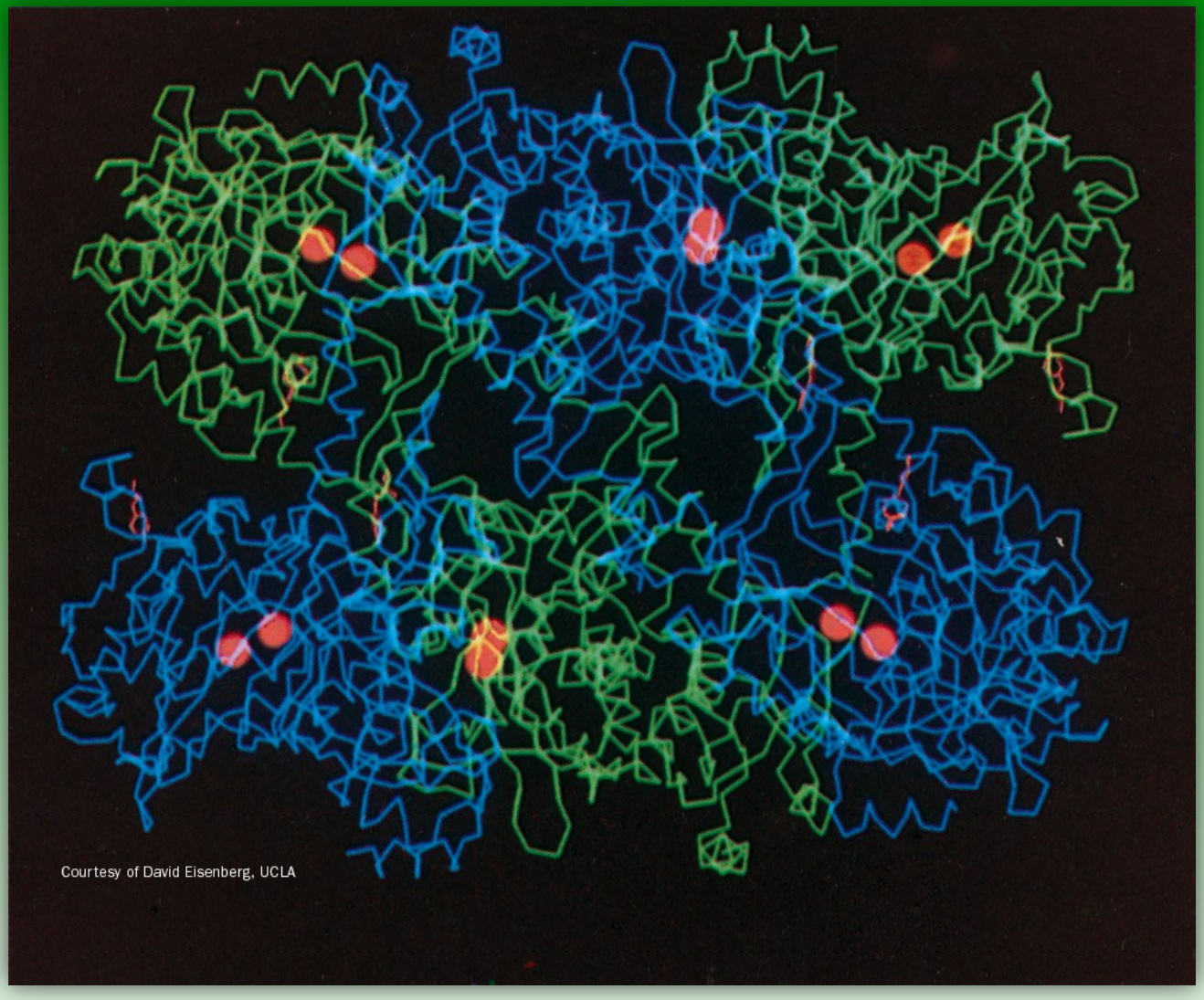
Some possible symmetries of proteins with identical protomers. Assemblies with symmetries C_2, C_3, and C_5.



