CHAPTER 2

Basic Anatomy and Muscle Biology

INTRODUCTION

THE anatomical structure of the major meat-producing poultry and the four major tissues composing the carcass (i.e., muscle, epithelial, nervous and connective tissues) will be described in this chapter. Greater emphasis will be given to the muscle tissue component, because it represents the major edible part important to processors and consumers.

The mechanism of muscle contraction is also described as a basis for understanding post-slaughter changes (e.g., onset of rigor mortis, pH decline) that are known to affect meat quality. The biochemical differences between red and white muscle fibers related to quality attributes of the so-called white and dark poultry meat are highlighted. Overall, this chapter serves as an introduction to the structure of poultry and to meat science as they relate to meat quality.

STRUCTURE OF MEAT-PRODUCING POULTRY

Figure 2.1 shows the overall structure of a chicken, which is fairly typical of avian species; the proportion and size of certain body parts vary depending on a specific bird's living environment. In the case of a chicken, the legs are fairly developed because chickens usually live in open spaces and forests where walking and standing represent a major activity. The wings are fairly developed in the wild ancestors of the domesticated chicken and serve for fast escaping from predators and relatively short flights. The breast muscles that support the wings are also fairly developed. However, today's meat-type birds are selected for heavy musculature, especially breast muscles, and are much heavier than their ancestors. A more extreme case is the domesticated turkey (Figure 2.2) which, due to intense selection for heavy musculature, is an almost flightless bird. The legs and toes are structured to allow walking and perching on branches in the case of chickens and turkeys. In the case of ducks (Figure 2.3), the feet are adapted to swimming and have webbing between the

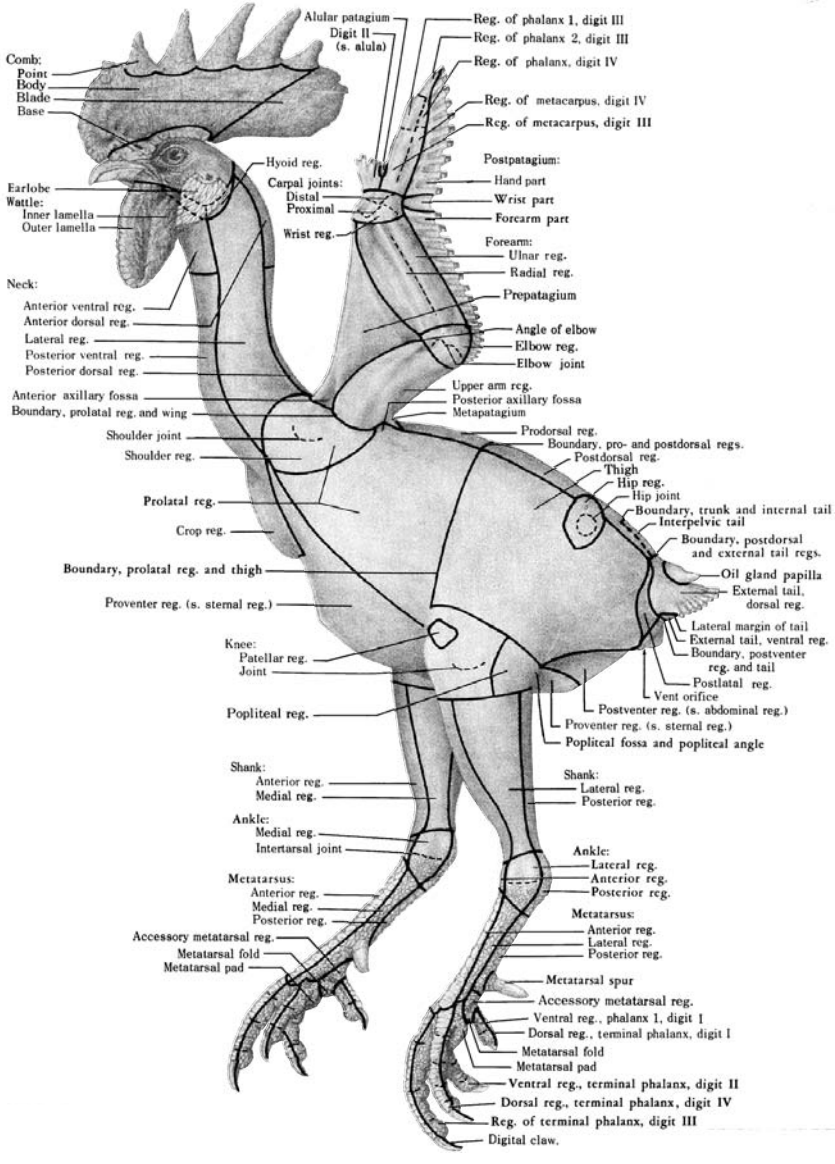

Figure 2.1. *Left Lateral View of the Chicken Showing the Different Regions. Abbreviations: Reg(s)., Region(s); s., Synonym. From Lucas and Stettenhiem (1972).*

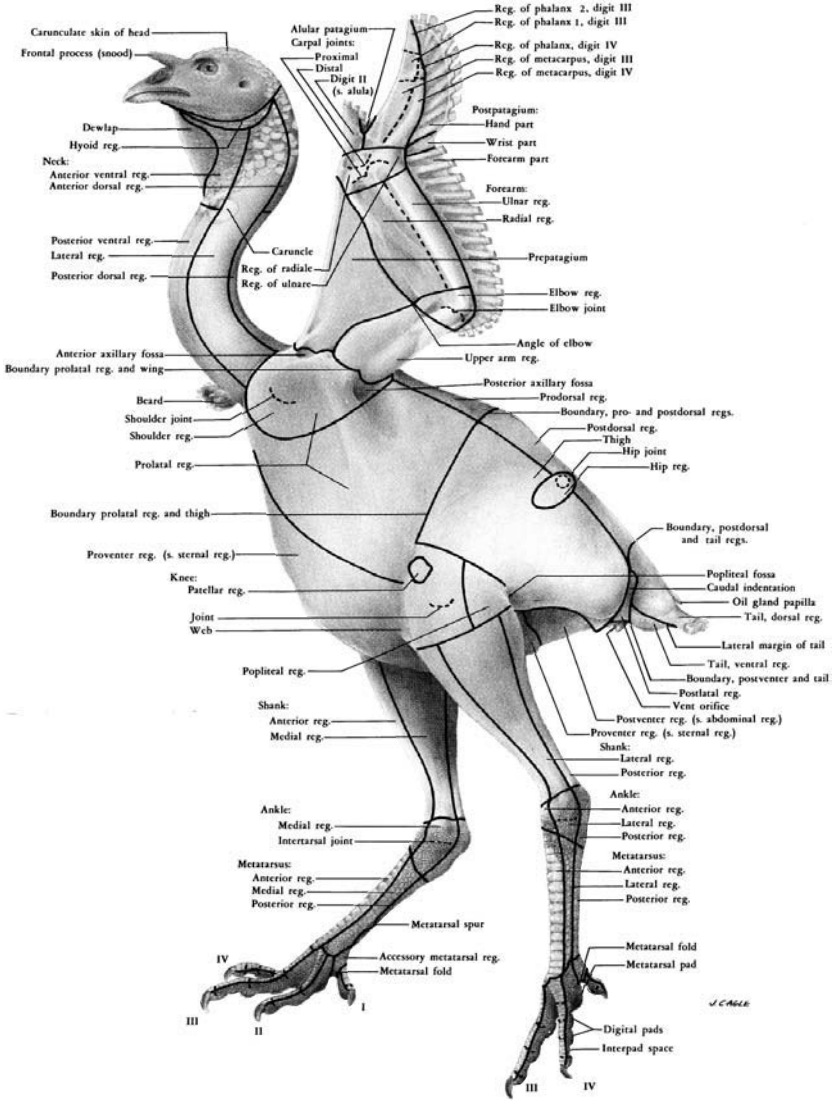

Figure 2.2. *Lateral View of a Turkey Showing the Different Regions. Abbreviations: Reg(s)., Region(s); s., Synonym. From Lucas and Stettenhiem (1972).*

toes, which serves as paddles during swimming. The feet are relatively short compared to turkey feet. The beak has also evolved to fit a marsh-type environment where a wider beak allows for the straining of water and for catching small fish and frogs. In the case of the pigeon (Figure 2.4), large wings in relation to the body size are used for long distance flying and gliding. The

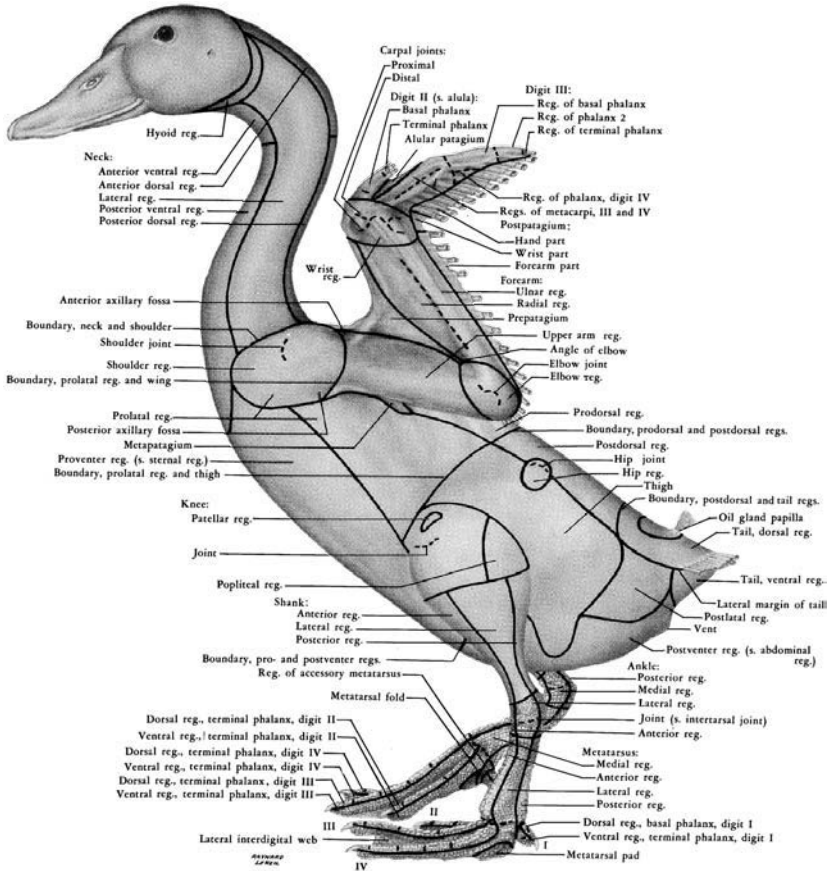

Figure 2.3. *Lateral View of the White Peking Duck Showing the Different Regions. Abbreviations: mar., Margin; Reg(s)., Region(s); s., Synonym. From Lucas and Stettenhiem (1972).*

overall structure of the wing bones resembles the basic structure found in mammals; however, major evolutionary modifications have occurred to allow the bird to fly.

