

Human body has more than 600 muscles. Muscles perform many useful functions and help us in doing everything in day-to-day life. Muscles are classified by three different methods, based on different factors:

- I. Depending upon the presence or absence of striations
- II. Depending upon the control
- III. Depending upon the situation.

■ DEPENDING UPON STRIATIONS

Depending upon the presence or absence of cross striations, the muscles are divided into two groups:

1. Striated muscle
2. Non-striated muscle.

1. Striated Muscle

Striated muscle is the muscle which has a large number of cross-striations (transverse lines). Skeletal muscle and cardiac muscle belong to this category.

2. Non-striated Muscle

Muscle which does not have cross-striations is called non-striated muscle. It is also called plain muscle or smooth muscle. It is found in the wall of the visceral organs.

■ DEPENDING UPON CONTROL

Depending upon control, the muscles are classified into two types:

1. Voluntary muscle
2. Involuntary muscle.

1. Voluntary Muscle

Voluntary muscle is the muscle that is controlled by the will. Skeletal muscles are the voluntary muscles. These muscles are innervated by somatic nerves.

2. Involuntary Muscle

Muscle that cannot be controlled by the will is called involuntary muscle. Cardiac muscle and smooth muscle are involuntary muscles. These muscles are innervated by autonomic nerves.

■ DEPENDING UPON SITUATION

Depending upon situation, the muscles are classified into three types:

1. Skeletal muscle
2. Cardiac muscle
3. Smooth muscle.

Features of these muscles are given in Table 28.1.

1. Skeletal Muscle

Skeletal muscle is situated in association with bones forming the skeletal system. The skeletal muscles form 40% to 50% of body mass and are voluntary and striated. These muscles are supplied by somatic nerves.

TABLE 28.1: Features of Skeletal, Cardiac and Smooth Muscles

Features	Skeletal muscle	Cardiac muscle	Smooth muscle
Location	In association with bones	In the heart	In the visceral organs
Shape	Cylindrical and unbranched	Branched	Spindle-shaped, unbranched
Length	1 cm to 4 cm	80 μ to 100 μ	50 μ to 200 μ
Diameter	10 μ to 100 μ	15 μ to 20 μ	2 μ to 5 μ
Number of nucleus	More than one	One	One
Cross-striations	Present	Present	Absent
Myofibrils	Present	Present	Absent
Sarcomere	Present	Present	Absent
Troponin	Present	Present	Absent
Sarcotubular system	Well developed	Well developed	Poorly developed
T tubules	Long and thin	Short and broad	Absent
Depolarization	Upon stimulation	Spontaneous	Spontaneous
Fatigue	Possible	Not possible	Not possible
Summation	Possible	Not possible	Possible
Tetanus	Possible	Not possible	Possible
Resting membrane potential	Stable	Stable	Unstable
For trigger of contraction, calcium binds with	Troponin	Troponin	Calmodulin
Source of calcium	Sarcoplasmic reticulum	Sarcoplasmic reticulum	Extracellular
Speed of contraction	Fast	Intermediate	Slow
Neuromuscular junction	Well defined	Not well defined	Not well defined
Action	Voluntary action	Involuntary action	Involuntary action
Control	Only neurogenic	Myogenic	Neurogenic and myogenic
Nerve supply	Somatic nerves	Autonomic nerves	Autonomic nerves

Fibers of the skeletal muscles are arranged in parallel. In most of the skeletal muscles, muscle fibers are attached to tendons on either end. Skeletal muscles are anchored to the bones by the tendons.

. Cardiac Muscle

Cardiac muscle forms the musculature of the heart. These muscles are striated and involuntary. Cardiac muscles are supplied by autonomic nerve fibers.

3. Smooth Muscle

Smooth muscle is situated in association with viscera. It is also called visceral muscle. It is different from skeletal and cardiac muscles because of the absence of cross-striations, hence the name smooth muscle. Smooth muscle is supplied by autonomic nerve fibers. Smooth muscles form the main contractile units of wall of the various visceral organs.

Structure of Skeletal Muscle

■ MUSCLE MASS

Muscle mass or muscle tissue is made up of a large number of individual muscle cells or myocytes. The muscle cells are commonly called muscle fibers because these cells are long and slender in appearance. Skeletal muscle fibers are multinucleated and are arranged parallel to one another with some connective tissue in between (Fig. 29.1).

Muscle mass is separated from the neighboring tissues by a thick fibrous tissue layer known as fascia. Beneath the fascia, muscle is covered by a connective tissue sheath called epimysium. In the muscle, the muscle fibers are arranged in various groups called bundles or fasciculi. Connective tissue sheath that covers each fasciculus is called perimysium. Each muscle fiber is covered by a connective tissue layer called the endomysium (Fig. 29.2).

