OUTLINES OF THE COMPARATIVE PHYSIOLOGY AND MORPHOLOGY OF ANIMALS

By Prof. JOSEPH LE CONTE.

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D. APPLETON AND COMPANY, NEW YORK.

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BY

JOSEPH LE CONTE

AUTHOR OF
RELIGION AND SCIENCE; ELEMENTS OF GEOLOGY; SIGHT,
AN EXPOSITION OF THE PRINCIPLES OF MONOCULAR
AND BINOCULAR VISION; EVOLUTION AND ITS
RELATION TO RELIGIOUS THOUGHT, ETC.

NEW YORK
D. APPLETON AND COMPANY
1900

PREFACE.

So many books have recently come out, and are still coming out, on zoölogy and biology that it seems necessary that I should say something of the reasons for this one.

Nearly all the books now coming out are devoted, and rightly so, to practical laboratory methods, and especially to the study of *selected types.* This method, first introduced by Rolleston and rendered popular by Huxley, was a reaction against the barrenness of the old text-book and lecture method. It was certainly timely and necessary; but there is danger that, like all reactions, it may have, and indeed has already, gone too far. Undoubtedly the teaching by types is indispensable in the early part of the course, in order to introduce the student into the true spirit and methods of science; but to continue it and "make it the main form of teaching is a serious mistake." * There is serious danger that in the attempt to explore thoroughly a few small spots here and there in the field we lose sight of the general connection of all parts to one another and to the whole —that in the microscopic clearness but narrowness of our knowledge we lose that general view of the whole which alone gives significance to any knowledge.

Such a general view of the physiology and morphology of the animal kingdom is, it seems to me, a great

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* Lankester, Nature, lviii, 25, 1898.

want in our teaching of zoölogy to-day—a want which is only now beginning to be recognized. It is just such a general view which I have attempted to give in this volume. The book is not intended to take the place of books already in the field, but to supplement them. It is intended to precede and accompany the special laboratory courses of our high schools, colleges, and universities. It must itself be preceded by the type method in the schools.

Some will think I have too much slighted the invertebrates. I can only say that this was unavoidable if I kept within the limits of a moderate-sized book. I have given only what every intelligent person would like to know.

Again, some will perhaps think that I dwell too much relatively on certain functions—e. g., the sense of sight and glycogeny. I can only answer that a perfectly balanced treatise on any wide and complex subject is well-nigh impossible, and I am not sure that it would be best even if it were possible. A certain insistence on points best known to and most thoroughly investigated by the teacher—a certain hobby riding, if not carried too far—is necessary to give life and interest to any subject.

Some may object to the order of treatment—descensive instead of ascensive. This, I believe, finds justification in the fact that physiology, not morphology, is the prominent point of view. This I explain fully in the book (page 27).

The work is the final embodiment of a course of lectures continued and compacted for many years, and given in connection with and preparatory to the laboratory courses in zoölogy in the University of California.

JOSEPH LE CONTE.

BERKELEY, CAL., *October, 1899.*

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OUTLINES OF COMPARATIVE PHYSIOLOGY AND MORPHOLOGY OF ANIMALS.

INTRODUCTORY.

SOME GENERAL PRINCIPLES.

SECTION I.

RELATIONS OF THE THREE KINGDOMS OF NATURE TO ONE ANOTHER.

NATURE is primarily divided into two kingdoms, the living and the nonliving. The living kingdom is subdivided into the animal and the plant kingdoms, thus:

Living..................	3. Animal. 2. Plant.
Nonliving..................	1. Mineral.

We may, indeed, divide Nature into three kingdoms—mineral, plant, and animal—as seen above; but, if so, it is necessary to remember that the gap between the organized and the unorganized, the living and the nonliving, is far greater than between the two divisions of the living kingdom, i. e., between plants and animals. The study of unorganized or nonliving Nature belongs to physics and chemistry; the study of organized or living Nature belongs to biology.