MUSCLE TISSUE

Muscle tissue is considered most important in terms of poultry meat further processing and will be described in detail below. The so-called white and dark muscle/meat in chickens and turkeys (i.e., the most commonly consumed poultry; see Chapter 1) represents the major edible parts of breast and

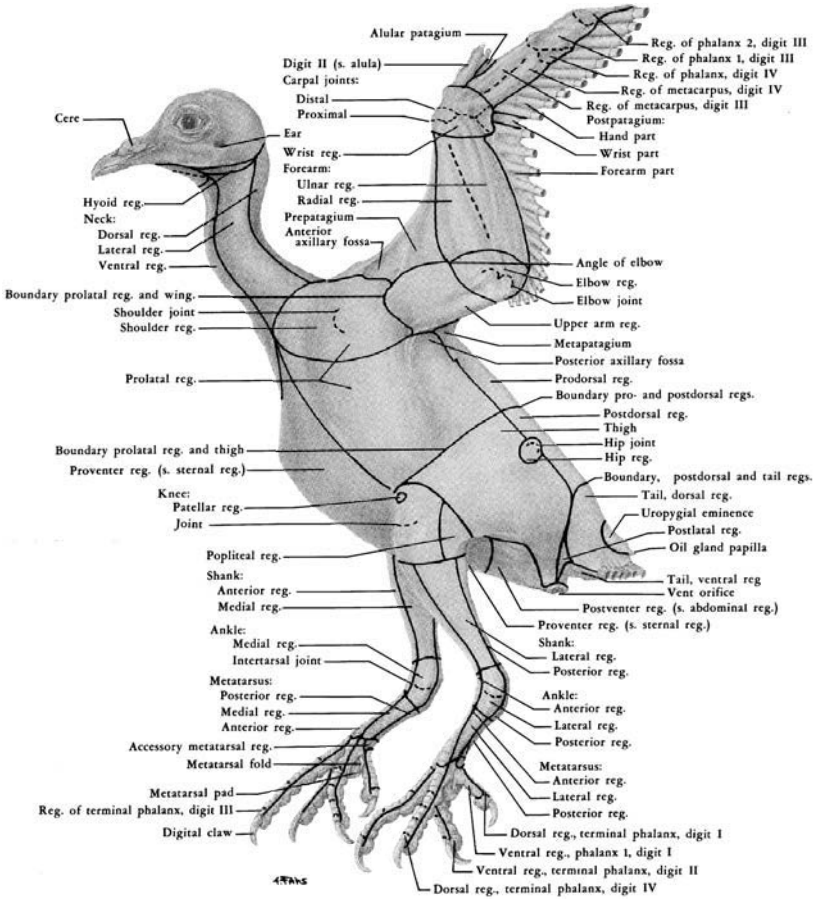

Figure 2.4. *Lateral View of the Common Pigeon Showing the Different Regions. Abbreviations: Reg(s)., Region(s); s., Synonym. From Lucas and Stettenhiem (1972).*

leg meat, respectively. However, in ducks, the breast meat appears red due to its high myoglobin content, as will be discussed later in the chapter. Regardless of bird type, a high yield of lean meat is sought by producers and processors.

In the live animal, muscles are used for various functions. The shape and structure of each muscle is designed to allow for the performance of a specific task. Muscle functions can range from locomotion (walking, flying) to pumping (heart muscle for circulating blood) and moving food along the guts by the involuntary muscles used in the digestive system. These three major activities are related to the three types of muscles found in the body: skeletal (movement), cardiac (pumping blood) and smooth muscle (involuntary activities).

Skeletal Muscle

The skeletal muscle is considered to be mostly a voluntary-type muscle, meaning that the animal has full or a certain degree of control over its activity. An overview of the major skeletal muscles in poultry is shown in Figure 2.5. The muscles range from very large muscles such as the breast muscle *(pectoralis major)* to very small muscles such as the ones controlling eye movement.

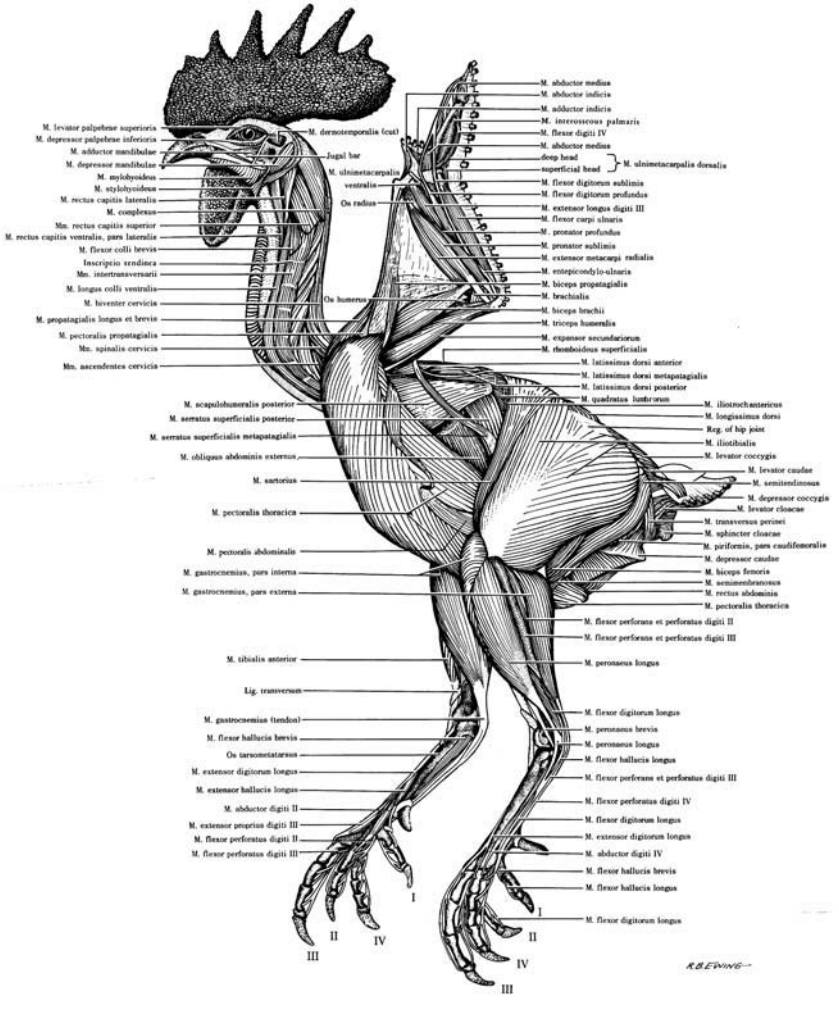

Figure 2.5. *Lateral View of the Superficial Musculature of a Single Comb White Leghorn Chicken. Abbreviations: Lig., Ligamentum; M(m)., Musculus(i); Reg., Region. From Lucas and Stettenhiem (1972).*

The skeletal muscles are also known as striated muscles because of the striated appearance they possess when stained and viewed under a light microscope. This appearance is the result of repetitive microstructure of the fibers and their components.

Figure 2.6 shows a schematic diagram of the muscle structure and its components. A large muscle such as the *biceps femoris* is composed of numerous

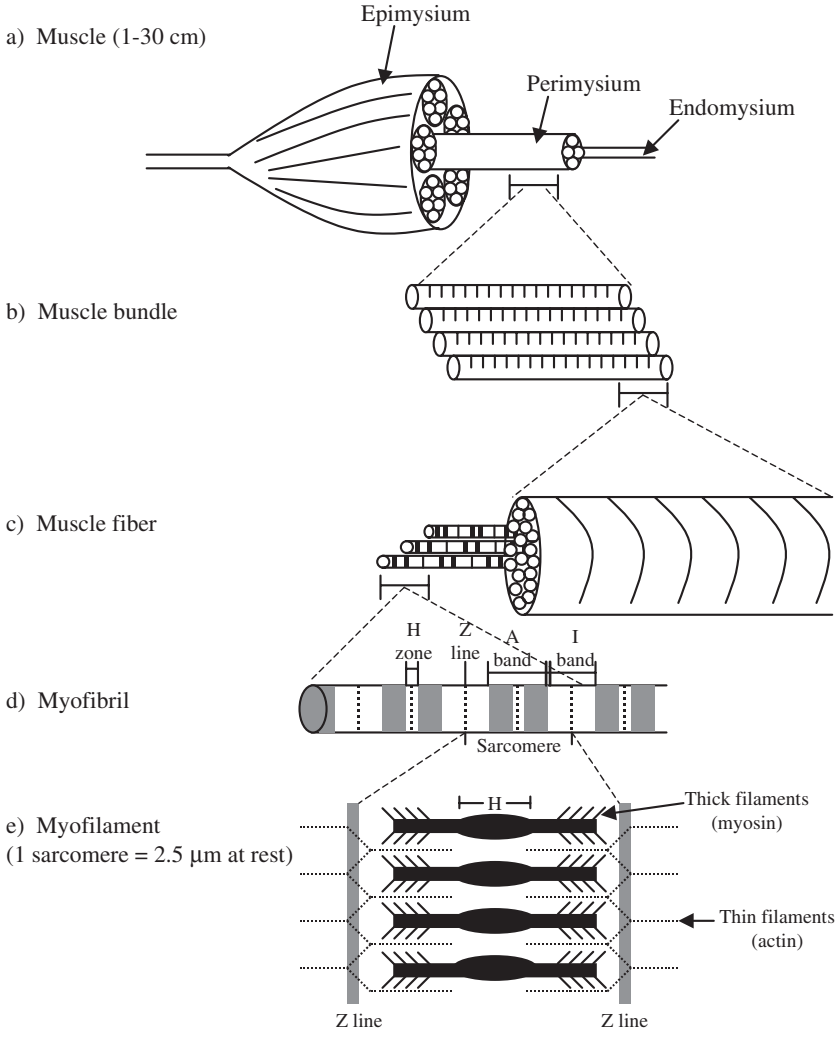

Figure 2.6. *Schematic Diagram Showing the Muscle Structure, Starting from a Cross Section of a Whole Muscle (a), Including the Different Layers of Connective Tissue, Going Down to the Muscle Bundle (b), Fiber (c), Myofibril (d) and Myofilaments (e). Please Note the Scale (1 meter = 100 centimeters = 1,000 millimeters = 10^6 microns = 10^9 nanometers = 10^{10} angstroms).*