■ MUSCLE FIBER

Each muscle cell or muscle fiber is cylindrical in shape. Average length of the fiber is 3 cm. It varies between 1 cm and 4 cm, depending upon the length of the muscle. The diameter of the muscle fiber varies from $10\ \mu$ to $100\ \mu$. The diameter varies in a single muscle.

Muscle fibers are attached to a tough cord of connective tissue called tendon. Tendon is in turn attached to the bone. Tendon of some muscles is thin, flat and stretched but tough. Such type of tendon is called aponeurosis.

Each muscle fiber is enclosed by a cell membrane called plasma membrane, that lies beneath the endomysium. It is also called sarcolemma (Fig. 29.3). Cytoplasm of the muscle is known as sarcoplasm.

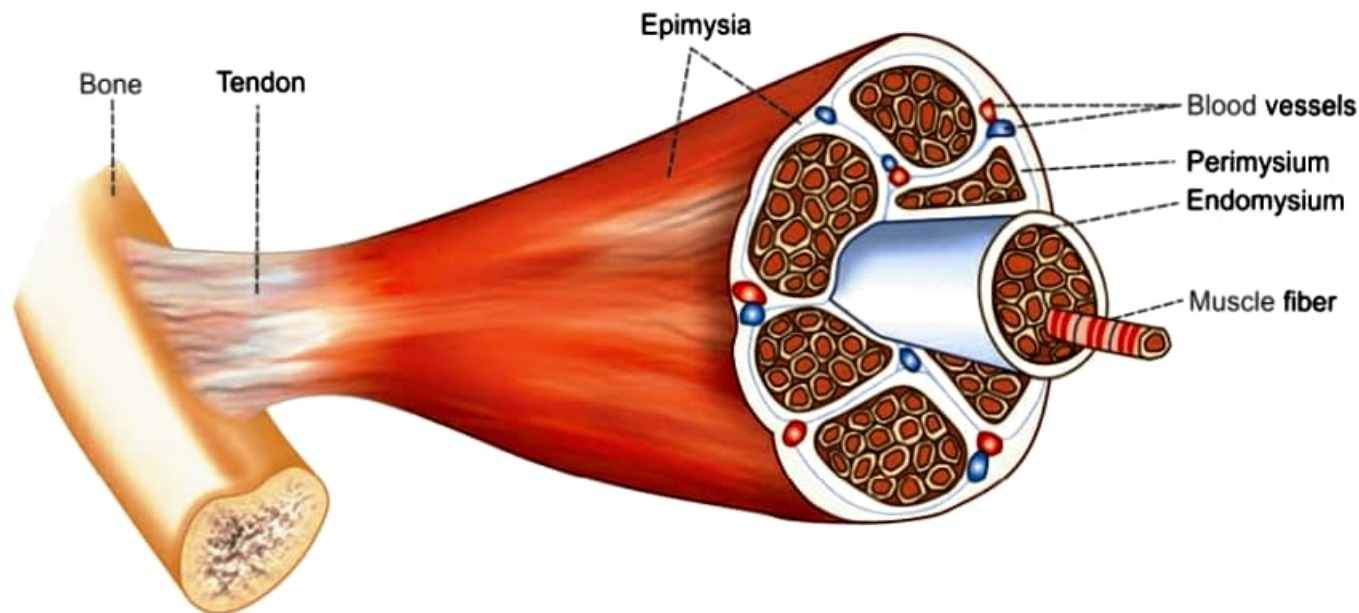


FIGURE 29.1: Structure of a skeletal muscle

Structures embedded within the sarcoplasm are:

1. Nuclei
2. Myofibril
3. Golgi apparatus
4. Mitochondria
5. Sarcoplasmic reticulum
6. Ribosomes
7. Glycogen droplets
8. Occasional lipid droplets.

Each muscle fiber has got one or more nuclei. In long muscle fibers, many nuclei are seen. Nuclei are oval or elongated and situated just beneath the sarcolemma. Usually in other cells, the nucleus is in the interior of the cell.

All the organelles of muscle fiber have the same functions as those of other cells.

■ MYOFIBRIL

Myofibrils or myofibrillae are the fine parallel filaments present in sarcoplasm of the muscle cell. Myofibrils run through the entire length of the muscle fiber.

In the cross-section of a muscle fiber, the myofibrils appear like small distinct dots within the sarcoplasm. Diameter of the myofibril is 0.2 to 2 μ . The length of a myofibril varies between 1 cm and 4 cm, depending upon the length of the muscle fiber (Table 29.1).

