Triple-Helix

A special type of structural protein is *collagen.* This is a particularly rigid and inextensible material that is a major constituent of tendons and many connective tissues. Analysis of collagen amino acid sequences shows them to be characterized by a repetitious tripeptide sequence, Gly-*X*-proline or Gly-*X*-hydroxyproline, where *X* can be any amino acid and hydroxyproline is a hydroxylated derivative of proline. Owing to the repeating proline residue, collagen polypeptide chains cannot adopt either an α-helical or a β-sheet conformation. Instead, individual collagen polypeptide chains tend to assume a left-handed helical conformation in which successive side-chain groups point toward the corners of an equilateral triangle when viewed down the polypeptide chain axis ('end-on') (Fig. 4-32*a*). The glycine occurrence every three residues is strictly required because there is no space for any other amino acid residue inside the triple helix, where the glycine *R* groups (H) are located. Each collagen helix is already extended (Fig. 4-32*b*), so it cannot easily stretch further like the α-helix. In contrast to the α-helix, formation of a single-chain collagen helix *cannot* be accompanied by the formation of hydrogen bonds among residues *within* each polypeptide chain (see, e.g., Fig. 4-28*e* and *f*). Instead, three collagen helical chains associate in a three-stranded "cable" with hydrogen bonds *between* each chain and its two neighbors. This produces a highly interlocked fibrous structure that is especially suited to its biological role of providing rigid connections between muscles and bones, as well as structural reinforcement in the skin and connective tissue.

Although additional types of protein exist, attention has been here focused on three arrangements whose structural properties are currently best understood. Two of these, the α-keratins and the silks, incorporate polypeptide secondary structures that also occur often in globular proteins. In contrast, collagen is a protein that evolution has developed to play a special, structural role.

Ramachandran Plots

The three-dimensional structures of proteins, and especially the *regular secondary structures*, are readily specified by employing two dihedral angles, ϕ and ψ. The ψ angle defines the rotation of the carbonyl group around the $C^{\alpha}-C'$ bond, whereas the ϕ angle defines the rotation of the NH group around the $C^{\alpha}-N$ bond. A plot of ψ against ϕ is called a *Ramachandran plot*, two examples of which are given in Figure 4-33*a* and *b*. The Ramachandran maps graphically define the regions of allowed secondary structures. The points in Figure 4-33*b* represent specific values of the ϕ and ψ angles for which the potential energy of the corresponding conformation is *minimal*, and, therefore, they represent *stable* conformations.

Sulfhydryls and Disulfide Bonds in Glycinin

Because the native glycinin is not readily hydrolyzed by proteases, it is thought that the native conformation is a tightly folded one, which is presumably maintained by disulfide bonds because denatured glycinin does *not* renature in the presence of mercaptoethanol, or DTT, but does renature about 70% if these disulfide bond-breakers are not present. Free SH groups of ~1.1 mole/mole protein are exposed to solvent and 10.1 SS groups are not exposed. The total, however, is about 37 S—S bonds.

Denaturation of Glycinin by Urea or Guanidine Hydrochloride

8M urea or 6M guanidine hydrochloride completely dissociates the 11S complex of glycinin and causes denaturation. After removing the 8M urea, renaturation occurs to about 70% of the basic structure.

7S/11S Gelling Behavior: Heat Effects

At low ionic strength glycinin dissociates into subunits at about 70°–80°C (heating for 10 min), while at high ionic strengths dissociation into subunits occurs between 90°C and 100°C.

Gels can be formed containing both glycinin and conglycinin, and the most important role played in holding these gels together is that of *disulfide bonding* (irreversible gelling). Hydrophobic interactions seem to be less important in this case, and hydrogen bonding may be involved in reversible gelling of these soy proteins.

Wheat and Corn Proteins

In this section we first discuss the distribution of protein in cereals and in the various parts of the grain. For example, at natural moisture levels, the protein content of all the common cereals averages around 10%, although individual samples of particular cereals might contain as little as 6% or more than 20% (e.g., Table 4-4).

The protein is distributed nonuniformly among the morphological tissues of the grain, the highest concentrations occurring in the outermost, or subaleurone, part of the so-called "starch endosperm" and in the germ and the aleurone layer of the endosperm. The inner endosperm has a lower protein content than that of the whole grain, and there is very little protein in the pericarp.

By manual dissection of whole grains and microanalysis of the parts, the distribution of protein in wheat and in corn was obtained (see Table 4-5).

Classes of Cereal Proteins

Proteins in cereal endosperm have been classified structurally in numerous ways. None of these classifications is entirely satisfactory, but all have made some contribution to our knowledge of cereal proteins.