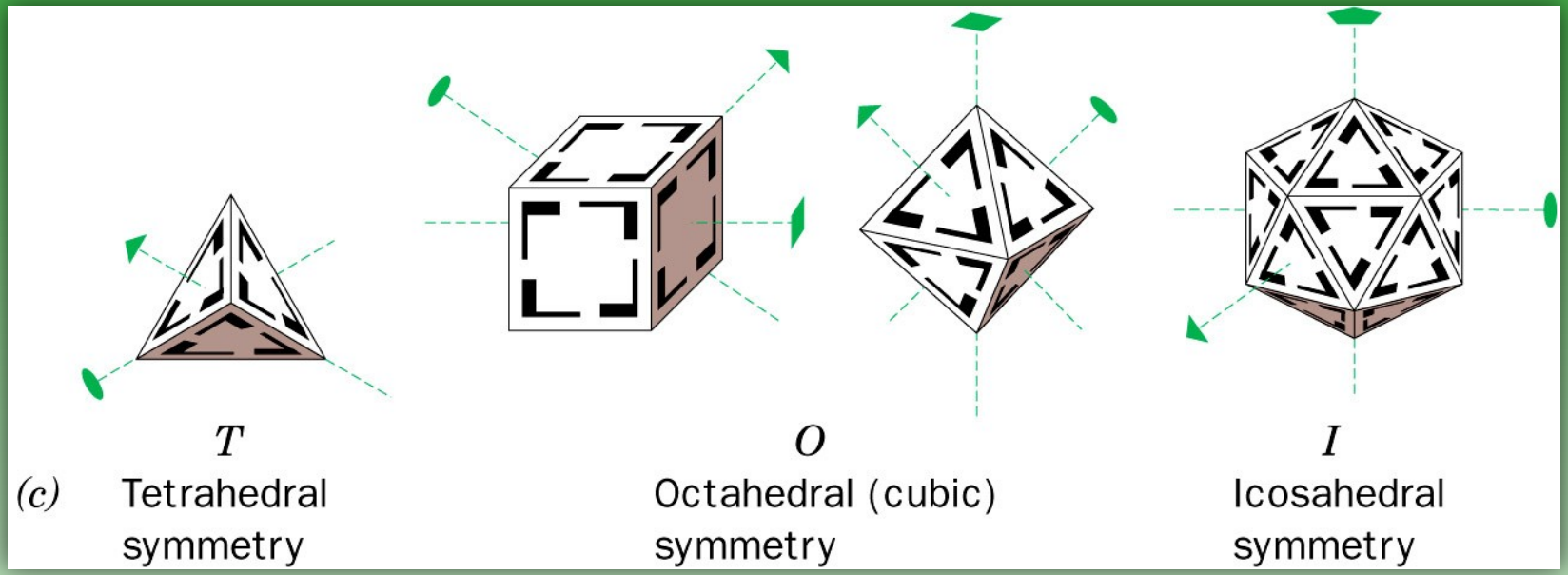
A dimer of transthyretin as viewed down its two-fold axis (*red symbol*).



X-ray structure of glutamine synthetase from *Salmonella typhimurium* - view down 6-fold symmetry axis (contains 12 subunits)



X-ray structure of glutamine synthetase from *Salmonella typhimurium* - view down one of the 2-fold symmetry axes



Some possible symmetries of proteins with identical protomers. Assemblies with *T*, *O*, and *I* symmetries.