In some muscle fibers, some of the myofibrils are arranged in groups called Cohnheim's areas or fields.

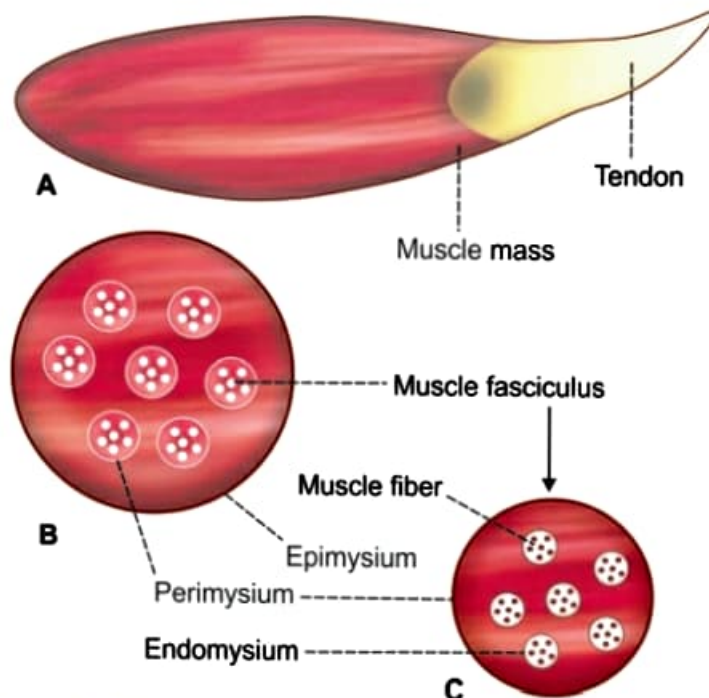


FIGURE 29.2: Diagram showing. A. Skeletal muscle mass; B. Cross-section of muscle; C. One muscle fasciculus.

■ MICROSCOPIC STRUCTURE OF A MYOFIBRIL

Light microscopic studies show that, each myofibril consists of a number of two alternating bands which are also called the sections, segments or disks. These bands are formed by muscle proteins.

The two bands are:

1. Light band or 'I' band.
2. Dark band or 'A' band.

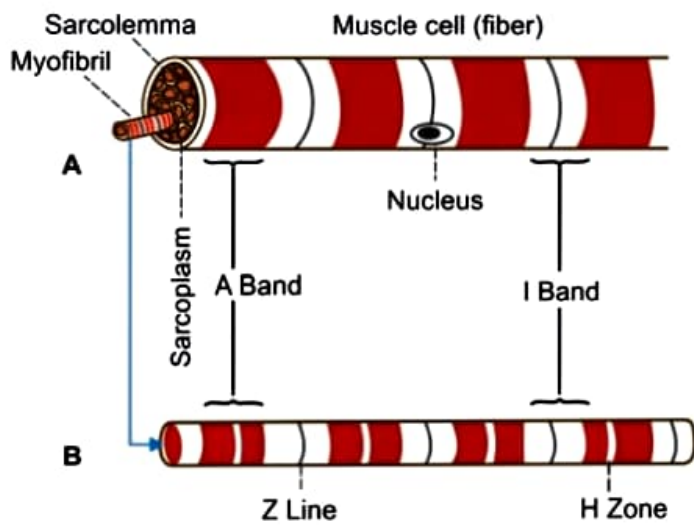


FIGURE 29.3: A. One muscle cell; B. One myofibril.

Light Band or 'I' Band

Light band is called 'I' (isotropic) band because it is isotropic to polarized light. When polarized light is passed through the muscle fiber at this area, light rays are refracted at the same angle.

Dark Band or 'A' Band

Dark band is called 'A' (anisotropic) band because it is anisotropic to polarized light. When polarized light is passed through the muscle fiber at this area, the light rays are refracted at different directions (An = not; iso = it; trop = turning). Dark band is also called 'Q' disk (Querscheibe = cross disk).

In an intact muscle fiber, 'I' band and 'A' band of the adjacent myofibrils are placed side-by-side. It gives the appearance of characteristic cross-striations in the muscle fiber.

I band is divided into two portions, by means of a narrow and dark line called 'Z' line or 'Z' disk (in German, zwischenscheibe = between disks). The 'Z' line is formed by a protein disk, which does not permit passage of light. The portion of myofibril in between two 'Z' lines is called sarcomere.

