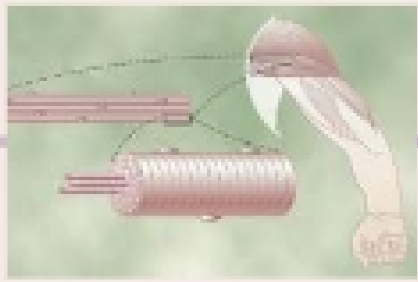

CHAPTER 6

UNIT II

Contraction of Skeletal Muscle

About 40% of the body is skeletal muscle, and perhaps another 10% is smooth and cardiac muscle. Some of the same basic principles of contraction apply to all these muscle types. In this chapter, we mainly consider skeletal muscle function; the specialized functions of smooth muscle are discussed in Chapter 8, and cardiac muscle is discussed in Chapter 9.

PHYSIOLOGICAL ANATOMY OF SKELETAL MUSCLE

Figure 6-1 shows that skeletal muscles are composed of numerous fibers ranging from 10 to 80 micrometers in diameter. Each of these fibers is made up of successively smaller subunits, also shown in Figure 6-1, and described in subsequent paragraphs.

In most skeletal muscles, each fiber extends the entire length of the muscle. Except for about 2% of the fibers, each fiber is usually innervated by only one nerve ending, located near the middle of the fiber.

The Sarcolemma Is a Thin Membrane Enclosing a Skeletal Muscle Fiber. The sarcolemma consists of a true cell membrane, called the plasma membrane, and an outer coat made up of a thin layer of polysaccharide material that contains numerous thin collagen fibrils. At each end of the muscle fiber, this surface layer of the sarcolemma fuses with a tendon fiber. The tendon fibers, in turn, collect into bundles to form the muscle tendons that then connect the muscles to the bones.

Myofibrils Are Composed of Actin and Myosin Filaments. Each muscle fiber contains several hundred to several thousand *myofibrils*, which are illustrated in the cross-sectional view of Figure 6-1*C*. Each myofibril (Figure 6-1*D* and *E*) is composed of about 1500 adjacent *myosin filaments* and 3000 *actin filaments*, which are large polymerized protein molecules that are responsible for the muscle contraction. These filaments can be seen in longitudinal view in the electron micrograph of Figure 6-2 and are represented diagrammatically in Figure 6-1*E* through *L*. The thick filaments in the diagrams are *myosin*, and the thin filaments are *actin*.

Note in Figure 6-1*E* that the myosin and actin filaments partially interdigitate and thus cause the myofibrils to have alternate light and dark bands, as illustrated in Figure 6-2. The light bands contain only actin filaments and are called *I bands* because they are *isotropic* to polarized light. The dark bands contain myosin filaments, as well as the ends of the actin filaments, where they overlap the myosin, and are called *A bands* because they are *anisotropic* to polarized light. Note also the small projections from the sides of the myosin filaments in Figure 6-1*E* and *L*. These projections are *cross-bridges*. It is the interaction between these cross-bridges and the actin filaments that causes contraction (Video 6-1).

Figure 6-1*E* also shows that the ends of the actin filaments are attached to a *Z disk*. From this disk, these filaments extend in both directions to interdigitate with the myosin filaments. The Z disk, which is composed of filamentous proteins different from the actin and myosin filaments, passes crosswise across the myofibril and also crosswise from myofibril to myofibril, attaching the myofibrils to one another all the way across the muscle fiber. Therefore, the entire muscle fiber has light and dark bands, as do the individual myofibrils. These bands give skeletal and cardiac muscle their striated appearance.

The portion of the myofibril (or of the whole muscle fiber) that lies between two successive Z disks is called a *sarcomere*. When the muscle fiber is contracted, as shown at the bottom of Figure 6-5, the length of the sarcomere is about 2 micrometers. At this length, the actin filaments completely overlap the myosin filaments, and the tips of the actin filaments are just beginning to overlap one another. As discussed later, at this length, the muscle is capable of generating its greatest force of contraction.