muscle bundles covered by *epimysium* [Figure 2.6(a)]. Each muscle bundle [Figure 2.6(b)] is separated from the others by a connective tissue called *perimysium*. The connective tissue is important in providing structural organization, anchoring the different components and transmitting the power generated by contraction of the small muscle units called the sarcomeres. (Note: additional discussion on the various types of connective tissue is found later in the chapter.) Blood vessels are also seen in a cross section of the muscle, as well as groups of nerves that are reaching the muscle fibers and controlling their contraction. The individual nerves are usually not visible by the naked eye, but some large white/silvery nerve trunks can be seen. The muscle bundle is composed of smaller muscle fibers [Figure 2.6(c)] that are covered by a thinner layer of connective tissue called *endomysium*. Each fiber consists of numerous myofibrils [Figure 2.6(d)] that have myofilaments inside of them. The myofibril's striated appearance is the result of the repetitive structure of overlapping thin and thick filaments. The dark area in a stained muscle preparation [Figure 2.6(d)] is the result of thin and thick filaments overlapping and is called the A-band. The A-band also consists of an area where no thin filaments are present and, therefore, it is slightly lighter and is called the H-zone [Figure 2.6(e)]. During muscle contraction, the thick filaments slide toward the Z-line and, by doing so, shorten the overall length of the sarcomere and cause movement; a detailed discussion on muscle contraction is found below.

Cardiac Muscle

The cardiac muscle cell has a striated appearance like a skeletal muscle, but it has one (and sometimes two) nucleus per cell, whereas a striated muscle cell has numerous nuclei (Figure 2.7). The average length of the cell is

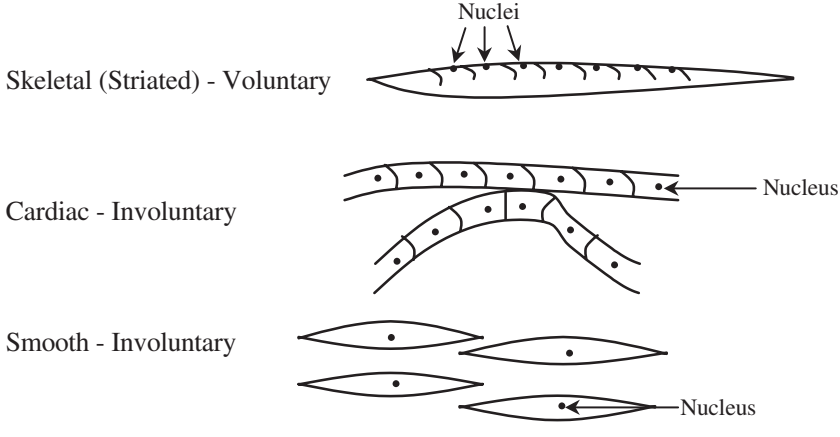

Figure 2.7. *Skeletal (Single Cell), Cardiac and Smooth Muscle Cells.*

about 50–100 μm, and its width is about 15 μm. The cardiac muscle has a unique rhythmic contraction that starts from the early embryonic stage and is triggered from the sinuatrial node. Another unique structural characteristic is that the fibers run in a mesh-like pattern and are branched. This allows the heart chambers to contract, reduce their volume and pump the blood forward.

Microscopic examination reveals unique structures called the intercalated disks that appear as dense lines at regular intervals along the longitudinal axis of the fiber. The disks provide a cohesive link between the heart muscle fibers and facilitate the transmission of contraction force from one fiber to the other. The heart is controlled by the sympathetic and parasympathetic nervous systems that are partly outside the central nervous system. The heart muscle is very active and has an extensive blood supply that results in its dark red color.

Smooth Muscle

The smooth muscle has relatively long and narrow cells with an average length of a few hundred μm and a diameter of 3–12 μm. The fibers have a single nuclei that is usually centrally located (Figure 2.7). The smooth muscle cells are associated with the involuntary systems in the body (e.g., digestive system, walls of arteries and parts of the reproductive system). The reason the muscle does not show a striated appearance is that the repetitive structure of the sarcomeres is not as well organized as in the skeletal and cardiac muscle fibers; thus, it is called a smooth muscle. In certain locations, such as the digestive system, a cross section reveals different layers of smooth muscle sheaths. Some of the sheaths are perpendicular, whereas others are parallel to the cut surface. This allows the muscles to decrease the diameter of the gut as well as elongate/contract its length. By performing this double action, the gut system can move food forward.

MUSCLE PROTEINS

Proteins represent essential building blocks of the muscle structure. The proteins consist of about 18–20% of the lean muscle weight, where water and fat represent about 75% and 5%, respectively. The muscle proteins can be divided into three major groups (Table 2.1) based on their water and salt solubility (Asghar et al., 1985). A common procedure used in a muscle biology laboratory to separate the muscle proteins is to homogenize a piece of lean muscle tissue (e.g., 1:1 meat to water) in a high speed mixer/homogenizer. Then, the homogenate is placed in a test tube and centrifuged to separate the aqueous phase that contains the water-soluble proteins, also called the sarcoplasmic proteins. After decanting the upper layer, a salt solution (e.g., 0.6 M NaCl or KCl) is added to the bottom layer, mixed well (or homogenized) and centrifuged. This

Table 2.1. The Major Proteins in an Average Lean Avian Muscle Divided into Three Groups According to Their Solubility (See Text) and Their Relative Percentage in the Wet Muscle (Based on 19% Total Protein).

Group	Protein	
Sarcoplasmic		(5.5)
	Myoglobin	0.2
	Hemoglobin	0.6
	Cytochromes	0.2
	Glycolytic enzymes	2.2
	Creatine kinase	0.5
Myofibrillar		(11.5)
	Myosin	5.5
	Actin	2.5
	Tropomyosin	0.6
	Troponin	0.6
	C-Protein	0.3
	α-Actinin	0.3
	β-Actinin	0.3
Stromal		(2.0)
	Collagen	1.0
	Elastin	0.05
	Mitochondrial	0.95

separates the salt-soluble proteins, called myofibrillar proteins, and the bottom layer of the nonsoluble proteins, called the stromal proteins.

Sarcoplasmic proteins are water soluble and are distributed within the cellular fluid (sarcoplasm). The liquid in which they are found after separation appears red because it contains the oxygen-carrying molecule, myoglobin (see structure in Chapter 13), and various enzymes (Table 2.1). The sarcoplasmic proteins consist of about 25% of the muscle's proteins.

Myofibrillar proteins, also known as the contractile or cytoskeletal proteins, consist of about 55% of the total proteins. This group of proteins makes up the thick and thin filaments (Figure 2.6) that are mainly made of myosin and actin, respectively. Additional discussion on the structure of myosin and actin, as well as their functions, is provided below.

Stromal proteins are the water- and salt-insoluble proteins consisting of about 10–15% of the muscle's proteins, mainly including the connective tissue proteins. The two major proteins are collagen and elastin. In the living muscle, they form various structural components including membranes surrounding cells, muscle bundles (*perimysium;* Figure 2.6), muscles *(epimysium),* ligaments and tendons, and they are found within joints as intermittent material. Overall, collagen is the most abundant protein in the animal's body (i.e., considering the entire body mass that includes bones, cartilage, etc.). The

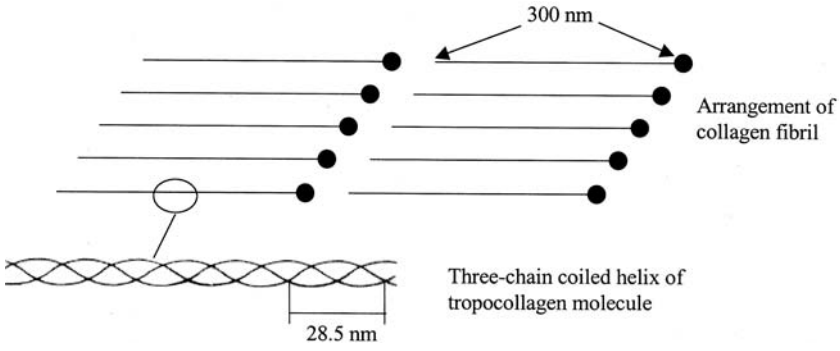

Figure 2.8. *Microstructure of a Collagen Fibril that Shows How the Fibril, Participating in Muscle Movement, Can Stretch. A Striation Pattern Is Seen at 64–67 nm Intervals Due to the Parallel Layout of the Tropocollagen Molecules. The Striation Can Be Seen after Negatively Staining a Sample with Heavy Metals and Viewing with an Electron Microscope.*

connective tissue sheaths surrounding muscles, muscle bundles and muscle fibers are known as "connective tissue proper." Cartilage and ligaments are known as the "supportive connective tissue" because they provide the body with support and structure. Collagen (Figure 2.8) is the main structural protein of the connective tissue. Its quantity varies among muscles, depending on the muscle's physical activity. Leg muscles, for example, have higher collagen because they are more active and are used to support the whole body. This higher amount of connective tissue makes leg meat tougher compared to less active muscles. See additional discussion regarding collagen structure and function later in the chapter.