TABLE 29.1: Dimensions of structures in skeletal muscle

Structure	Length	Diameter
Muscle fiber	1 cm to 4 cm	10 μ to 100 μ
Myofibril	1 cm to 4 cm	0.2 μ to 2 μ
Actin filament	1 μ	20 \AA
Myosin filament	1.5 μ	115 \AA

SARCOMERE

Definition

Sarcomere is defined as the structural and functional unit of a skeletal muscle. It is also called the basic contractile unit of the muscle.

Extent

Each sarcomere extends between two 'Z' lines of myofibril. Thus, each myofibril contains many sarcomeres arranged in series throughout its length. When the muscle is in relaxed state, the average length of each sarcomere is 2 to 3 μ .

Components

Each myofibril consists of an alternate dark 'A' band and light 'I' band (Fig. 29.4). In the middle of 'A' band, there is a light area called 'H' zone (H = hell = light – in German. H = Henson – discoverer). In the middle of 'H' zone lies the middle part of myosin filament. This is called 'M' line (in German-mittel = middle). 'M' line is formed by myosin binding proteins.

ELECTRON MICROSCOPIC STUDY OF SARCOMERE

Electron microscopic studies reveal that the sarcomere consists of many thread-like structures called **myofilaments**.

Myofilaments are of two types:

1. Actin filaments
2. Myosin filaments.

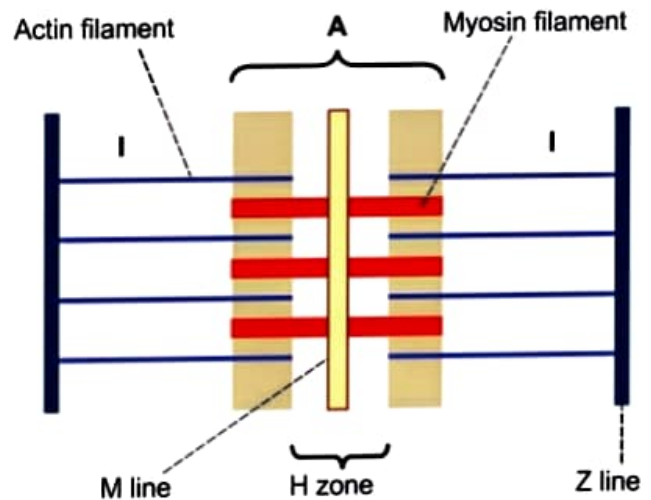


FIGURE 29.4: Sarcomere. A = A band, I = I band.

Actin Filaments

Actin filaments are the thin filaments with a diameter of 20 Å and a length of 1 μ. These filaments extend from either side of the 'Z' lines, run across 'I' band and enter into 'A' band up to 'H' zone.

Myosin Filaments

Myosin filaments are thick filaments with a diameter of 115 Å and a length of 1.5 μ. These filaments are situated in 'A' band.

Cross-bridges

Some lateral processes (projections) called cross-bridges arise from each myosin filament. These bridges have enlarged structures called myosin heads at their tips. Myosin heads attach themselves to actin filaments. These heads pull the actin filaments during contraction of the muscle, by means of a mechanism called sliding mechanism or ratchet mechanism.

During the contraction of the muscle, the actin filaments glide down between the myosin filaments towards the center of 'H' zone and approach the corresponding actin filaments from the next 'Z' line (Fig. 29.5). The 'Z' lines also approach the ends of myosin

