muscles to contract. The number of vibrations noted by Helmholtz was 19½ per second; but the sound heard was the first overtone, or the octave, the fundamental tone being too low to be appreciated by the ear.

Some physiologists have denied the supposed identity between the tetanic contraction produced by a rapid succession of stimuli applied to a motor nerve and voluntary muscular contraction. Complete fusion of contraction occurs with twenty-seven or more stimuli per second applied to a nerve; but it is stated that stimuli applied to the motor cerebral centres, even when very rapid, do not produce more than eight to thirteen muscular contractions, the average being ten per second (Horsley and Schäfer, 1887). The average in voluntary muscular contraction is about the same. From these observations it is argued that the rate of so-called vibration in voluntary muscular contraction has an average of about ten per second. This conclusion is based upon actual myographic tracings. It is difficult, however, to reconcile these results with those obtained by Marey, Helmholtz and others. It is a fact, also, that distinct muscular contractions may be produced very rapidly by an effort of the will. It is not difficult for any one to make five taps of the finger per second for a few seconds, and skillful performers on musical instruments are able, by using the same muscle or set of muscles, to make movements that are very much more rapid, each movement presumably requiring a distinct nervous impulse. It may be that in an unweighted muscle, the contractions are discontinuous, and that the average number of waves is about ten per second; but it is probable that the estimate of Helmholtz—19½ waves per second—is nearly correct for muscles in a condition of powerful contraction. In a series of observations by Griffiths (1888), it was found that voluntary contraction of the biceps weighted with a little more than eleven pounds (5,000 grammes), for one hundred seconds, gave an average of eighteen waves per second, the average for the unweighted muscle being fourteen waves per second for thirty-three seconds.

The nerves are not capable of conducting an artificial stimulus for an indefinite period, nor are the muscles able to contract for more than a limited time upon the reception of such an excitation. The electric current may be made to destroy for a time both the nervous and muscular excitability; and these properties become gradually extinguished, the parts becoming fatigued before they are completely exhausted. Precisely the same phenomena are observed in the physiological action of muscles. When a muscle is fatigued artificially, a tetanic condition is excited more and more easily, but the power of the contraction is proportionally diminished. Muscles contracting in obedience to an effort of the will pass through the same stages of action. It is probable that constant contraction is excited more and more easily as the muscles become fatigued, because the nervous force gradually diminishes in intensity; but it is certain that the vigor of contraction at the same time progressively diminishes.

The phenomena of muscular contraction thus far considered are those produced by voluntary effort or by stimulation of motor nerves; but many important phenomena have been observed in muscles detached from the body

and stimulated directly. These observations have generally been made on the gastrocnemius of the frog, the phenomena being recorded by a registering apparatus, the simplest form of which is the myograph of Helmholtz. This instrument is used in recording muscular contractions by causing the recording point to play upon a smoked paper moving at a known rate. If the muscle of the frog, slightly weighted, be stimulated by a single induction-shock, there is first a latent period, when there is no contraction, then a contraction followed by relaxation, and finally a slight, elastic vibration before the muscle becomes quiescent. These phenomena are illustrated in the curve given in Fig. 156 in which, however, the latent period is not measured.

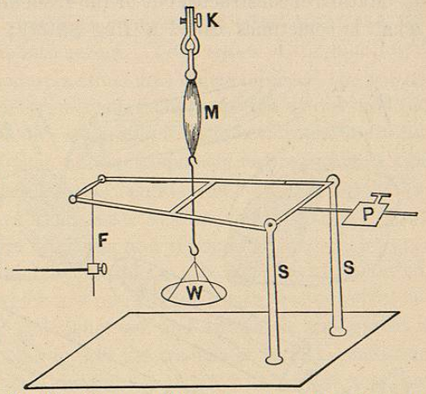

Fig. 155.—*Diagram of the myograph of Helmholtz* (Landois).
M, muscle fixed by the clamp (K) by a portion of the femur; F, recording point; P, counterpoise used to balance the lever; W, pan for weights; S, S, supports for the lever.

In a muscle prepared in this way, the maximum of stimulation and the maximum of power measured by a weight lifted can readily be ascertained, and certain phenomena due to fatigue of the muscle have been observed. In a fatigued muscle, the latent period is lengthened and the elevation of the curve of contraction is not so high, showing a slower and longer action. When a muscle is excited to tetanic contraction by a rapidly interrupted current of considerable strength, the elevation produced by the initial contraction is nearly vertical, and is followed by a horizontal straight line which marks the tetanic condition. The phenomena induced by direct stimulation of muscles are somewhat exaggerated when the stimulus is applied to the motor nerve.