MUSCLE CONTRACTION

The phenomenon we observe as movement is the result of muscle contraction, which is actually a very complex chain of events. Overall, it is the result of many sarcomeres (the smallest contracting unit) moving in harmony that produces tension, which is observed as a pulling in a certain part of the body. In the process, chemical energy, which is stored as a high-energy bond within the adenosine triphosphate (ATP) molecule, is converted into physical movement (Swatland, 1994). The following section will briefly describe the major proteins involved in muscle contraction, their unique structure and three-dimensional arrangement.

Myosin forms the thick filaments in the muscle and constitutes about 45% of the myofibrillar proteins. It is an elongated rod-shaped protein [Figure 2.9(a)] with a high molecular weight of around 450,000 daltons. It is composed of two

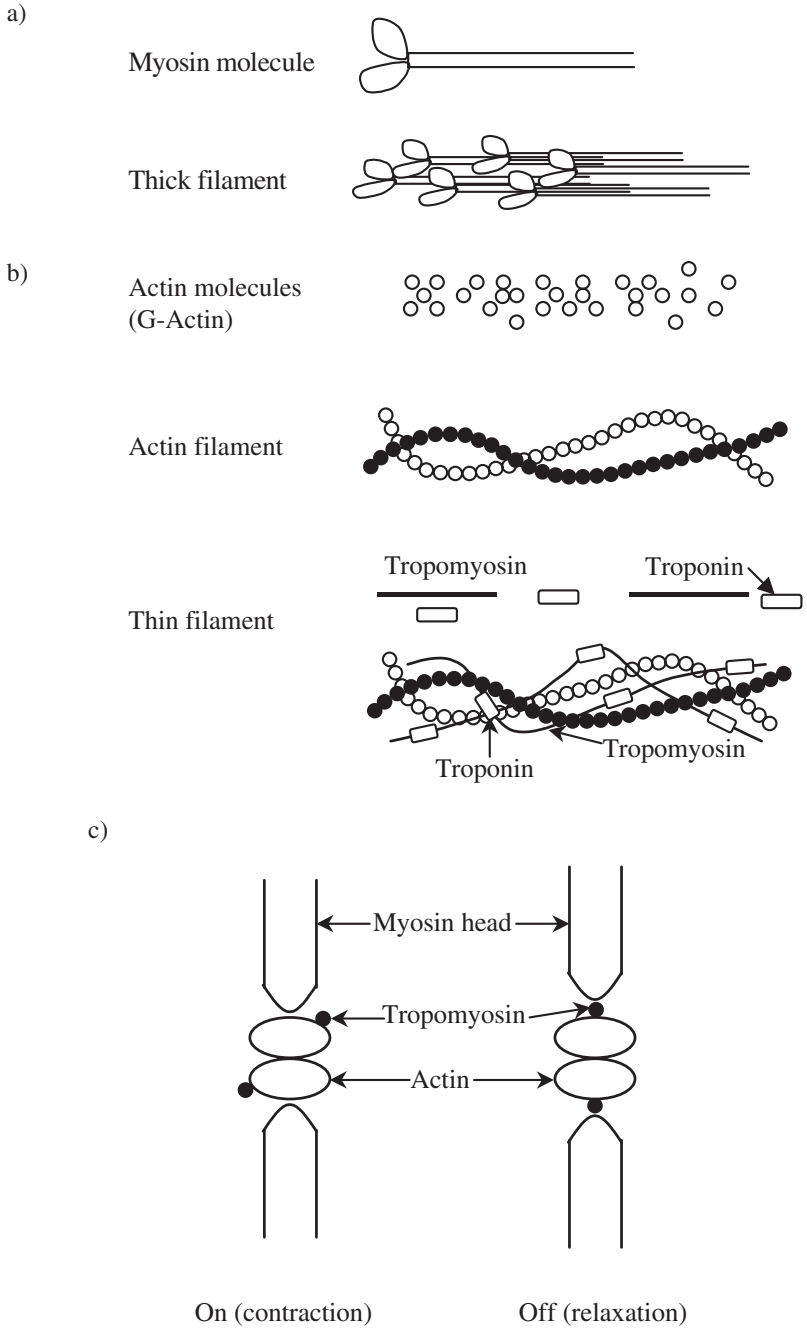

Figure 2.9. *The Microstructure of the Major Proteins Participating in Muscle Movement. Myosin that Builds the Thick Filaments (a); Actin, Troponin and Tropomyosin that Make Up the Thin Filament (b); and a Cross Section of the Thick and Thin Filaments (c) during Rest (Off) and during Contact (On).*

heavy and two light chains, that can be separated when myosin is subjected to a specific proteolytic enzyme activity. The heavy chains consist of the myosin's heads that are unique in their ability to split the ATP molecule into adenosine diphosphate and phosphate (ADP + PO_4). During movement, the heads form cross bridges with the actin molecules, using energy to change their orientation (i.e., bend), and by that, generating movement.

Actin forms the thin filament and has a lower molecular weight of 42,000 daltons. It consists of two chains of G-actin that are formed from individual F-actin molecules [Figure 2.9(b)]. This process takes place at a specific salt concentration that favors the formation of the chain. The thin filament is made up of two chains twisted together forming the so-called double helix of actin molecules.

Tropomyosin is a rod-like protein that surrounds the actin helical structure and constitutes about 5% of the myofibrillar proteins. There is one tropomyosin molecule for every seven actin molecules [Figure 2.9(b)]. It lies alongside the actin molecule and is positioned in the groove of the helical structure of the actin double helix.

Troponin is a globular protein that constitutes about 5% of the myofibrillar proteins. It is also present in the groove between the two actin filaments, where it lies within the tropomyosin strands. The troponin units are positioned in a repetitive pattern along the actin filament [Figure 2.9(b)]. There are three types of troponin: troponin-C which binds Ca^{++}, troponin-I which inhibits ATP and troponin-T which binds tropomyosin.

Different explanations have been proposed to explain muscle contraction. The most acceptable explanation is the so-called sliding-filament theory. According to this theory, the thick myosin filaments are sliding in between the thin actin filaments toward the Z-lines [Figure 2.6(e)]. During this process, one can measure the depletion of the energy-rich molecule ATP into ADP. As mentioned earlier, the myosin heads have a site capable of splitting the ATP, and by that, releasing the energy needed to bend or twist the heads and pull the myosin molecule toward the Z-line (Figure 2.10).

The trigger for starting the contraction process comes from the brain and is transferred via the nervous system (Figure 2.11). The signal travels through the nerve by depolarizing the membrane and changing the inside electrical potential from about −80 mV to +20 mV. During rest, the nerve membrane actively pumps positive sodium ions out of the cell and maintains the potential difference between the inside and outside of the cell. When a message is passed through the cell (also called action potential), a fast reverse of the electrical potential is seen. The overall change in polarization is very fast and takes about 1 millisecond before the original base condition is restored. When the signal arrives to the nerve's ending (Figure 2.11; motor end plates), the message is transferred to the muscle by chemical means. *Acetylcholine* is released from the nerve ending and causes the muscle cell's membrane to depolarize. It should be mentioned that this chemical messenger is broken down

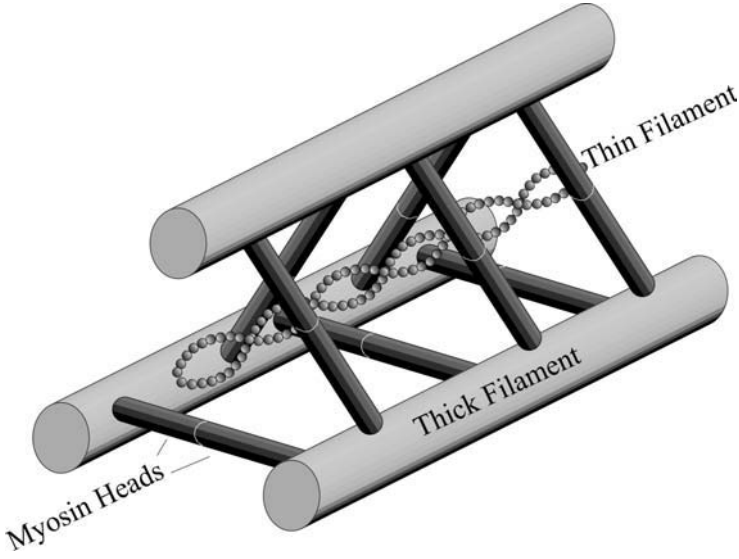

Figure 2.10. *Schematic Diagram of the Sliding Filament Theory. Adapted from Pollack (1990).*

very quickly (i.e., to prevent continuous signaling to the muscle) by an enzyme called *acetycholinesterase*. The chemical message is then causing an electrical depolarization in the muscle cell's membrane and is transferred to the myofibrils via a special arrangement of T-tubules within the sarcoplasmic reticulum. This triggers muscle contraction that consists of the following:

- calcium release from the sarcoplasmic reticulum's terminal cisternae into the sarcoplasm
- free calcium is quickly bound by troponin-C
- this, in turn, causes the tropomyosin to shift from the actin binding sites
- actin and myosin molecules form cross bridges [Figure 2.9(c)]
- the repeated formation and breaking of the cross bridges results in sliding of the thick filaments toward the Z-line and, hence, sarcomere shortening

During the relaxation phase, the signal coming from the nerve is stopped:

- the sarcolemma and the T-tubules are re-polarized, making them ready for the next signal
- the calcium pump, within the sarcoplasmic reticulum, is resequestering the calcium
- the actomyosin bridges are broken