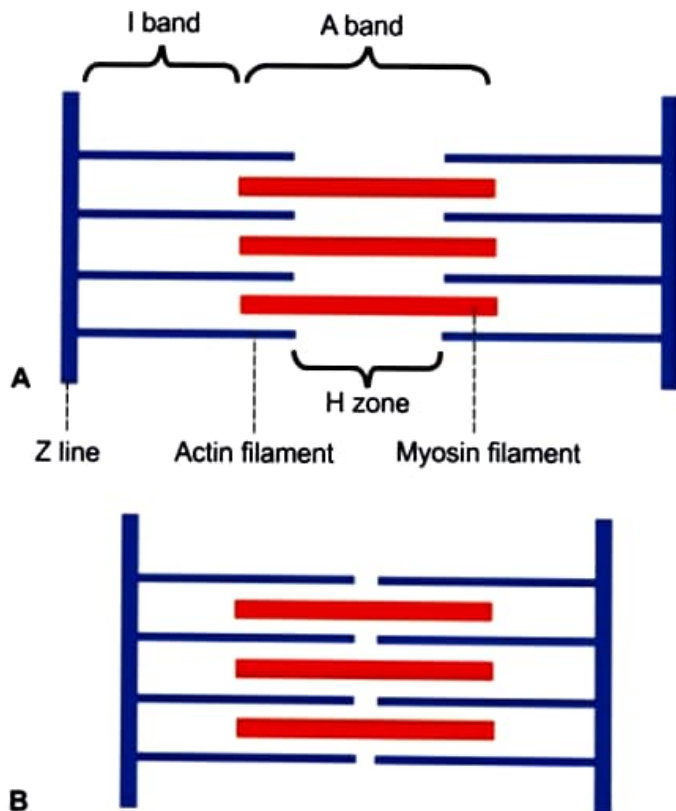


FIGURE 29.5: Sarcomere in resting muscle A. Contracted muscle; B. During contraction; Z lines come close, H zone and I band are reduced and no change in A band.

filaments, so that the 'H' zone and 'I' bands are shortened during contraction of the muscle. During the relaxation of the muscle, the actin filaments and 'Z' lines come back to the original position.

CONTRACTILE ELEMENTS (PROTEINS) OF MUSCLE

Myosin filaments are formed by myosin molecules. Actin filaments are formed by three types of proteins called actin, tropomyosin and troponin. These four proteins together constitute the contractile proteins or the contractile elements of the muscle.

MYOSIN MOLECULE

Each myosin filament consists of about 200 myosin molecules. Though about 18 classes of myosin are identified, only myosin II is present in the sarcomere.

Myosin II is a globulin with a molecular weight of 480,000. Each myosin molecule is made up of 6 polypeptide chains, of which two are heavy chains and four are light chains (Fig. 29.5). Molecular weight of each heavy chain is 200,000 ($2 \times 200,000 = 400,000$). Molecular weight of each light chain is 20,000 ($4 \times 20,000 = 80,000$). Thus, total molecular weight of each myosin molecule is 480,000 ($400,000 + 80,000$).

Portions of Myosin Molecule

Each myosin molecule has two portions:

1. Tail portion
2. Head portion.

Tail portion of myosin molecule

It is made up of two heavy chains, which twist around each other in the form of a double helix (Fig. 29.6).

Head portion of myosin molecule

At one end of the double helix, both the heavy chains turn away in opposite directions and form the globular head portion. Thus the head portion has two parts. Two light chains are attached to each part of the head portion of myosin molecule (Fig. 29.6).

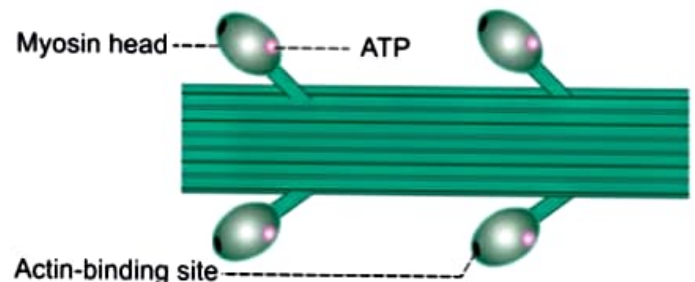


FIGURE 29.6: Diagram showing myosin filament. ATP = Adenosine triphosphate.

Each myosin head has two attachment sites. One site is for actin filament and the other one is for one ATP molecule (Fig. 29.7). Myosin head is absent in the central part of myosin filament, i.e. in the 'H' zone.

■ ACTIN MOLECULE

Actin molecules are the major constituents of the thin actin filaments. Each actin molecule is called F-actin and it is the polymer of a small protein known as G-actin. There are about 300 to 400 actin molecules in each actin filament. The molecular weight of each molecule is 42,000. The actin molecules in the actin filament are also arranged in the form of a double helix.

Each F-actin molecule has an active site to which the myosin head is attached (Fig. 29.8).

■ TROPOMYOSIN

About 40 to 60 tropomyosin molecules are situated along the double helix strand of actin filament. Each tropomyosin molecule has the molecular weight of 70,000. In relaxed condition of the muscle, the tropomyosin molecules cover all the active sites of F-actin molecules.

■ TROPONIN

It is formed by three subunits:

1. Troponin I, which is attached to F-actin
2. Troponin T, which is attached to tropomyosin
3. Troponin C, which is attached to calcium ions.

■ OTHER PROTEINS OF THE MUSCLE

In addition to the contractile proteins, the sarcomere contains several other proteins such as:

1. Actinin, which attaches actin filament to 'Z' line.
2. Desmin, which binds 'Z' line with sarcolemma.
3. Nebulin, which runs in close association with and parallel to actin filaments.
4. Titin, a large protein connecting 'M' line and 'Z' line. Each titin molecule forms scaffolding (framework) for sarcomere and provides elasticity to the muscle.