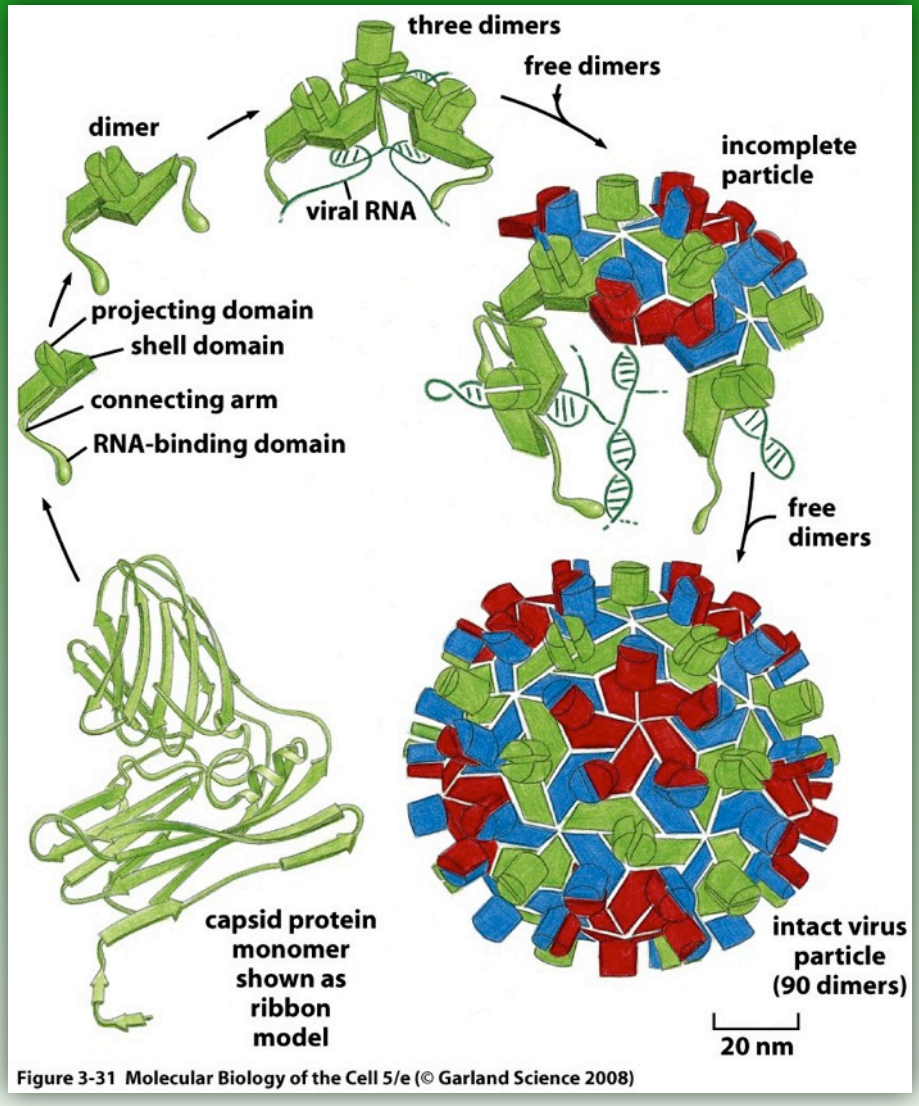


Figure 3-31 Molecular Biology of the Cell 5/e (© Garland Science 2008)

Assembly of a spherical virus (capsid formation): the tomato bushy stunt virus (TBSV).

33 nm in diameter

180 copies of a 386 aa capsid protein subunit

RNA genome of 4500 nucleotides

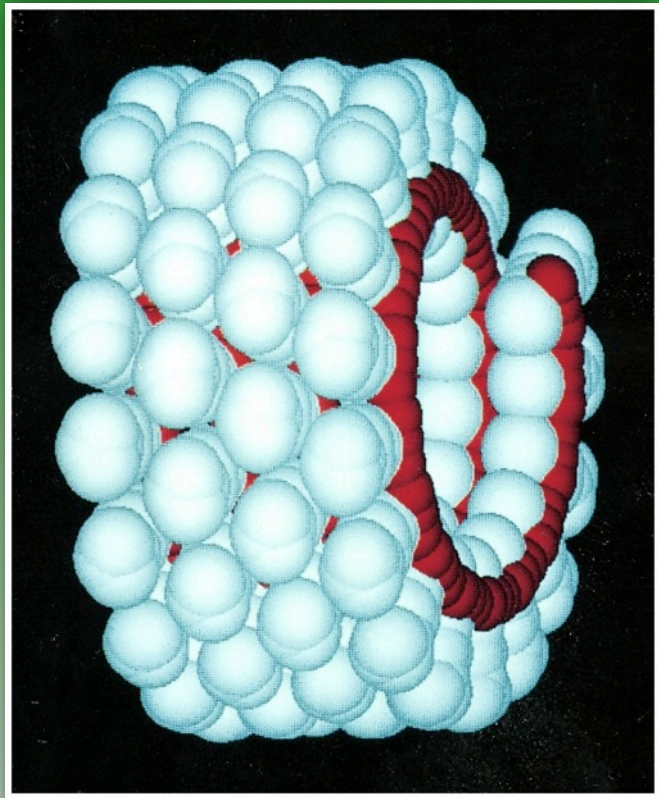
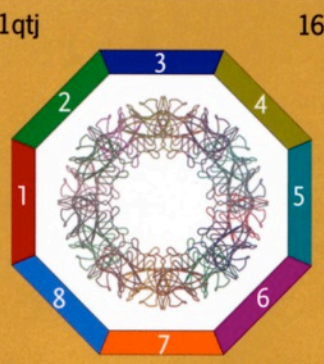


Figure 3-32b Molecular Biology of the Cell 5/e (© Garland Science 2008)

A structural representation of the tobacco mosaic virus (TMV):
A single long RNA molecule (6395 nucleotides) is enclosed in a cylindrical protein (helical coat) composed of 2130 identical protein subunits each containing 158 amino acids.