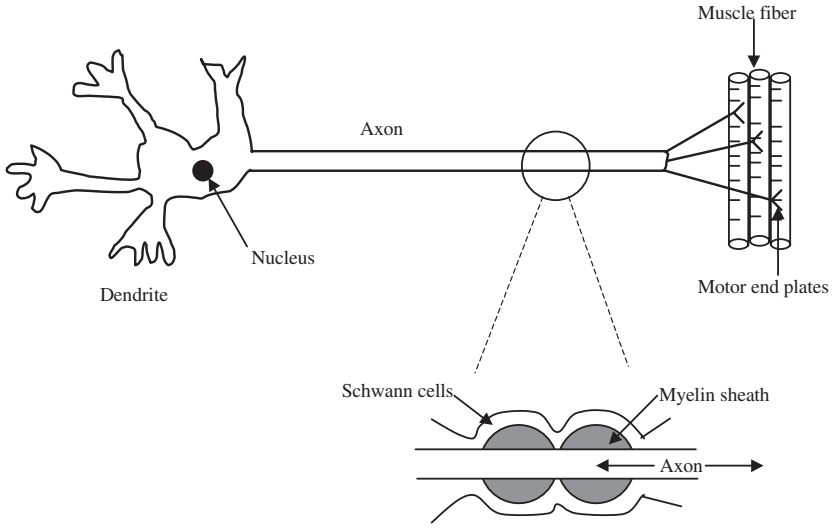

Figure 2.11. *A Schematic Drawing of a Neuron with Motor End Plates.*

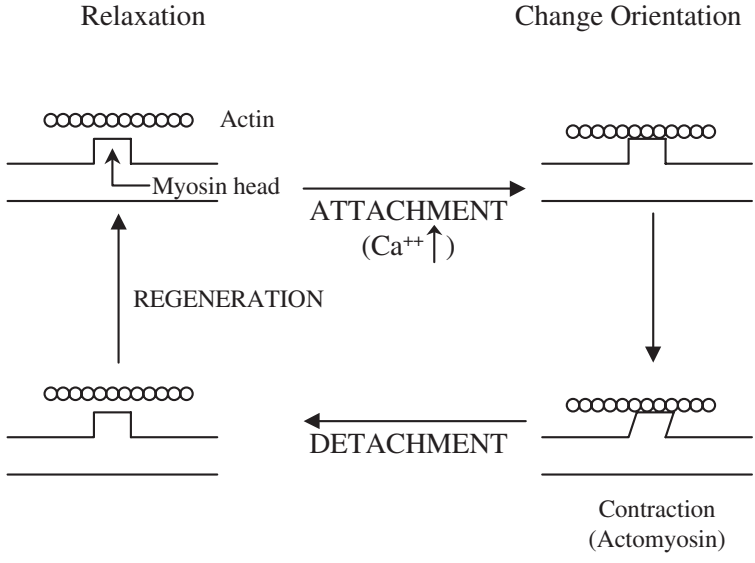

Figure 2.12. *A Schematic Illustration of the Steps Involved in Muscle Contraction.*

- the tropomyosin molecules return to the actin binding sites [Figure 2.9(c)]
- passive sliding of the filaments is observed, and the sarcomeres return to their resting state.

Calcium concentration in the sarcoplasm controls muscle contraction. During rest, the concentration of free calcium is below 10^{-8} mole/liter. When calcium is released, the concentration goes up to a level around 10^{-5} mole/liter. This causes the troponin-C to bind calcium which in turn triggers movement of the tropomyosin-troponin system away from the myosin binding sites on the actin molecules. During relaxation, free calcium is resequestered, and its concentration goes back to around 10^{-8} mole/liter.

A schematic illustration of the steps described above is provided in Figure 2.12 to assist the reader in understanding the sequence of events.

FIBER TYPE

In the poultry meat trade, there is a clear distinction between white and dark meat. White meat refers to the breast muscle from chicken and turkey, whereas dark meat refers to the leg meat. This classification is based on the overall color of the meat. In chicken and turkey, it can be said that this is also related to the relative proportion of red and white fibers within the muscle. Generally speaking, most muscles contain a mixture of red and white fibers; very few muscles are composed of all white or red fibers. The dark/red chicken/turkey meat has a high proportion of red fibers compared to white meat.

There are important metabolic and functional differences between red and white muscle fibers; some of the key ones are summarized in Table 2.2. It

Table 2.2. Relative Comparisons between Red and White Muscle Fibers in Poultry.

	Red Fiber	White Fiber
Myoglobin (concentration)	High	Low
Color	Red	White
Contraction speed	Slow	Fast
Mitochondria (number)	High	Low
Mitochondria (size)	Large	Small
Glycogen content	Low	High
Glycolytic activity	Low	High
Lipid content	High	Low
Oxidative metabolism	High	Low
Fiber diameter	Small	Large

should be pointed out that these differences are judged on a relative scale, and variation can exist within each characteristic. There is also an intermediate fiber type, not described here, that has intermediate characteristics. Overall, red muscle fibers have a higher myoglobin content (see myoglobin structure in Chapter 13) that results in a redder appearance. The red fibers contract more slowly but have the capacity to operate for a longer period of time (i.e., slower but sustained activity). The presence of a higher number and larger mitochondria than in white fibers, and the higher lipid content, allow the fibers to contract for a longer period of time. Muscles with a high proportion of red fibers are used to support the skeleton in an upright position and, because of their unique metabolism, are less easily fatigued. A good oxygen supply is important and, together with a high proportion of enzymes involved in oxidative metabolism (Table 2.2), the fibers can function for extended periods of time.

White fibers have less myoglobin and a lower oxidative enzyme activity than red fibers. The glycolytic metabolism, which predominates in the white fibers, can occur in either the presence or absence of oxygen, i.e., aerobic and anaerobic metabolism, respectively. Muscles dominated by white fibers show lower capillary density because they do not rely on fast nutrient transfer. Muscles with a high proportion of white fibers are known to contract more rapidly in shorter bursts (e.g., quickly flap the wings and lift a chicken off the ground) and are relatively easily fatigued. It should be mentioned that in some of the active wild-type birds, such as ducks and geese who fly far during their migration, the breast muscle appears fairly dark/red. This indicates that there is a higher proportion of red fibers, and the muscle can operate for extended periods of time.

From a marketing standpoint, the difference in muscle color can affect consumer acceptability and price in different markets. In North America, the price of white meat is much higher than dark meat. In some Far East regions, the situation is reversed, and dark poultry meat sells at a premium. Further discussion on meat quality and functionality is provided in the following chapters.

EPITHELIAL TISSUE

The main component of this tissue is the skin. The skin (Figure 2.13) serves as a protective layer that prevents microorganisms from entering the body and protects the body from environmental stresses such as drying. It also protects the body against mechanical damage and serves a major role in insulation and heat regulation. The two major parts of the skin are the epidermis, which is the ectodermal portion, and the dermis, which is the mesodermal portion (Figure 2.13). Poultry skin has pigmented cells that contain

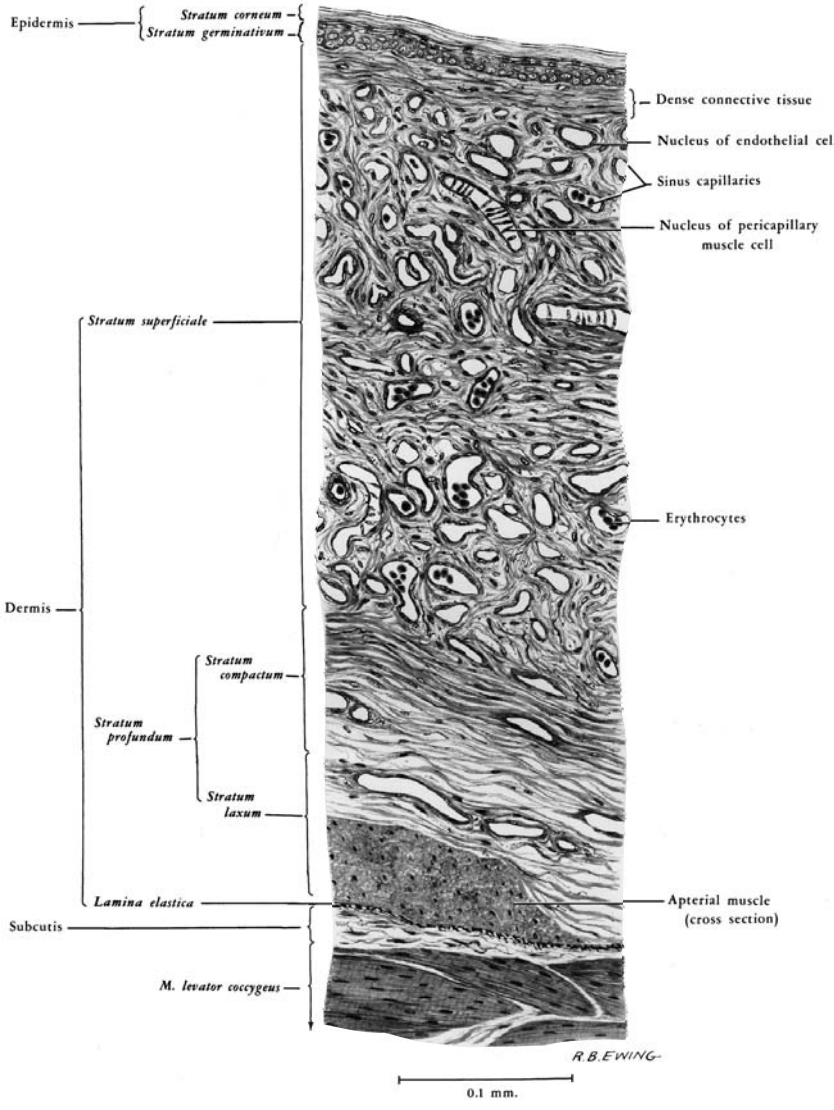

Figure 2.13. *Structure of a Mature Chicken Skin. Section Stained with Hematoxylin and Eosin. Abbreviation: M., Musculus. From Lucas and Stettenhiem (1972).*

melanin and, together with other plant pigments (e.g., xanthophyll, absorbed in the diet and can be deposited in the skin), give it a certain color (see discussion in Chapter 13). For the meat processor, the characteristics of the skin are important in terms of color (presentation), flavor and texture. The crispiness of fried chicken, for example, is due to the properties of the epithelial

tissue and the underlying connective tissues. Other organs that contain epithelial tissue are the liver, kidney and the lining of the digestive system. The epithelial tissue is usually characterized by the shape of the cells and the number of layers forming it. The cells in the epithelial tissue are usually laid down with little extracellular material. The cell shape can vary from elongated columnar-type cells to very thin and flat cells called squamous cells. In addition, cuboidal cells also form single or multiple layers on external or internal surfaces of the body. In organs such as the liver and kidney, the cells secrete different enzymes, while in the digestive system, they absorb different nutrients from the gut. Of major importance in poultry are the feathers that are formed by epithelial tissue. Figure 2.14 shows the structure of a feather, and Figure 2.15 shows a cross section of a feather follicle. The feathers represent a complex derivative of the epithelial tissue. Size alone often has a very wide range, with the longest tail feathers of a roaster being about 1,000 times as long as the feathers on its eyelids. The predominant feathers on a bird's body