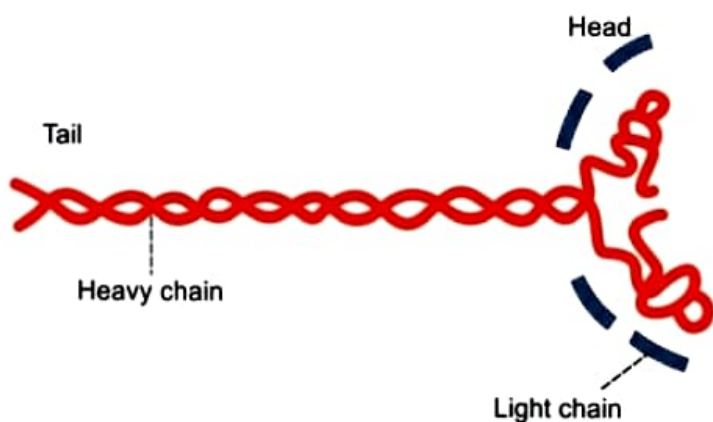


FIGURE 29.7: Myosin molecule formed by two heavy chains and four light chains of polypeptides

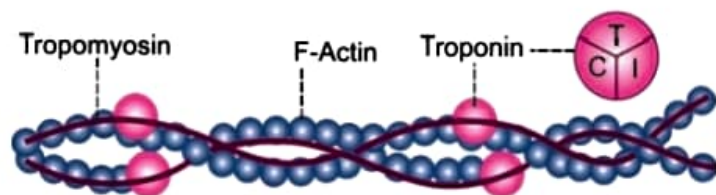


FIGURE 29.8: Part of actin filament. Troponin has three subunits, T, C and I.

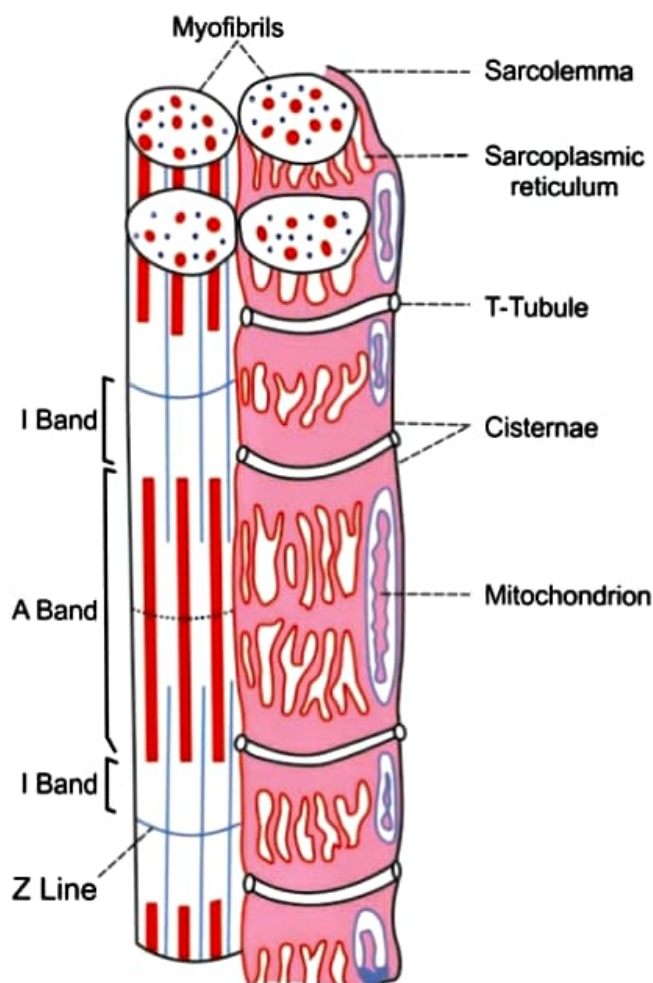


FIGURE 29.9: Diagram showing the relation between sarcolemma and parts of sarcomere. Only few myofibrils are shown in the myofibril drawn on the right side of the diagram.