Titin Filamentous Molecules Keep the Myosin and Actin Filaments in Place. The side-by-side relationship between the myosin and actin filaments is maintained by a large number of filamentous molecules of a protein called *titin* (Figure 6-3). Each titin molecule has a molecular weight of about 3 million, which makes it one of the largest protein molecules in the body. Also, because it is filamentous, it is very *springy*. These springy titin molecules act as a framework that holds the myosin and actin filaments in place so that the contractile machinery of

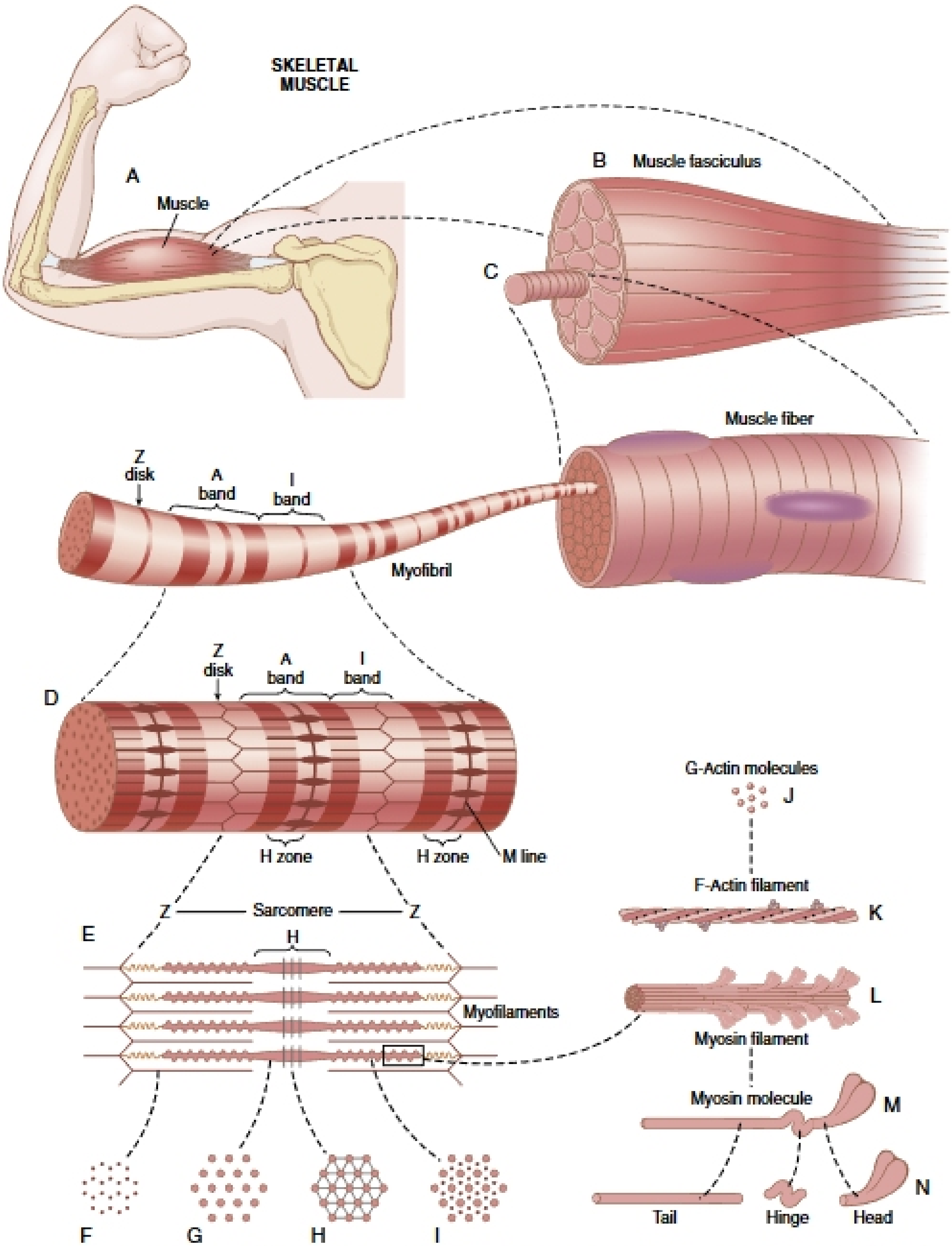

Figure 6-1 A–E, Organization of skeletal muscle, from the gross to the molecular level. F–I, Cross sections at the levels indicated.