Living vs. Nonliving.—Besides the essential properties belonging to all matter, living things have certain additional and distinctive properties. These are all connected with the *endowment of life.* But we know nothing of life except by its properties. The same, however, is true of all other forces of Nature. We know not what they are, but only what they do, how they behave. Life, like all other forces of Nature, is a *specific form of energy* characterized by a peculiar group of phenomena, the subject-matter of a distinct science —biology. What, then, are the peculiar phenomena of life?

1. **Organization.**—All living things are *organized*—i. e., consist of different parts having different functions and all co-operating for one given end, the conservation of the organism. It may at first seem that by this definition a machine, say a steam engine, is living; but there is this essential difference: the steam engine requires an external force determining the co-operation, while in living things the co-operation is *self-determined.*

2. **Cellular Structure.**—All living things are wholly made up of cells, as completely as a brick building is made up of bricks. Now there is an unorganized cellular structure also—such, for example, as in foam, in soapsuds, in vesicular lava, etc. But there is again this essential difference: in unorganized cellular structure there is simply a homogeneous mass full of hollow spaces, while, on the contrary, in organized cellular structure each cell is a living entity—the organized body is a community of living cells.

3. **Growth.**—All living things grow. But do not nonliving things grow also? Take a saturated solution of sugar, or alum, or salt. By evaporation crystals are formed. Small at first, they grow from hour to hour, from day to day, until they become as large as a walnut or even as one's fist. But again, we find essential differences in the kind of growth: 1. The growth of the

crystal is by additions to the *outside*, layer by layer; the growth of the living thing is by material taken into every part of each cell—*interstitial growth.* 2. Again, the growth of the crystal is by materials exactly like itself already existing in the liquid, not made by the crystal; whereas the living thing *makes* the material of its growth; it *manufactures material like itself out of material wholly different from itself, and then uses it for growth—growth by assimilation.*

4. **Life History.**—All living things pass through a regular cycle of changes determined by forces within itself. They are born, increase, culminate, decay, and finally die. No such cycle of changes is observed in nonliving things. Whatever changes they undergo are accidental and the result of *external* causes.

5. **Reproduction.**—As living things have a definite term of existence, they must *reproduce* their kind; otherwise the organic kingdom would speedily pass out of existence. This also is characteristic of living things.

6. **Waste and Supply—Metabolism.**—Continual change of the material composing the body in every part is very characteristic of living things. The living body has been compared to a whirlpool: the *matter* is continually changing while the form remains. In the living body the change is in some sense self-determined. This ceaseless internal change by waste and supply is called *metabolism.* It is rapid in proportion as the life is high.

We are concerned here only with living things. All dead things and the sciences which concern them are therefore put aside; but we must still limit our field. We are not concerned with *all* living things, but only with animals. We must therefore distinguish between animals and plants.

Animals vs. Plants.—The distinctions between animals and plants are apparently so obvious that it may seem useless to draw attention to them, but it is so only to careless view and in comparing the higher members of the two kingdoms. As we descend in the scale the two kingdoms approach more and more, until they absolutely come together—in other words, the living kingdom in its lowest members consists of beings which are both animals and plants, or else neither. They are living things *without further qualification.* In the present state of our knowledge they may be claimed by either botany or zoölogy, and it is proposed to call them *Protista*, or lowest living beings. From these lowest beginnings the two kingdoms separate more and more as we rise. Where they first separate we call them Protozoa (first or lowest animals) and Protophyta (first or lowest plants). Then follow the more distinctive animals and plants, but the animals rise the higher, as in Fig. 1.

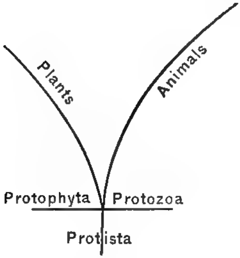

FIG. 1.—Diagram representing the differentiation of animals and plants from *Protista*.