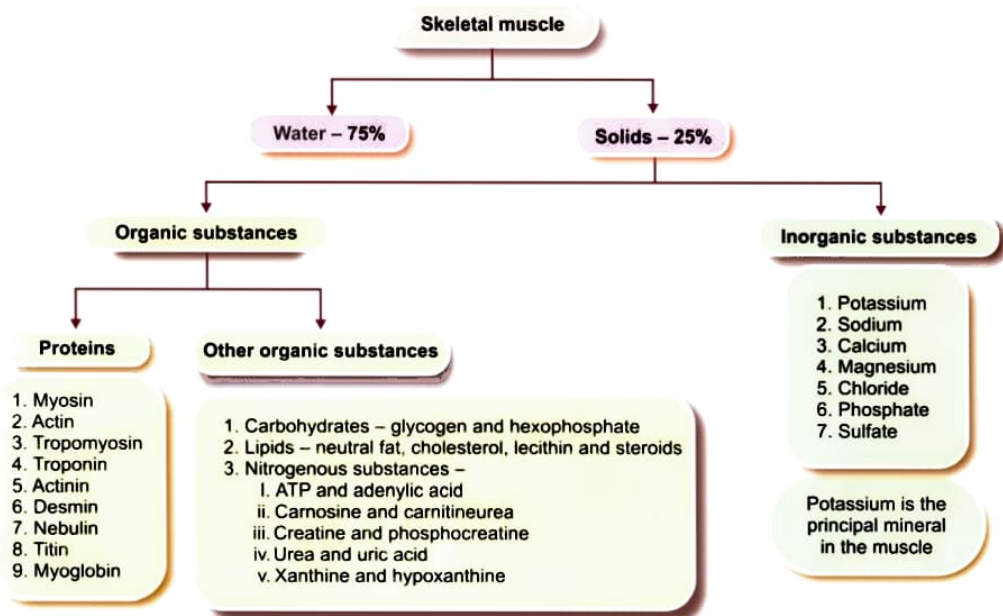


FIGURE 29.10: Composition of skeletal muscle

When the muscle is stretched, the **titin** unfolds itself. However, if the stretching is more, it offers resistance and protects the sarcomere from overstretching.

5. **Dystrophin**, a rod-shaped large protein that connects actin filament to dystroglycan. Dystroglycan is a transmembrane protein, present in the sarcolemma. Dystrophin and dystroglycan form dystrophin-dystroglycan or dystrophin-glycoprotein complex.

■ SARCOTUBULAR SYSTEM

Sarcotubular system is a system of membranous structures in the form of vesicles and tubules in the sarcoplasm of the muscle fiber. It surrounds the myofibrils embedded in the sarcoplasm (Fig. 29.9).

■ STRUCTURES CONSTITUTING THE SARCOTUBULAR SYSTEM

Sarcotubular system is formed mainly by two types of structures:

1. T-tubules
2. L-tubules or sarcoplasmic reticulum.

T-Tubules

T-tubules or transverse tubules are narrow tubules formed by the invagination of the sarcolemma. These tubules penetrate all the way from one side of the muscle fiber to another side. That is, these tubules penetrate the muscle cell through and through. Because of their origin from sarcolemma, the T-tubules open to the exterior of the muscle cell. Therefore, the ECF runs through their lumen.

L-Tubules or Sarcoplasmic Reticulum

L-tubules or longitudinal tubules are the closed tubules that run in long axis of the muscle fiber, forming sarcoplasmic reticulum. These tubules form a closed tubular system around each myofibril and do not open to exterior like T-tubules.

L-tubules correspond to the endoplasmic reticulum of other cells. At regular intervals, throughout the length of the myofibrils, the L-tubules dilate to form a pair of lateral sacs called terminal cisternae. Each pair of terminal cisternae is in close contact with T-tubule. The T-tubule along with the cisternae on either side is called the triad of skeletal muscle.

In human skeletal muscle, the triads are situated at the junction between 'A' band and 'I' band. Calcium ions are stored in L-tubule and the amount of calcium ions is more in cisternae.

■ FUNCTIONS OF SARCOTUBULAR SYSTEM

Function of T-Tubules

T-tubules are responsible for rapid transmission of impulse in the form of action potential from sarcolemma to the myofibrils. When muscle is stimulated, the action potential develops in sarcolemma and spreads through it. Since T-tubules are the continuation of sarcolemma, the action potential passes through them and reaches the interior of the muscle fiber rapidly.

Function of L-Tubules

L-tubules store a large quantity of calcium ions. When action potential reaches the cisternae of L-tubule, the calcium ions are released into the sarcoplasm. Calcium ions trigger the processes involved in contraction of the muscle. The process by which the calcium ions cause contraction of muscle is called excitation-contraction coupling (Chapter 31).

■ COMPOSITION OF MUSCLE

Skeletal muscle is formed by 75% of water and 25% of solids. Solids are 20% of proteins and 5% of organic substances other than proteins and inorganic substances (Fig. 29.10).