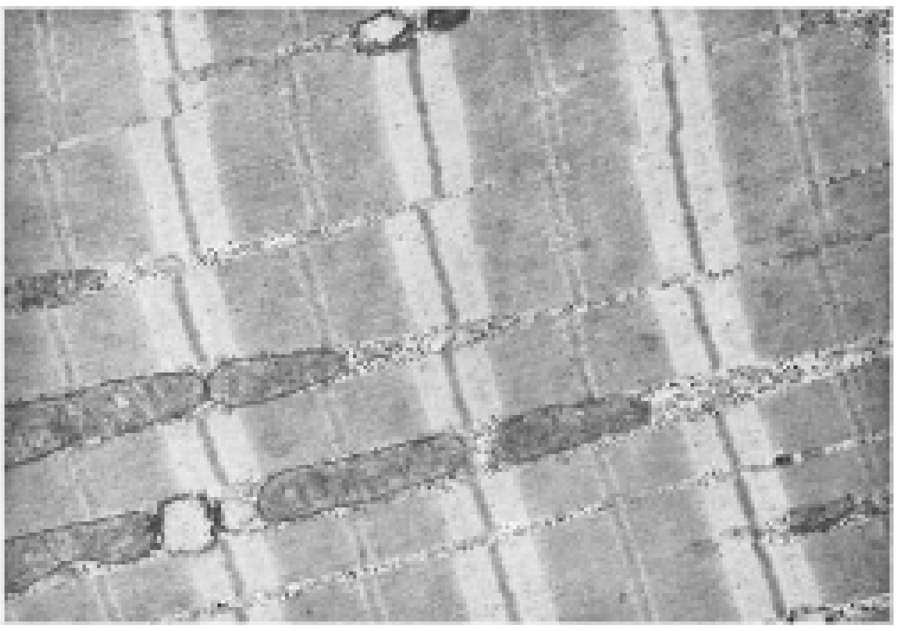

Figure 6-2 Electron micrograph of muscle myofibrils showing the detailed organization of actin and myosin filaments. Note the mitochondria lying between the myofibrils. *(From Fawcett DW: The Cell. Philadelphia: WB Saunders, 1981.)*

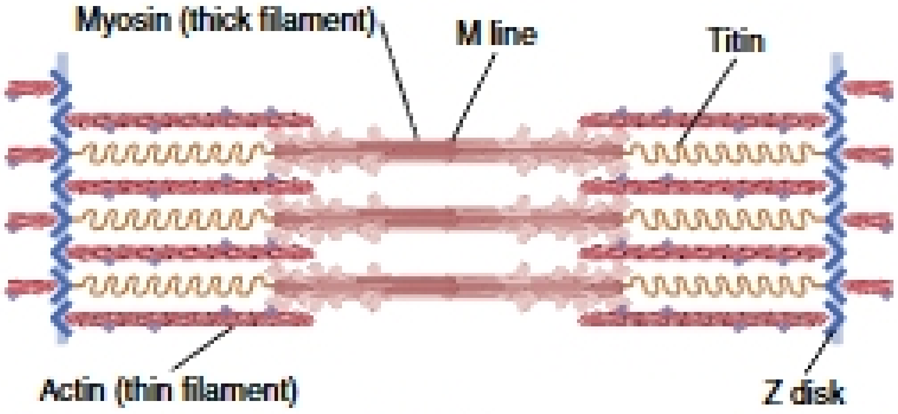

Figure 6-3 Organization of proteins in a sarcomere. Each titin molecule extends from the *Z disk* to the *M line*. Part of the titin molecule is closely associated with the myosin thick filament, whereas the rest of the molecule is springy and changes length as the sarcomere contracts and relaxes.

the sarcomere will work. One end of the titin molecule is elastic and is attached to the Z disk, acting as a spring and changing length as the sarcomere contracts and relaxes. The other part of the titin molecule tethers it to the myosin thick filament. The titin molecule may also act as a template for the initial formation of portions of the contractile filaments of the sarcomere, especially the myosin filaments.