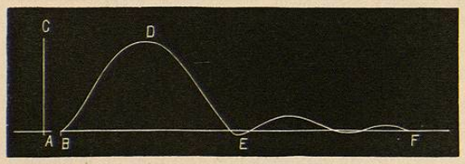

Fig. 156.—*Curve of a single muscular contraction* (Landois).
A F, abscissa; A C, ordinate; A B, latent period; B D, period of contraction; D E, period of relaxation; E F, elastic vibration.

Electric Phenomena in Muscles.—It was ascertained a number of years ago, by Matteucci, that all living muscles present electric currents. The direction of these currents is from the longitudinal surface to the transverse, or cut surface of the muscle, as is shown in Fig. 157. A simple method of demonstrating the muscular current is to prepare the leg of a frog with the crural nerve attached, and to apply one portion of the nerve to the deep parts of an incised muscle and the other to the surface. As soon as the connection is made, a contraction of the leg takes place. The current

may also be demonstrated with an ordinary galvanometer; but the evidence obtained by the frog's leg is sufficiently conclusive.

Matteucci constructed out of the fresh muscles from the thigh of the frog, what is sometimes called a frog-battery; which is made by taking the muscles of the lower half of the thigh from several frogs, removing the bones, and arranging them in a series, each with its conical extremity inserted into the central cavity of the one below. In this way the external surface of each thigh except the last is in contact with the internal surface of the one below. If the two extremities of the pile be connected with a galvanometer, quite a powerful current from the internal to the external surface of the muscle may be demonstrated. In a pile formed of ten elements, the needle of a galvanometer was deviated 30° to 40°.

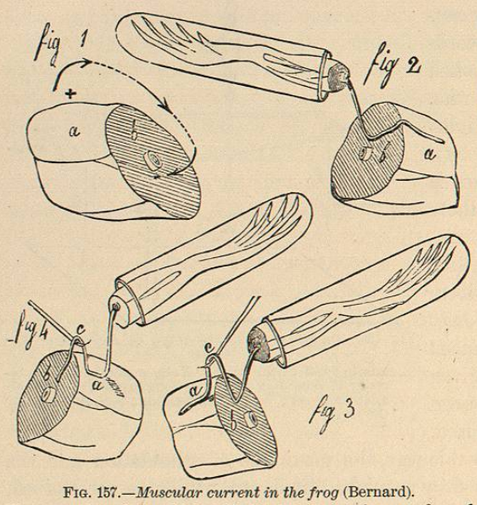

FIG. 157.—*Muscular current in the frog* (Bernard).

Fig. 1, portion of the thigh, with the skin removed; *a*, surface of the muscles; *b*, section; the direction of the current is indicated by the arrow.

Fig. 2, the nerve of a frog's leg (the leg enclosed in a glass tube) is applied to the section and the surface of the muscle. There is no contraction, because it is necessary that a portion of the nerve should be raised up.

Fig. 3, a portion of the nerve is raised with a glass rod. The contraction of the galvanoscopic leg occurs at the making of the circuit, because the current follows the course of the nerve, or is descending.

Fig. 4, the contraction here occurs at the breaking of the circuit, because the direction of the current is opposite the course of the nerve, or is ascending.

Electric currents are observed in all living muscles, but they are most marked in the mammalia and warm-blooded animals. They exist, also, for a certain time after death. Artificial tetanus of the muscles, however, instead of intensifying the current, causes the galvanometer to recede. If, for example, the needle of the instrument show a deviation of 30° during repose, when the muscle is excited to tetanic contraction, it will return so as to mark only 10° or 15°, or it may even return to zero. This phenomenon, which is called negative variation of the muscular current, is observed only during a continued muscular contraction and it does not attend a single contraction.

Muscular Effort.—The mere voluntary movement of parts of the body, when there is no obstacle to be overcome or no great force is required, is very different from a muscular effort. For example, in ordinary progression there is simply a movement produced by the action of the proper muscles, almost without consciousness, and this is unattended with any considerable modification in the circulation or respiration; but in attempting to lift a heavy weight, to jump, to strike a powerful blow or to make any vigorous

effort, the action is different. In the latter instance, a certain preparation for the muscular effort is made by inflating the lungs, closing the glottis and contracting more or less forcibly the expiratory muscles so as to render the thorax rigid and unyielding; and by a concentrated effort of the will, the proper muscles are then brought into action. This action of the muscles of the thorax and abdomen, due to simple effort and independent of the particular muscular act that is to be accomplished, compresses the contents of the rectum and bladder and obstructs very materially the venous circulation in the large vessels. It is well known that hernia frequently is produced in this way; the veins of the face and neck become turgid; the conjunctiva may become ecchymosed; and sometimes aneurismal sacs are ruptured. An effort of this kind is generally of short duration, and it can not, indeed, be prolonged beyond the time during which respiration can be conveniently arrested.