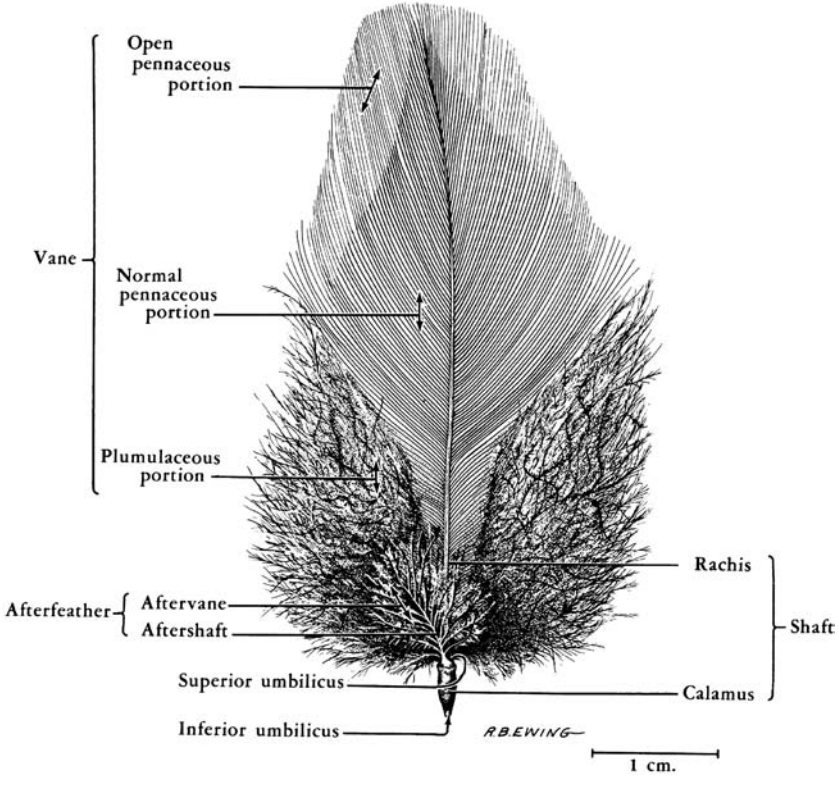

Figure 2.14. *A Structure of a Feather from the Middle of the Dorsal Tract of a White Leghorn Chicken. From Lucas and Stettenhiem (1972).*

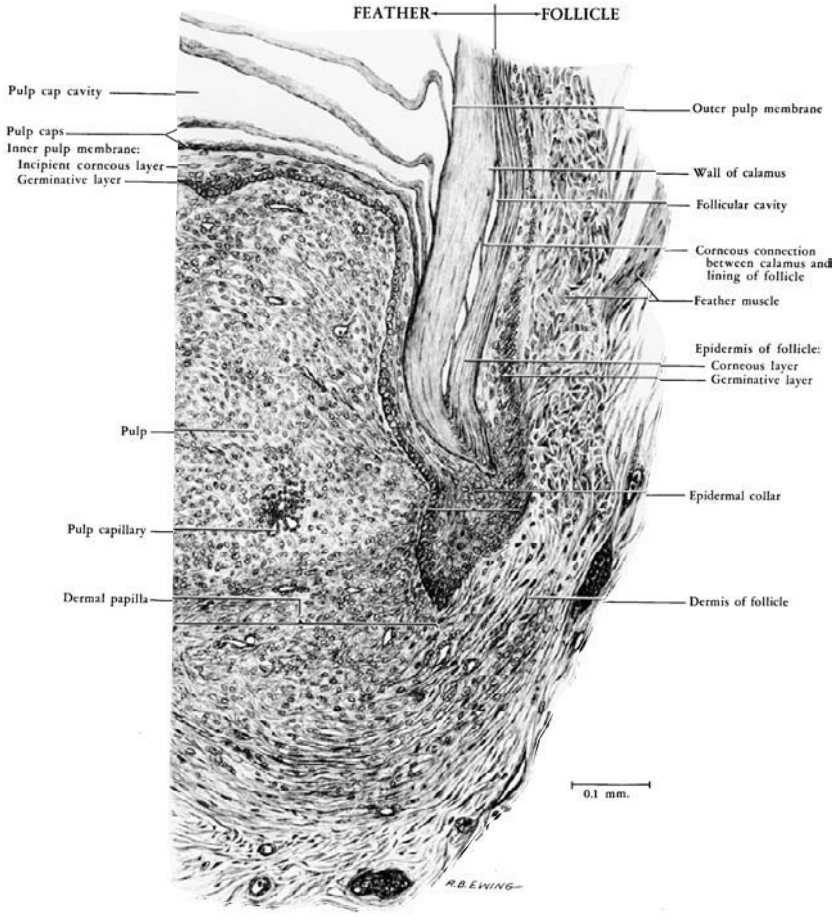

Figure 2.15. *A Longitudinal Microscopical Section through a Feather Follicle of a White Leghorn Chicken. From Lucas and Stettenhiem (1972).*

are called contour feathers and are composed of a shaft with the plates or vanes on either side (Figure 2.14).

The feather grows in a follicle (Figure 2.15). The follicle and its feather are both tubes of modified integument, showing a gradient from dermis to keratinized, highly flattened epidermis. The wall of the follicle appears to be drawn upward in some way by the sheath of the growing feather. The epidermis of the follicle, in a full-grown feather, has a single layer of germinative cells, which are low cuboidal cells and contain large nuclei (Lucas and Stettenheim, 1972).

NERVOUS TISSUE

The nervous system represents a small part of the edible meat, usually less than 1%. However, understanding its structure is important in explaining postmortem changes and meat quality issues. There are two main structural components. The first is the central nervous system that consists of the brain and the spinal cord. The second is the peripheral system that consists of the nerve cells that are part of the body. The nerve cell, or neuron (Figure 2.11), represents the basic structure of the nervous tissue. Neurons have a fairly distinct structure that consists of a cell body with an elongated fiber-type structure called axon. A nucleus is found within the polyhedrally shaped cell body. A few short branched structures called dendrites come out from the body. In a motor neuron, a long single axon branches when it reaches the muscle; the ends are called motor end plates (Figure 2.11). As can be seen in the figure, one nerve reaches a number of muscle fibers and triggers them all at the same time. The action potential that goes through the nerve (i.e., from the cell's body through the axon and the motor end plates) is transferred to the muscle or to other nerves (i.e., their dendrite portion) in an area called synapse. At this point, there is no physical connection of the two structures, but there is a small gap where in motor neurons a chemical messenger, called acetylcholine, is used to transfer the message to the muscle. (Note: within the brain and other locations, other chemical messengers are used.) Certain toxins can block acetylcholine and cause serious problems to an animal. One such toxin is produced by *Clostridium botulinum* and is associated with cases of food poisoning (see Chapter 11 for further discussion).

In the muscle, nerve trunks consisting of a group of axons can be observed as silvery lines. This trunk arrangement helps to protect the axons, which run parallel to each other, and provide strength to the structure. The peripheral nerve fibers are covered with Schwann cells and, in addition, the large fibers are covered with a myelin sheath (Figure 2.11). The small peripheral fibers do not have the myelin sheath and are only covered by Schwann cells. Therefore, nerve fibers are commonly referred to as myelinated and unmyelinated fibers. The position of the Schwann cells along the fiber assists in accelerating the movement of the action potential along the fiber.

CONNECTIVE TISSUE

The connective tissue is used, as the name implies, to connect and hold different parts of the body. It consists of bones, ligaments, tissue covering muscles, muscle bundles and fibers. As indicated before, the tissue responsible for building bones and cartilage is called "supportive connective tissue" because

it provides structural support. The part that surrounds muscles, muscle bundles and fibers is called "connective tissue proper." The two types of connective tissue have many similarities in their composition and functionability. Usually, both consist of a few cells and a lot of extracellular substance. The substance can range from very soft to very tough material and contains embedded fibers that provide structure to the tissue. In bones, the extracellular substance is much tougher than in other locations and, in addition, contains calcium salts. In cartilage, the extracellular substance is more rubbery and soft. The unique structure of the collagen molecule provides strength and elasticity. Tropocollagen molecules are the basic structural units of the collagen fiber. They are composed of three α chains that form a triple helix (Figure 2.8). There are 12 types of collagen molecules that have different functional properties and, therefore, can be found in different locations. The different types of collagen result from at least 19 different α chains that can be combined in different ways to form a triple-chained coiled helix. During filament assembly, the tropocollagen molecules are aligned longitudinally, end to end, and laterally in a slightly overlapping stagger. This overlapping results in the unique striated appearance of the collagen fibers, which is different from the striation seen in skeletal muscle (Hedrick et al., 1994). It should be mentioned that not all types of collagen form fibers. Type I and III form large and fine fibers, respectively. Type IV collagen is non-fibrous and forms a chicken wire-like sheath that surrounds individual muscle fibers. In Type V and VIII collagen, the tropocollagen molecules are aligned longitudually and form microfilaments. In general, the number of collagen fibrils found at a certain muscle depends on the activity, load and stress that the muscle is expected to endure. Another factor that contributes to strength is the formation of intermolecular cross-linkages among the collagen fibrils. In young animals, there are less cross-linkages, and the ones present are easily broken. In an older animal, the number of cross-linkages increases, and the bonds are more difficult to break. Therefore, meat from an older animal is considered to be tougher.

The other major connective tissue protein, elastin (Table 2.1), has a different structure and possesses a much more rubbery texture (i.e., elastin fibers can be easily stretched, compared to collagen, and later return to their original length). Elastin is more commonly present in ligaments and arteries and provides the structure of certain organs.