Legend

PDB code for reference structure ▼ — Number of subunits ▼



▲ Protein name ▲

Point group symmetry (Schoenflies nomenclature) ▲

Point group symmetry (International nomenclature) ▲

1 Multiple sites, cross-linking, membrane association
2 Cooperativity/allosterism
3 Cavities, channels and pores
4 Functional (active) site formation
5 Size and stability
6 Economy of genetic material
7 "Rulers" (exact separation between binding sites)
8 Multiple functions (in hetero-oligomers)

Yellow background indicates dihedral symmetry

Gray background indicates cubic/ icosahedral symmetry

WILEY-VCH

Oligomeric Proteins

Highest Order Rotation Axis

1	2	3	4	5	6	7	>7
1aqd 2 — C_1 1 — HLA class II	1wrp 2 — C_2 2 — Trp repressor	1rtm 3 — C_3 3 — C-type mannose binding protein	1bl8 4 — C_4 4 — Potassium channel	1lts 5 — C_5 5 — Heat labile enterotoxin (B subunit)	1do0 6 — C_6 6 — HslU ATPase	1i8f 7 — C_7 7 — SmAP	1igh 16 — C_8 8 — LHC II Rhodospirillium molischianum
3hvt 2 — C_1 1 — HIV reverse transcriptase	2pol 2 — C_2 2 — Bacterial polymerase III β subunit (E. coli)	1cd5 6 — D_3 32 — Glucosamine 6-P deaminase	1cuk 4 — C_4 4 — RUVA (DNA recombination protein)	1msl 5 — C_5 5 — Mechanosensitive channel	1g8y 6 — C_6 6 — Helicase RepA of plasmid RSF 1010	7ahl 7 — C_7 7 — Alpha-hemolysin	1nkz 18 — C_9 9 — LHC II Rhodopseu-domonas acidophila
1hzh 4 — C_1 1 — IgG	3phv 2 — C_2 2 — HIV protease	1raa 12 — D_3 32 — Aspartate transcarb-amoylase	1dhn 8 — D_4 422 — 7,8-Dihydroneopterin aldolase	1gtp 10 — D_5 52 — GTP cyclohydrolase I	1y12 6 — C_6 6 — Protein secretion apparatus (HCP1)	1grl 14 — D_7 72 — GroEL	1wap 11 — C_{11} 11 — TRP RNA binding attenuation protein (TRAP)
2aai 2 — C_1 1 — Ricin	4hhb 4 — C_2 2 — Human haemoglobin	1dps 12 — T 23 — DNA binding protein Dps	1a6d 16 — D_4 422 — Thermosome	1rvv 60 — I 532 — Icosahedral lumazine synthase (B. subtilis)	1f52 12 — D_6 622 — Glutamine synthase	1pma 28 — D_7 72 — Proteasome	1qtj 16 — D_8 822 — SAP from horseshoe crab
	4pfk 4 — D_2 222 — Phosphofructokinase	3pcg 24 — T 23 — Protocatechuate 3,4-dioxygenase	2fha 24 — O 432 — Ferritin	1stm 60 — I 532 — Satellite panicum mosaic virus	1g3k 24 — D_6 622 — HslUV ATP dependent protease		