There are degrees of effort which are not attended with this powerful action of the muscles of the chest and abdomen, and in which the glottis is not completely closed; and an opening into the trachea or larynx, rendering immobility of the thorax impossible, does not interfere with certain acts that require considerable muscular power. If the glottis be exposed in a dog, when he makes violent efforts to escape, the opening is firmly closed. This is often observed in vivisections; but Longet has shown that dogs with an opening into the trachea are frequently able to run and leap with "astonishing agility." He also saw a horse, with a large canula in the trachea, that performed severe labor and drew heavily loaded wagons in the streets of Paris.

PASSIVE ORGANS OF LOCOMOTION.

It would be out of place to describe fully and in detail all of the varied and complex movements produced by muscular action. Many of these, such as the movements of deglutition and of respiration, are necessarily considered in connection with the functions of which they form a part; but others are purely anatomical questions. Associated and antagonistic movements, automatic and reflex movements etc., belong to the history of the motor nerves and will be fully considered in connection with the physiology of the nervous system.

The study of locomotion involves a knowledge of the physiological anatomy of certain passive organs, such as the bones, cartilages and ligaments. Although a complete history of the structure of these parts trenches somewhat upon the domain of anatomy, a brief description of their histology will practically complete the account of the tissues of the body, with the exception of the nervous system and the organs of generation, which will be taken up hereafter.

Locomotion is effected by the muscles acting upon certain passive, movable parts. These are the bones, cartilages, ligaments, aponeuroses and tendons. The fibrous structures have already been described, and it only remains to study the structure of bones and cartilages.

Physiological Anatomy of the Bones.—The bones are composed of what is called the fundamental substance, with cavities and canals of peculiar form.

The cavities contain corpuscular bodies called bone-corpuscles. The canals of larger size serve for the passage of blood-vessels, while the smaller canals (canaliculi) connect the cavities with each other and finally with the vascular tubes. Many of the bones present a medullary cavity, filled with a peculiar structure called marrow. In almost all bones there are two distinct portions; one, which is exceedingly compact, and the other, more or less spongy or cancellated. The bones are also invested with a membrane, containing vessels and nerves, called the periosteum.

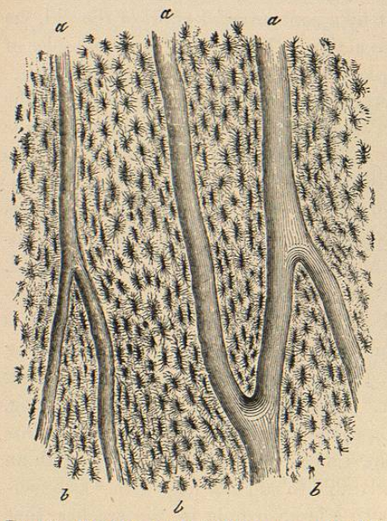

FIG. 158.—*Vascular canals and lacunæ, seen in a longitudinal section of the humerus; magnified* 200 *diameters* (Sappey).

a, a, a, vascular canals; *b, b, b*, lacunæ and canaliculi in the fundamental substance.

The fundamental substance is composed of an organic matter, called osseine, combined with various inorganic salts, in which calcium phosphate largely predominates. In addition to calcium phosphate, the bones contain calcium carbonate, calcium fluoride, magnesium phosphate, sodium phosphate and sodium chloride. The relative proportions of the organic and inorganic constituents are somewhat variable; but the average is about one-third of the former to two-thirds of salts. This proportion is necessary to the proper consistence and toughness of the bones.

Anatomically, the fundamental substance of the bones is arranged in the form of regular, concentric lamellæ, about $\frac{1}{3000}$ of an inch (8 μ) in thickness. This matter is of an indefinitely and faintly striated appearance, but it can not be reduced to distinct fibres. In the long bones the arrangement of the lamellæ is quite regular, surrounding the Haversian canals and forming what are sometimes called the Haversian rods, following in their direction the length of the bone. In the short, thick bones the lamellæ are more irregular, frequently radiating from the central portion toward the periphery.