The amount of connective tissue in a muscle/meat sample is usually assessed by the quantity of the imino acid hydroxyproline, which is unique to the collagen molecule structure. As indicated before, older animals are known to have tougher meat, but both processors and consumers should know that collagen can be broken down by exposure to heat. Therefore, prolonged moist heating is recommended for cooking tough cuts of meat, including spent hen meat. Heating results in breaking the cross bridges and eventually turning col-

lagen into gelatin. The collagen becomes soluble during cooking (starting melting point ≈ 67°C) and, as exposure time and temperature increase, more will be converted to gelatin. After cooking, if the meat and its juices are left to cool, the juices will turn into a jello-like texture. Elastin, on the other hand, cannot be broken down by heat, and cuts of meat high in elastin should either be discarded or tenderized by mechanical means (e.g., small blades/needle tenderization; see Chapter 8).

Adipose tissue is also part of the connective tissue, and it consists mainly of cells and less extracellular fibers, as its main function is to store fat. The adipose tissue is usually found enclosed in areas surrounded by a sheath of collagen fibers. The young adipose cells are called adipoblast and, when they mature and fill with fat, are called adipocyte. The adipoblast grow from about 1–2 μm to a size of up to 100 μm, while accumulating small lipid droplets that later fuse to form a large fat globule. The development of the adipose tissue is related to age of the bird and the abundance/lack of nutrition. In young animals, the first fat deposit usually appears in the visceral area. Later, subcutaneous fat (under the skin) is developed, followed by a limited amount of intermuscular fat, which is deposited in between muscles. It should be mentioned that poultry is fairly unique, as compared to red meat animals, because intermuscular fat (or marbling) does not appear in most muscles (e.g., pectoralis). The adipose tissue represents an energy storage for the animal and is used in response to certain needs. Migrating birds, for example, can go through a large increase of their adipose tissue mass just before migration. In any case, the adipose tissue has a fairly dynamic metabolism, meaning that the lipids stored are constantly mobilized.

The bone structure in poultry is unique in its ability to provide great physical strength with relatively light weight. This is essential for the flying bird as opposed to the heavy bone structure found in red meat animals. The bone tissue consists of an organic matrix and inorganic salts. The first contains the collagen fibers and ground substance consisting of proteins and sugar complexes. The inorganic part is primarily made up of calcium and phosphate salts that form crystals deposited within the collagen fibers of the organic matrix. The structure consists of bone cells distributed within the matrix and arranged in small cylindrical elements called *lacuna*. These structures form a network of canals between the cell cavities, which is important in allowing for proper cell feeding. The structure of a long bone such as the humerus and femur is shown in Figure 2.16. The central shaft, called diaphysis, is hollow and filled with compact bone material. Both ends are enlarged to allow enough surface area for connecting with other bones (via cartilage-mediated medium) and are called epiphyses. The cartilage region separating the diaphysis and the epiphysis of the growing animal is called the epiphyseal plate and is the section responsible for elongating the bone. The central hollow part of the bone contains the bone marrow that produces new red blood cells. The bone

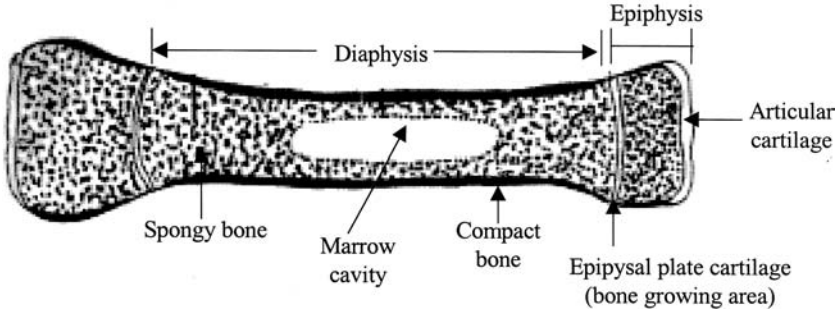

Figure 2.16. *The Structure of a Long Bone.*

represents a very dynamic system in terms of calcium deposition and withdrawal. It is interesting to note that the laying hen is used as a research model to study osteoporosis in humans because of the very fast calcium turnaround seen during the laying period. The overall skeletal structure of a chicken is shown in Figure 2.17. The figure shows a chicken skeleton, which is a fair representation of other birds; however, there are some differences between chickens, turkeys, quails, ducks and pigeons. It should be mentioned that the number of vertebrae of the axial skeleton varies among birds and also among individuals of the same species; the neck of a chicken can have 16 or 17 vertebrae (Lucas and Stettenheim, 1972).

Cartilage is part of the connective tissue used to connect and support different skeletal elements. The cells, called chondrocytes, are found in clusters located in small cavities within the extracellular material. The interlacing collagen form a delicate network of cartilage. Cartilage can differ in the relative amount of collagen fibers and extracellular material. This results in the formation of cartilage with different properties that can be divided into three main categories. The first is the hyaline cartilage found between individual vertebrae, on the surfaces of joints and bones and on the dorsal tips of vertebrae. The second type is the fibrocartilage found in tendons attaching bones and within ligaments of the joints. The fibrocartilage has numerous collagen fibers and can resist repetitive stress. The third type is the elastic collagen that consists of a number of branched elastin fibers that provide its elastic characteristics.

The blood and lymph systems are also part of the connective tissue system. The blood consists of a large portion of extracellular material in which various cellular components are suspended; the cell component usually represents about 40% of the blood volume. The red blood cells or erythrocytes transfer gases, such as oxygen, from the lungs to the body. The white blood cells, leukocytes, are part of the body's defense mechanism against infections.

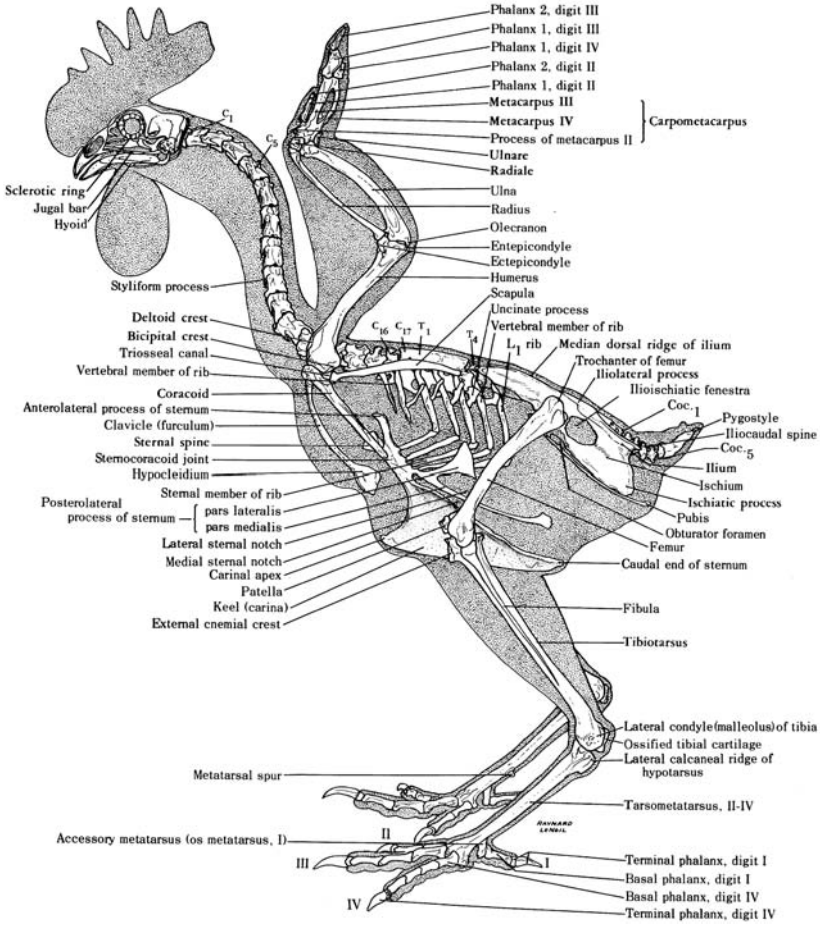

Figure 2.17. *A Lateral View of the Skeleton of a Leghorn Chicken. Abbreviations: C., Cervical Vertebra; Coc., Coccygeal Vertebra; L., Lumber Vertebra; T., Thoracic Vertebra. From Lucas and Stettenhiem (1972).*

POSTMORTEM CHANGES

Understanding the structure and mechanism of muscle contraction in the living animal is essential in comprehending the changes taking place during the conversion of muscle to meat. The living muscle is a complex system that is used to provide movement. In the living animal, all the organs are working in harmony, where it is essential that the internal environment is kept balanced within a very narrow range of temperature, pH, oxygen, CO_2 concentration, etc. Maintaining balanced conditions is called homeostasis, and it is essential

for the body's operation in different environments such as high/low temperatures and relative humidity. The body employs thousands of nerve sensors sensitive to physical pressure, temperature, gas concentration, blood pressure, etc., to collect data about external and internal conditions. The information is processed and, if required, corrective actions, such as fluffing the feathers and running to find shelter, are prescribed.

During the conversion of muscle to meat, many of the homeostatic mechanisms are disrupted (e.g., oxygen supply). Stress conditions prior to slaughter also affect homeostatic conditions (see Chapter 3) and, later, meat quality. Stress can arise from activities such as transportation, unloading and immobilization. Immobilization of poultry, which refers to rendering the bird unconscious, is usually the first step in the process. In most countries, there are regulations requiring the use of human immobilization methods to minimize animal pain and distress. For poultry, electrical stunning and gas (CO_2, argon) immobilization are commonly employed (see Chapter 5). In addition to using a proper immobilization method, attention should be given to reducing stress, such as wing flapping before and during stunning (i.e., to minimize hemorrhages in the muscle and incidences of broken bones). The next step after stunning is known as exsanguination or the removal of blood. This step represents the beginning of the major changes seen during the postmortem phase. The removal of as much blood as possible is required, because an excessive amount of blood left in the muscle will result in an overall dark appearance or dark spots. Usually, only around 35–50% of the total blood volume is removed (Chapter 5), and the remaining is mainly held within the vital organs. This occurs because when the blood pressure starts to drop, peripheral blood vessels constrict in an attempt to maintain blood pressure. The removal of blood stops the line of support between the muscle and internal organs such as the lungs, liver and kidney that provide oxygen, detoxify and regulate water, respectively. The first and most serious effect of ceasing the blood flow is the interruption in oxygen supply. In the healthy animal, the oxygen is transferred from the lungs via the red blood cells to the tissue. Once the oxygen supply is cut off, the normal aerobic tricarbocylic acid (TCA) cycle stops. At this point, energy metabolism is switched into an anaerobic pathway that provides the muscle with energy for some extra time. It should be remembered that such an anaerobic pathway occurs in a living, heavily exercised muscle and can be carried out for a certain period of time. In the living cell, lactic acid is produced (i.e., via an anaerobic metabolism pathway) and is then transported to the liver to be resynthesized into glucose or to the heart where it is broken down into water and CO_2 via a specialized enzyme system (Hedrick et al., 1994). When the blood stops circulating, lactic acid will accumulate in the muscle until most of the glycogen stored in the muscle (about 1% of the rested muscle weight) is depleted or until the pH becomes too low for glycolytic enzymes to operate.