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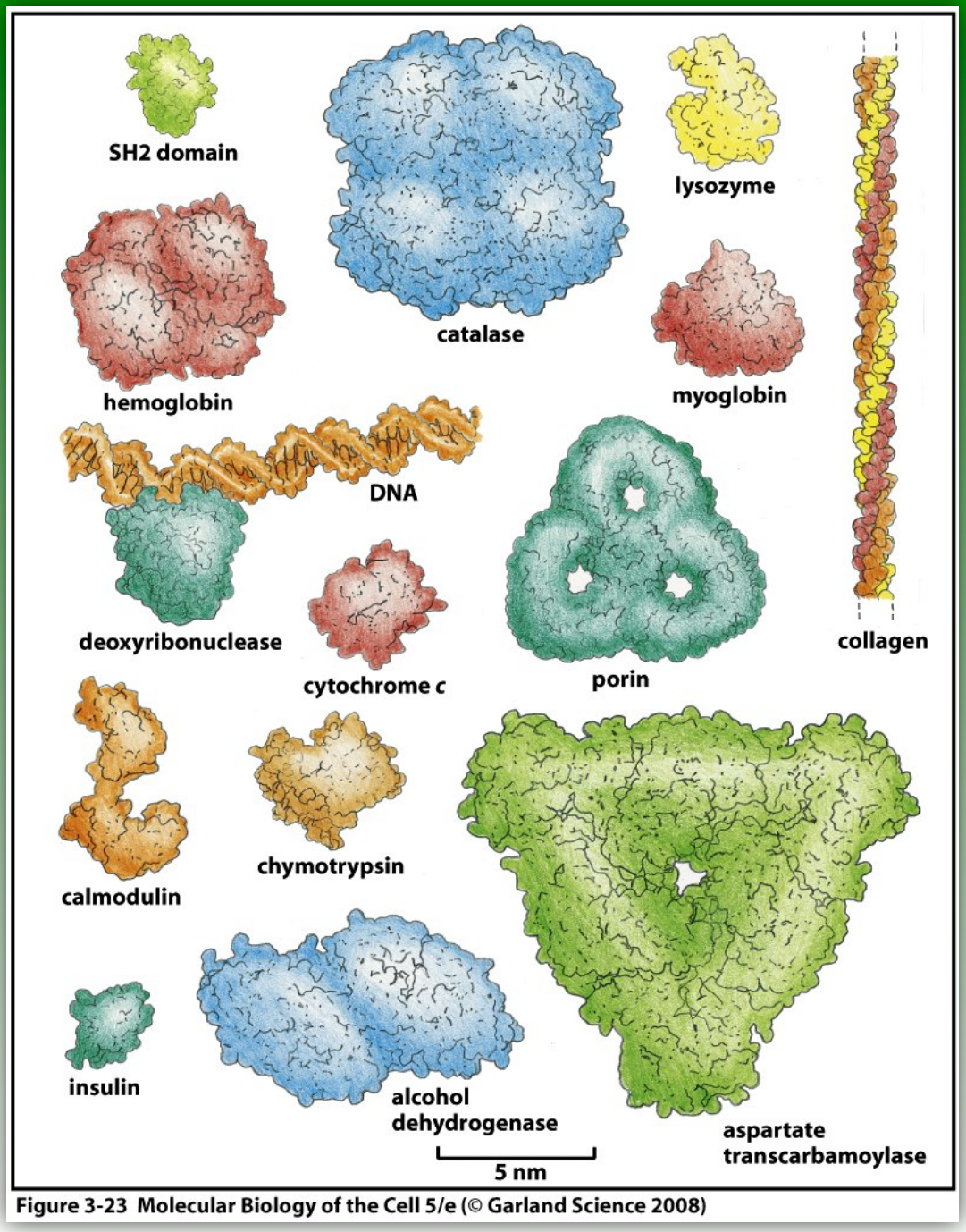