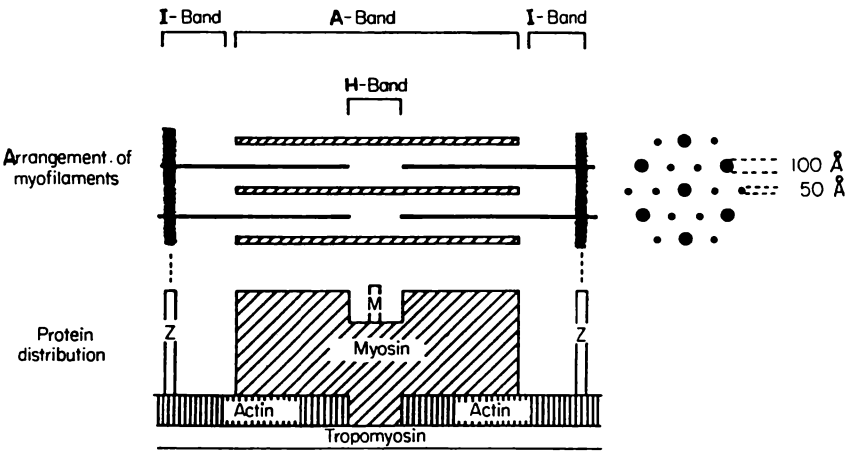

FIGURE 4-40. Schematic representation of the arrangement of myofibrillar proteins within the *I*-, *A*-, and *H*-bands in muscle based on electron micrographs of muscle structure such as those illustrated in Figure 4-39.

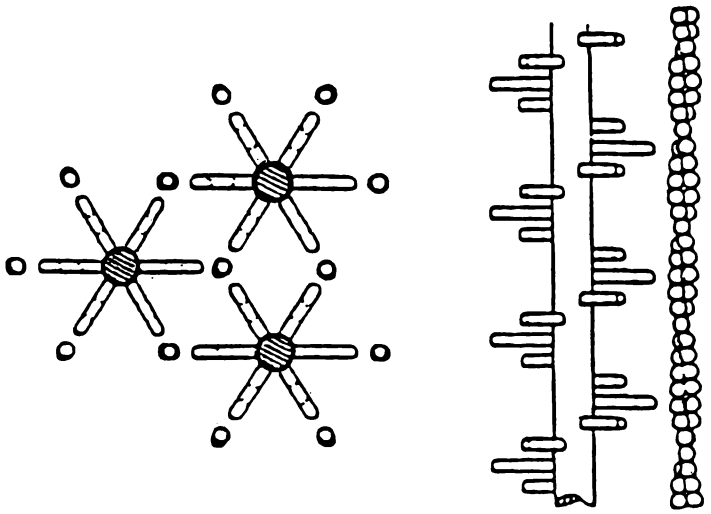

FIGURE 4-41. Diagram to show the structure of the actin (thin) and myosin (thick) filaments. Note (*left*) the alignment of one actin filament, opposite each row of feet, in cross section; (*right*) the double-stranded beaded structure of actin, the pitch of the spiral being about 350°; and the six staggered rows of "feet" on the myosin filament.

where h is the order in the series, C_h are coefficients that need to be determined, x is the lattice point at which $\rho(x)$ is to be calculated, a is the repeat distance in the lattice along one of the three axes of the unit cell, and ϕ_h is the phase angle, fixed by the value of this function at the chosen origin, $x = 0$.

An artificial, *one-dimensional* lattice with atoms distributed at regular intervals along a single line would give a one-dimensional X-ray diffraction pattern corresponding to the electron density in equation (5-2). The intensity of an X-ray reflection or diffraction spot is then found to be proportional to the square of the coefficients C_h in equation (5-2). The latter are therefore called *structure factors* and are denoted by F_h. The structure factor sums up the scattering effects of all the atoms in the unit cell, and could be calculated for a given structure by superimposing all the scattered beams from the various atoms with suitable phase differences. For the single one-dimensional case considered here

$$F_h = \sum_i F_i \cdot \cos 2\pi \left[\frac{hx_i}{a} + \phi_i(h) \right] \tag{5-3}$$

where i labels the particular coordinate x_i for which a term F_h is being evaluated, F_i is the scattering power of the atom i, and a is the repeat distance in the one-dimensional lattice. The phase angle ϕ_i is determined by the distance of the atom i from the point in the unit cell that was chosen as the origin ($x = 0$). An example of such a one-dimensional X-ray diffraction pattern from oriented erythrocyte membranes is presented in Figure 5-4, and is further analyzed in Chapter 17, Volume II of this book.

For a periodic three-dimensional lattice the structure repeats in three directions, **a**, **b**, and **c**, with repeat distances (unit cell dimensions), a, b, and c. In the latter case, the structure factors have a form similar to the simpler one-dimensional lattice previously considered (eq. (5-3)), except that three sets of indices, h, k, and l, are needed to specify the lattice planes. Thus, the structure factors of a crystal lattice are

$$F(h, k, l) = \sum_i F_i \cdot \cos 2\pi \left[\frac{hx_i}{a} + \frac{ky_i}{b} + \frac{lz_i}{c} + \phi(h, k, l) \right] \tag{5-4}$$

The electron-density distribution in the crystal lattice can then be expressed as

$$\rho(x, y, z) = \frac{1}{V_o} \sum_h \sum_k \sum_l F(h, k, l) \cdot \cos 2\pi \left[\frac{hx}{a} + \frac{ky}{b} + \frac{lz}{c} + \phi(h, k, l) \right] \tag{5-5}$$