The rate of pH decline (Figure 2.18) and the final point to which it reaches, known as the ultimate pH, are very important in terms of meat quality and color development. A normal pH reduction pattern is shown by the middle line in Figure 2.18. This represents a gradual decrease from the neutral pH of the living breast muscle to about 5.8. In some animals where glycogen storage has been depleted prior to slaughter, due to extended activity or struggling, the pH drop will be minimal, and the ultimate pH will stay high. This results from initial low levels of glycogen and, later, limited amounts of lactic acid production; the meat is known as dark firm and dry (DFD). The dry appearance results from a high ultimate pH that is further away from the isoelectric points of the muscle proteins and, therefore, exhibits higher water-holding capacity (see Chapter 14). On the other extreme, the meat's pH can drop very quickly at the beginning of the postmortem process, and this will result in the so-called pale soft and exudative (PSE) meat (Barbut, 1998). In this case, a rapid drop in the pH within the first hour, while the meat temperature is still high, can cause some protein denaturation and, hence, exudative meat. The partially denaturated proteins cannot hold water very well, and the surface appears wet (Hedrick et al., 1994). The color of the meat is pale, and this is the result of more light reflected from the loose muscle structure as compared to the tight structure of the DFD meat.

The process of rigor mortis, which means in Latin "stiffness of death," follows the depletion of energy from the muscle and results in a temporary toughening of the muscle. This state does not take place immediately after slaughter but rather at a certain time after slaughter (Figure 2.19). The reason for this occurrence is the gradual depletion of glycogen and other energy sources (e.g., creatin phosphate) within the cell. When all the energy has been depleted, the actomyosin cross-bridges formed within the muscle structure (between the

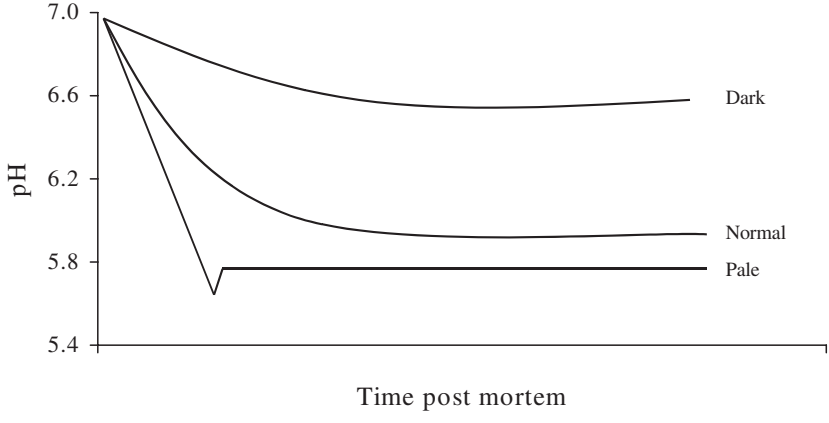

Figure 2.18. *Rate and Extent of Postmortem pH Decline of Chicken Breast Muscle.*

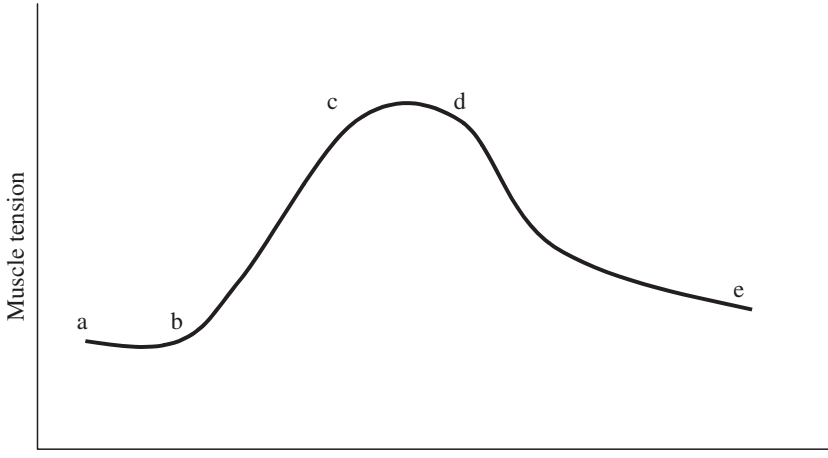

Figure 2.19. *Development of Rigor Mortis Expressed as Muscle Tension Over Time. The Regions Represent: Delay Time a-b; Development of Rigor Mortis b-c; Full Rigor Development c-d; and Rigor Resolution d-e. Time for Each Section Depends on Factors Such as Specie, Degree of Exercise Prior to Slaughter, Stunning Method and Temperature. Adapted from Hedrick et al. (1994).*

thick and thin filaments; Figure 2.12) cannot be broken. The time between slaughter and the onset of rigor mortis is called the delay phase. When all the energy sources have been depleted, the muscle becomes inextensible. After a certain period of time, the muscle starts to become flexible again (Figure 2.19), but this is the result of proteolytic enzymes slowly breaking down the sarcomere components. Some of the major structural changes during the so-called aging process include the degradation of the Z-line (leading to fragmentation and weakening of the myofibrils) and degradation of the proteins titin, nebulin and desmin. The proteolytic enzymes responsible for the degradation consist of two major systems: the calpains and cathepsins. The enzymes vary in their calcium requirements for activation; calcium is available after it was released from the sarcoplasmic reticulum and mitochondria during postmortem aging. Because the enzymes are activated by calcium, some have suggested calcium infusion (i.e., into the meat) to improve tenderness. This actually works and is used more in the red meat industry, where tough meat is a bigger problem. Experiments have also shown that chelating the calcium ion inhibits/slows these enzymes and prevents further improvement in tenderness. It should be noted that at the early stages of the postmortem period, collagen degradation is minimal and does not contribute to improved tenderness.

Temperature during the postmortem process is a critical factor in obtaining high quality meat. An optimal temperature for the postmortem process is

between 15–20°C. Therefore, it is recommended to start reducing the muscle temperature as soon as possible after slaughtering. However, very fast temperature reduction can also cause meat tenderness problems. Fast temperature reduction to sub-zero temperatures, prior to the completion of rigor mortis, can result in a condition known as thaw rigor. This is caused by a severe muscle contraction that takes place during thawing, and it is triggered by an excessive calcium release from the sarcoplasmic reticulum into the sarcoplasm. Such a severe contraction results in a release of water and toughening of the muscle. An unrestrained muscle (i.e., dissected and not attached by ligaments to bones) can shorten to over 50% of its original length after thawing (Hedrick et al., 1994). The condition results from a sudden release of calcium ions triggering an intense muscle contraction prior to the depletion of all the ATP. A microscopical examination of such muscles reveals a severe contraction of the sarcomers and the almost complete disappearance of the I-band.

A less severe shortening can occur when the temperature is reduced to below 15°C, but above freezing, prior to the onset of rigor mortis. This situation is known as cold shortening and is also the result of an extensive muscle contraction (Bilgili et al., 1989). The condition is more common than thaw shortening, and damage to the muscle is not as severe; however, it can still cause toughening and moisture loss problems.

Increasing the muscle temperature to above 50°C (higher than normal body temperature) during the rigor process can also result in excessive shortening known as heat rigor. This results from a rapid depletion of ATP and creatin phosphate. However, this problem is not commonly seen by the industry.

Overall, the information presented above indicates that an optimum temperature should be maintained during the rigor mortis process so as to prevent shortening and/or toughening of the muscle during the process. It is commonly suggested that the temperature be kept at 18 +/− 2°C so it is above 15°C but still lower than body temperature (≈39°C for chickens) to suppress microbial growth. Because the rigor process in poultry is much faster than in beef (1–3 hours vs. 12–24 hours, respectively), poultry carcass chilling in modern processing plants starts at about 30–60 min after slaughter and reaches 15°C when rigor is completed or almost completed.

Electrical stimulation can be used after slaughter to speed up the rigor process and overcome some of the problems that might be encountered during rapid chilling. Originally, the process was developed for red meat animals to allow an accelerated processing (i.e., deboning the meat at an earlier stage compared to nonelectrically stimulated carcasses). The process of electrical stimulation includes passing an electrical current through the carcass, which triggers muscle contraction by stimulating the nervous system (Hedrick et al., 1994). Such contraction results in depleting the energy within the muscle and in a rapid onset of the rigor mortis process. Because the electrical pulse used to stimulate the muscle is much larger than the one employed in the live

animal, excessive muscle contraction can occur. This, in turn, may result in physical damage to the sarcomere structure (ripping of some of the sarcomeres), which actually also adds to the tenderization effect of electrical stimulation. Besides accelerating the rigor mortis process and allowing deboning at an earlier stage, electrical stimulation can also be helpful in preventing or minimizing cold shortening problems (Sams, 1999). It should be mentioned that the use of electrical stimulation is not as common with poultry as with large beef animals, which have tougher meat to begin with and in which rigor mortis takes about 12–24 hours to complete (vs. 1–3 hours in chickens and turkeys). However, there are currently some poultry processing operations in the United States and elsewhere that are employing the process. Additional discussion on the procedure and equipment used can be found in Chapter 4.

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