It is not so easy, then, to define the limits of the animal kingdom. Popularly, perhaps, animals would be defined as beings capable of *motion*; but this will not do, for many plants also move under stimulus, as, for example, the sensitive plant. Or perhaps *locomotion* is supposed to be characteristic of animals; but this also fails, because many of the lower plants and the embryos of some higher ones move about with such rapidity that they can hardly be observed carefully under the microscope. On the other hand, many animals somewhat high in the scale, such as oysters, corals, etc., are incapable of locomotion. What, then, are the differences?

1. **Sensation and Volition.**—Doubtless conscious sensation and voluntary motion are characteristic of animals, but the difficulty is in applying the test. We conclude, and probably rightly, that the motions of plants are unconscious and involuntary. In the case of any motion, if we could be certain that it was attended with consciousness, we would rightly conclude that the moving thing was an animal. But how are we to know? Very many of the motions of animals, and even motions within our own bodies, such as motions of the heart, stomach, etc., are wholly unconscious and involuntary.

2. **Nature of the Food and the Relation to the Mineral Kingdom.**—Plants feed on the mineral kingdom directly; animals feed on plants or on one another. The food of plants is *mineral matter*; the food of animals is organic matter made by plants. More specifically, the food of plants is $CO_2.H_2O$ and NH_3. These purely mineral matters are taken and decomposed. Some parts are thrown away, and the remainder are made to combine into new substances not made elsewhere—i. e., organic substances, such as starch, sugar, cellulose, and especially protoplasm. Thus all the organic substance in the world is created by plants, under the influence of sunlight. Animals, so far from creating, are constantly destroying organic matter and resolving it into its original components. Thus the relations of

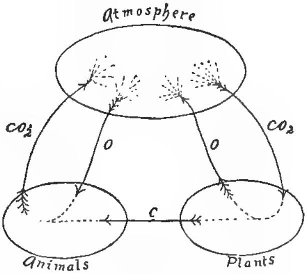

FIG. 2.—Diagram illustrating the circulation of carbon and oxygen.

the two living kingdoms to the mineral kingdom are the converse of one another: plants making organic matter from minerals, and animals destroying organic matter and returning it again to the mineral kingdom. Limiting our view now to one of these mineral plant-foods, CO_2: plants decompose CO_2, returning the oxygen to the air and retaining the carbon to make with other elements organic matter; animals contrarily take carbon from plants in the form of organic matter of food, and oxygen from the air in respiration, combine these, and restore them to the air as CO_2. Thus there is a continual circulation of carbon and oxygen between these three kingdoms, as shown in the diagram, Fig. 2. Thus the plant kingdom is a necessary intermediary between the mineral and the animal kingdoms.

This is probably the best and most philosophical distinction between the two kingdoms; but even in this there is a gradation as we go down the scale of life. In any case we want an easier and more practical test. We find this in

3. **The Possession of a Stomach.**—Animals have stomachs, plants have not. This is really a philosophical distinction, because it is closely connected with the nature of the food. The food of plants is mineral. This mineral food exists in *solution* in water, or else in a gaseous state in the atmosphere. It is therefore already in condition to be at once absorbed without further preparation. It is thus absorbed by the surface of the roots and of the leaves—*external absorption.* But the food of animals, being organic matter, is usually in a more or less solid condition, and can not be absorbed until it is dissolved; and this requires time. Therefore animals must have a reservoir in which the food is stored until it is reduced to a liquid condition fit for absorption—*internal absorption.* This reservoir is the

stomach. All animals therefore must have a stomach. In the very lowest animals, however, this organ is extemporized for use when wanted. A single cell, an almost microscopic spherule of gelatinous protoplasm, meets its food, flows around it, takes it in, and digests it (Fig. 156, p. 240).