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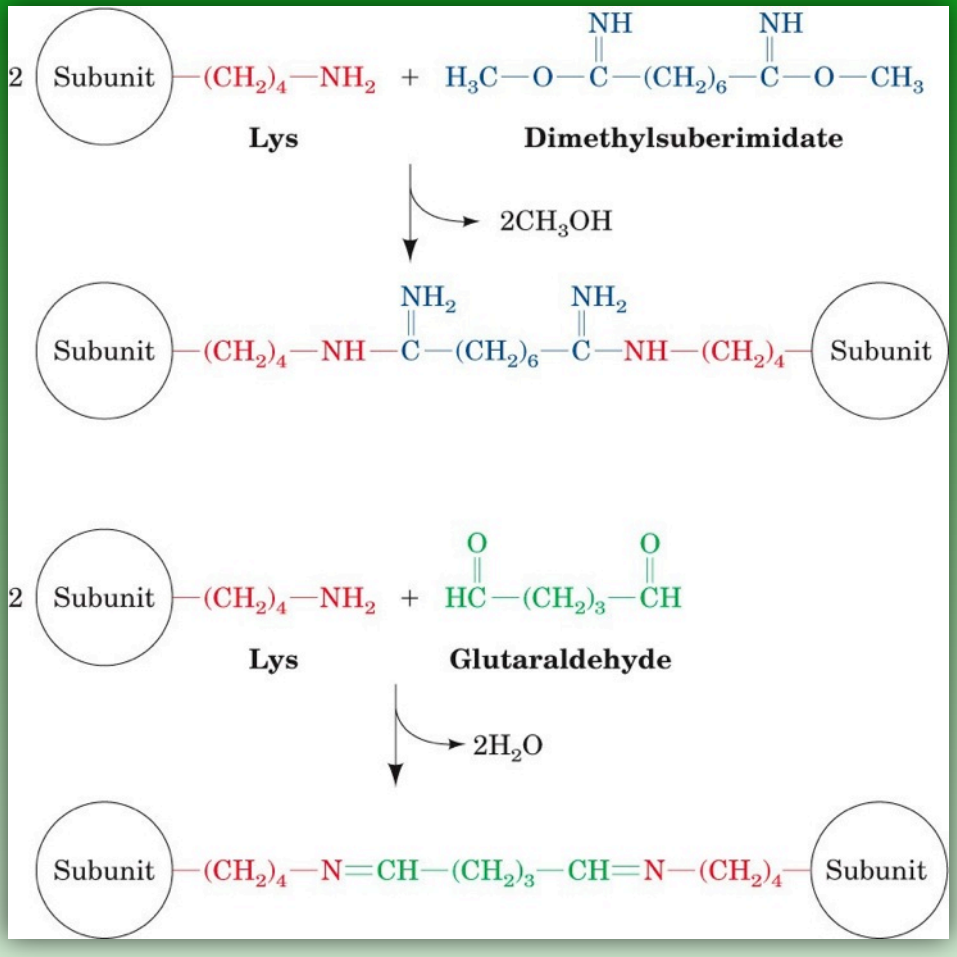
A collection of proteins shown on the same scale



Characterization of oligomeric proteins: Some chemical cross-linking agents (bifunctional reagents) used to stabilize protein quaternary structure

Protein-protein interactions (binding): Three common ways in which two proteins can bind to each other.

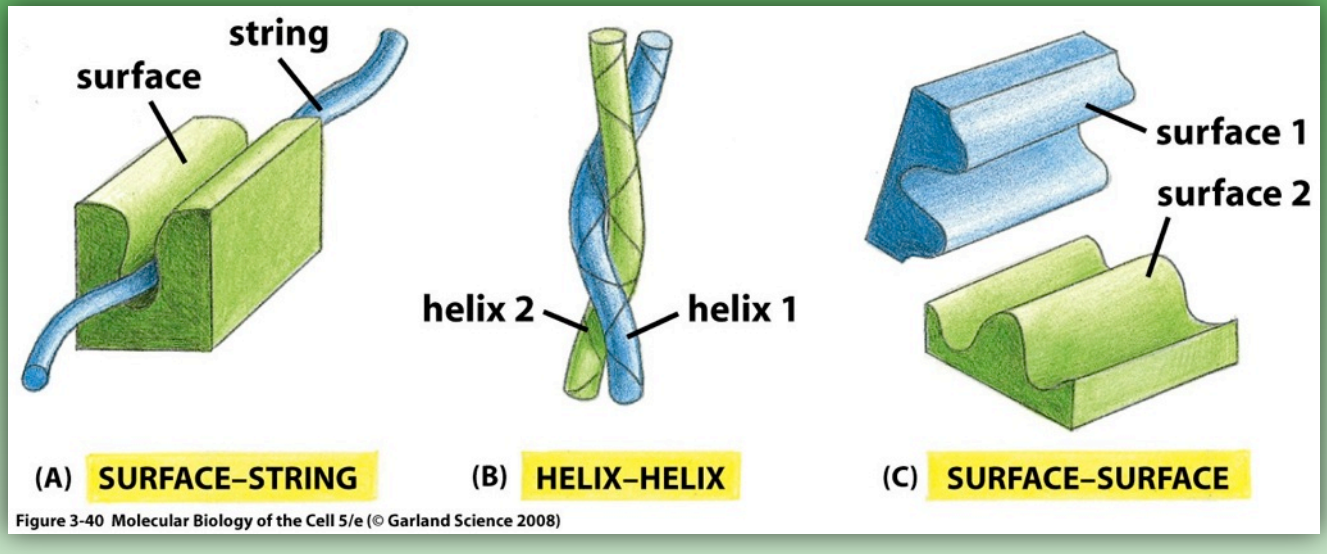


Figure 3-40 Molecular Biology of the Cell 5/e (© Garland Science 2008)