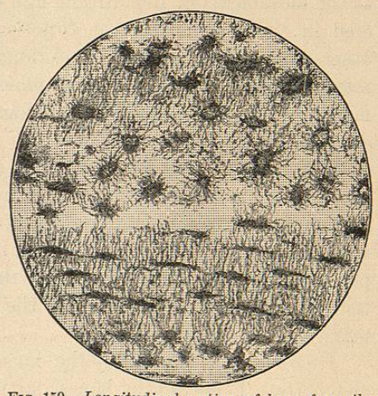

FIG. 159.—*Longitudinal section of bone, from the shaft of the human femur; magnified* 180 *diameters* (from a photograph taken at the United States Army Medical Museum).

The Haversian canals exist in the compact bony structure. They are either absent or are very few in the spongy and reticulated portions. Their form is rounded or ovoid, the larger canals being sometimes quite irregular. In the long bones their direction is generally longitudinal, although they anastomose by lateral branches. Each one of these canals contains a blood-vessel, and their disposition constitutes the vascular arrangement of the bones. They are all connected with the openings on the surface of the bones, by which the arteries penetrate and the veins emerge. Their size, of course, is variable. The largest are about $\frac{1}{60}$ of an inch (400 μ) and the smallest, $\frac{1}{800}$ of an inch (30 μ) in diameter (Sappey). Their average size is $\frac{1}{250}$ to $\frac{1}{200}$ of an inch (100 to 125 μ). In a transverse section of a long bone, the Haversian canals may be seen cut across and surrounded by twelve to fifteen lamellæ.

Lacunæ.—The fundamental substance is everywhere marked by irregular, microscopic excavations, of a peculiar form, called lacunæ. They are connected with little canals, giving them a stellate appearance. These canals are most abundant at the sides of the lacunæ. The lacunæ measure $\frac{1}{1250}$ to $\frac{1}{800}$ of an inch (20 to 30 μ) in their long diameter, by about $\frac{1}{2500}$ of an inch (10 μ) in width.

Canaliculi.—These are little, wavy canals, connecting the lacunæ with each other and presenting a communication between the first series of lacunæ and the Haversian canals. Each lacuna presents eighteen to twenty canaliculi radiating from its borders. The length of the canaliculi is $\frac{1}{800}$ to $\frac{1}{600}$ of an inch (30 to 40 μ), and their diameter is about $\frac{1}{25000}$ of an inch (1 μ). The arrangement and relations of the Haversian canals, lacunæ and canaliculi are shown in Fig. 160.

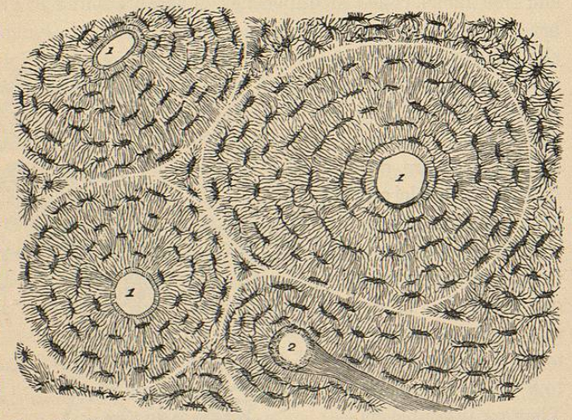

FIG. 160.—*Vascular canals and lacunæ, seen in a transverse section of the humerus; magnified* 200 *diameters* (Sappey).

1, 1, 1, section of the Haversian canals; 2, section of a longitudinal canal divided at the point of its anastomosis with a transverse canal. Around the canals, cut across perpendicularly, are seen the lacunæ (with their canaliculi), forming concentric rings.

Bone-cells or Corpuscles.—These structures are stellate, granular, with a large nucleus and several nucleoli, and are of exactly the size and form of the lacunæ. They send out prolongations into the canaliculi, but it has been impossible to ascertain positively whether or not they form membranes lining the canaliculi throughout their entire length.

Marrow of the Bones.—The marrow is found in the medullary cavities of the long bones, filling them completely and moulded to all the irregularities of their walls. It is also found filling the cells of the spongy portion. In other words, with the exception of the vascular canals, lacunæ and canaliculi, the marrow fills all the spaces in the fundamental substance. The cavities of the bones are not lined with a membrane corresponding to the periosteum, and the marrow is applied directly to the bony substance. In the fœtus and in very young children the marrow is red and very vascular. In the adult it is yellow in some bones and gray or gelatiniform in others. It contains certain peculiar cells and nuclei, with amorphous matter, adipose vesicles, connective tissue, blood-vessels and nerves. Robin has described little bodies, existing both in the form of cells and free nuclei, called medullocells. These are found in greater or less number in the bones at all ages, but they are more abundant in proportion as the amorphous matter and fat-cells are deficient. The nuclei are spherical, sometimes with irregular borders, generally without nucleoli, finely granular, and $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch (5 to 8 μ) in diameter. They are insoluble in acetic acid. The cells, which are less abundant than the free nuclei, are spherical or slightly polyhedric, contain a few pale granulations, are rendered pale but are not dissolved by acetic acid, and they measure about $\frac{1}{1700}$ of an inch (15 μ) in diameter. Irregular, nucleated patches, described by Robin under the name of myeloplaxes, more abundant in the spongy portions than in the medullary canals,