Sarcoplasm Is the Intracellular Fluid Between Myofibrils. Many myofibrils are suspended side by side in each muscle fiber. The spaces between the myofibrils are filled with intracellular fluid called *sarcoplasm*, containing large quantities of potassium, magnesium, and phosphate, plus multiple protein enzymes. Also present are tremendous numbers of *mitochondria* that lie parallel to the myofibrils. These mitochondria supply the contracting myofibrils with large amounts of energy in the form of adenosine triphosphate (ATP) formed by the mitochondria.

Sarcoplasmic Reticulum Is a Specialized Endoplasmic Reticulum of Skeletal Muscle. Also, in the sarcoplasm surrounding the myofibrils of each muscle fiber, is an extensive reticulum (Figure 6-4), called the *sarcoplasmic reticulum*. This reticulum has a special organization that is extremely important in regulating calcium storage, release, reuptake and therefore muscle contraction, as discussed in Chapter 7. The rapidly contracting types of muscle fibers have especially extensive sarcoplasmic reticula.

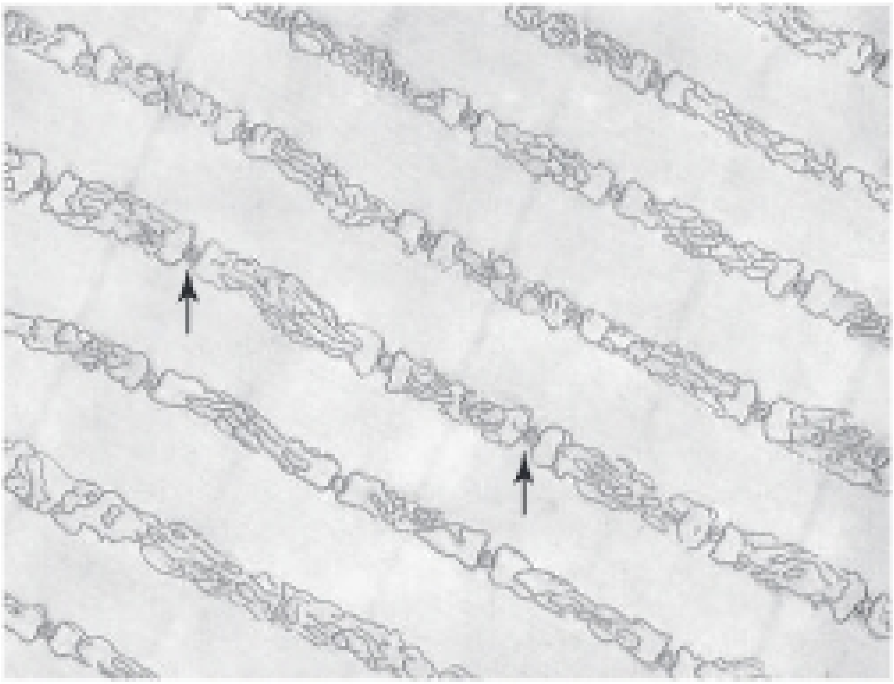

Figure 6-4 Sarcoplasmic reticulum in the spaces between the myofibrils, showing a longitudinal system paralleling the myofibrils. Also shown in cross section are T tubules (*arrows*) that lead to the exterior of the fiber membrane and are important for conducting the electrical signal into the center of the muscle fiber. *(From Fawcett DW: The Cell. Philadelphia: WB Saunders, 1981.)*

GENERAL MECHANISM OF MUSCLE CONTRACTION

The initiation and execution of muscle contraction occur in the following sequential steps.

1. An action potential travels along a motor nerve to its endings on muscle fibers.
2. At each ending, the nerve secretes a small amount of the neurotransmitter *acetylcholine*.
3. Acetylcholine acts on a local area of the muscle fiber membrane to open acetylcholine-gated cation channels through protein molecules floating in the membrane.
4. The opening of acetylcholine-gated channels allows large quantities of sodium ions to diffuse to the interior of the muscle fiber membrane. This action causes a local depolarization that in turn leads to the opening of voltage-gated sodium channels, which initiates an action potential at the membrane.
5. The action potential travels along the muscle fiber membrane in the same way that action potentials travel along nerve fiber membranes.
6. The action potential depolarizes the muscle membrane, and much of the action potential electricity flows through the center of the muscle fiber. Here it causes the sarcoplasmic reticulum to release large quantities of calcium ions that have been stored within this reticulum.