Among the proteins, the first eight proteins are already described in this chapter. Myoglobin is present in sarcoplasm. It is also called myohemoglobin. Its function is similar to that of hemoglobin, that is, to carry oxygen. It is a conjugated protein with a molecular weight of 17,000.

HISTOLOGICAL STRUCTURE

The skeletal muscle fibers are cylindrical in shape. These elongated cells have multiple nuclei. In the bulk, the extent of the muscle fibers may be from:

- One end to the other
- One end to somewhere at midway
- Both the ends within the muscle having no attachments with either side.

The length of the muscle fibers varies from 1.0 to 40 mm. The breadth varies from 0.01 to 0.1 mm. Albeit, the fiber size varies within the same muscle, yet there is some association between the thickness and size of the fibers and the amount of work to be done by the muscle. The thickness of the muscle fibers depends greatly on the nourishment of the individual. With the help of the regular exercise, total fiber volume increases along with the improvement of blood supply. The fiber number remains constant.

Sarcolemma

The transparent cell membrane of the muscle fiber is called as sarcolemma. With the help of electron micrography, it is observed that it is made up of plasmalemma and an extrinsic coat of amorphous material (similar to basement membrane). This amorphous layer is pierced and encircled by reticular fibers. The plasmalemma consists of two protein layers enclosing a lipid one having a thickness of 100A. Inside the plasmalemma, elongated multiple nuclei and transversely striated myofibrils are embedded in the sarcoplasm.

Sarcoplasm

The sarcoplasm contains numerous mitochondria, a small Golgi apparatus near each nucleus, myoglobin (protein pigment), lipid,

glycogen, sarcoplasmic reticulum, etc. The muscle fibers that are richer in sarcoplasm are darker in color and vice versa.

Mitochondria

They are the major noncontractile components of muscle fibers. The mitochondria are found in two sites, i.e. (i) subsarcolemmal and (ii) intermyofibrillar sites. The subsarcolemmal site accumulates within oxidative (type I and IIA) fibers and a high concentration is often adjusted to a capillary in oxidative fibers. The mitochondrial volume can be changed quickly in response to altered activity levels. This again reflects the adaptability of the fiber to maximize its use of space in response to the physical activity.

Nuclei

A muscle fiber is multinucleated. They are oval- or elongated-shaped and situated just beneath sarcolemma. Because of its multinucleated condition, the muscle fiber is divided into a mosaic of overlapping regions or domains, each controlled by a nucleus. Within the domain, the nucleus controls the structural proteins. During postnatal development, muscle growth is rapid. More nuclei must be added to accommodate the increased fiber size at that time. When the incorporation of additional nuclei is inhibited, growth stunts (Rosenblatt et al. 1994). When nuclear distribution is measured, slow twitch (type I) fibers generally contain more nuclei than the fast twitch (type II) fibers. However, the volume per nucleus is higher in fast type than slow type fibers.

Myofibrils

These are the fine parallel filaments presents in sarcoplasm of the muscle fibers. The myofibrils extent through the entire length of the muscle fiber. Depending upon the length of the muscle fiber, the length of a myofibril varies from 1 to 4 cm with the diameter ranges from 0.2 to 2 microns. Studying the cross-section of a muscle fiber, it is found that the myofibrils are separated from one another by the sarcoplasm. Sometimes, some of the myofibrils are arranged in groups. These groups of myofibrils are known as Cohnheim's areas or fields.

Under the light microscope, it is found that myofibrils have alternate light and dark shades (transverse striations) and thick longitudinal strands. Electron micrography reveals that the longitudinal striation is due to the presence of the myofibrils of

different thickness and transverse striation for the presence of alternate light and dark segments of longitudinally arranged elements.

Under polarized microscope, the dark band is anisotropic, hence the name A-band (sometimes called Q-band). The light band is isotropic hence the name I band (sometimes called J-band). This I-band is bisected at the midpoint by a thin darkly-stained line called as Z-line (sometimes called Dobie's line). It is also called as Krause's membrane. The portion of myofibril in between two Z-lines (in German, *Zwischenscheibe* = between disk) is called sarcomere. In certain exceptional preparations, central portion of the A- band is paler in color, called H-band (Hensen's line). At the midpoint of the H-band, there is a narrow dark line – the M-line or M-band. Myosin filaments are thickened here. At the peripheral dark portion of A-band where the myosin and actin filaments are overlapped, the portion is called O-band. A comparatively darker, thin, transverse line, called N-line, is found somewhere in the mid region of the I-band on the both the sides of the Z-line.