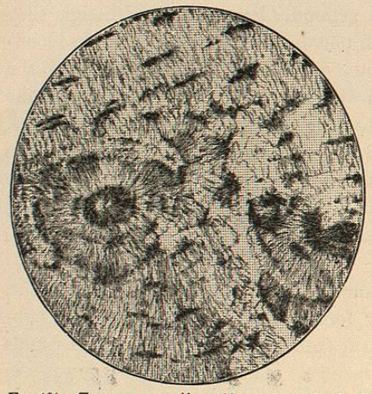

FIG. 161.—*Transverse section of bone, from the shaft of the human humerus; magnified* 180 *diameters* (from a photograph taken at the United States Army Medical Museum).

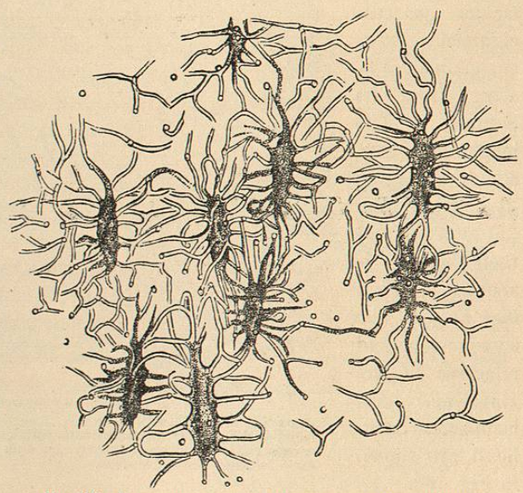

FIG. 162.—*Bone-corpuscles, with their prolongations* (Rollett).

are found applied to the internal surfaces of the bones. They are very irregular in size and form (measuring $\frac{1}{1200}$ to $\frac{1}{250}$ of an inch, or 20 to 100 μ in diameter), are finely granular, and present two to twenty or thirty nuclei. The nuclei are clear and ovoid and are generally provided with a distinct nucleolus. The myeloplaxes are rendered pale by acetic acid, and the nuclei are then brought distinctly into view. They are particularly abundant in the red marrow.

In addition to the anatomical elements just described, the marrow contains a few very delicate bundles of connective tissue, most of which accompany the blood-vessels. In the fœtus the adipose vesicles are few or may be absent; but in the adult they are quite abundant, and in some bones they seem to constitute the whole mass of the marrow. They do not differ materially from the fat-cells in other situations. Holding these different structures together, is a variable quantity of semi-transparent, amorphous or slightly granular matter.

The nutrient artery of the bones sends branches to the marrow, generally two in number for the long bones, which are distributed between the various anatomical elements and finally surround the fatty lobules and the fat-vesicles with a delicate capillary plexus. The veins correspond to the arteries in their distribution. The nerves follow the arteries and are lost when these vessels no longer present a muscular coat. Nothing is known of the presence of lymphatics in any part of the bones or in the periosteum.

The chief physiological interest connected with the marrow of the bones is in its relations to the formation of blood-corpuscles. This question has already been discussed in connection with the development of the corpuscular elements of the blood.

Periosteum.—In most of the bones the periosteum presents a single layer of fibrous tissue, but in some of the long bones two or three layers may be demonstrated. This membrane adheres to the bone but can generally be separated without much difficulty. It covers the bones completely, except at the articular surfaces, where its place is supplied by cartilaginous incrustation. It is composed mainly of ordinary fibrous tissue with small elastic fibres, blood-vessels, nerves and a few adipose vesicles.

The arterial branches ramifying in the periosteum are quite abundant, forming a close, anastomosing plexus, which sends small branches into the bony substance. There is nothing peculiar in the arrangement of the veins. The distribution of the veins in the bony substance itself has been very little studied.

The nerves of the periosteum are very abundant and form in its substance quite a close plexus.

The adipose tissue is very variable in quantity. In some parts it forms a continuous sheet, and in others the vesicles are scattered here and there in the substance of the membrane.

The importance of the periosteum to the nutrition and regeneration of the bones is very great. Instances are on record where bones have been removed, leaving the periosteum, and in which the entire bone has been