Again, the food of plants is *everywhere* present. In the form of solution it bathes the roots, in the form of gases it bathes the surface of the leaves. The food-taking is *passive*. Animals *seek* their food, and usually, but not always, *move about* to gather it. This, again, requires a *reservoir* in which to keep it while it is being prepared for absorption. Both the kind of food and the mode of taking it require a stomach. All these four—viz., *kind of food*, the possession of a *stomach*, power of *voluntary motion*, and the seeking of food or *desire*—are closely connected with one another; and the *kind* of food—i. e., organic matter—is the basis of all. For this necessitates appetite, therefore seeking of food, and this locomotion and a reservoir to store; therefore all are characteristic of animals.

4. **Waste and Supply.**—Continual internal change, as already seen, is coextensive with life. But this internal change is far more rapid in animals than in plants. In plants, supply is always in excess of waste, and therefore plants grow as long as they live. In animals, on the contrary, in early life supply is in excess of waste, in maturity they balance and there is no growth, in age waste is in excess. Again, as we shall see hereafter, the whole of animal force is derived from waste, while in plants only a small part is thus derived, the rest being derived from sunlight.

We have now delimited our field of study from other kingdoms of Nature—it is *animals;* and our science from other departments of science—it is *zoölogy*. But the field of zoölogy is far too extensive; we can occupy but a small part.

SECTION II.

DEFINITION OF ZOÖLOGY AND THE SCOPE AND LIMITS OF THIS COURSE.

ZOÖLOGY is the science of animals. It embraces every scientific question that may be raised concerning animals—their form, structure, functions, habits, their affinities, their distribution in time geologically and in space geographically. The subject of this course is only a part of zoölogy.

The most fundamental divisions of zoölogy may be clearly brought out by considering an animal in different ways. We may study the external form of the whole and of each part; then cut into and dissect and determine the form and structure of the internal organs as far as the naked eye can see. Then with the microscope we determine the minute structure of every tissue and organ. All of this is *anatomy*, although the naked-eye anatomy is often called *morphology*, and the minute anatomy *histology*. All this can best be studied in the dead animal.

Or, again, we may study the *functions* of the *living* animal—i. e., the work that each part or organ performs, and the manner in which they all co-operate for the common life and happiness of the animal. This is called *physiology*, and can be studied only in the living animal.

But, again, we may study not only the living mature animal, but the living *growing* animal. Commencing with the yet, apparently, unorganized egg, we may trace the gradual development of each part and of the function which it performs to its completion in the mature condition. This is *embryology.*

Now, if there were but one kind of animal in the world, the study of that species from these three points of view would still be inexhaustible. But the field of study becomes far wider when we remember that there are an almost infinite variety of kinds, of every degree of complexity of organization, and that it is only or chiefly by comparison of these kinds with one another that general laws are reached. Thus each of these departments must be made *comparative* before it can become truly scientific. Thus, then, the three fundamental departments of zoölogy thus far found are (1) *comparative anatomy,* (2) *comparative physiology,* and (3) *comparative embryology.*

But the number and variety of animals is so great, the material of science is so immense, that it is wholly unmanageable and even bewildering unless arranged and classified in an orderly way. Therefore animals are divided and subdivided into groups, according to their *affinities* or their differences and resemblances; those of the larger groups united with one another by the most general characters, and separated from other groups by the most profound differences, the smaller groups being united by smaller but more numerous resemblances, and separated by less profound differences. This is called (4) *taxonomy,* or classification.

But such orderly arrangement can not be made without extensive knowledge of animals in all parts of the world, such as no one man can individually acquire. Therefore it is necessary to *describe* all the kinds of animals, each in its proper place in the orderly arrangement. But this can be done only by the co-operation of all zoölogists in all parts of the world, and the publication of these results, so that each can use the work of *all.* This is called (5) *descriptive zoölogy.* This constitutes, along with taxonomy, *systematic zoölogy.*

But the scope of the subject is not yet exhausted. The earth has been inhabited for millions of years, and the animal forms have been changing during all this time according to certain definite laws. The study of extinct forms, and especially the laws of succession of forms, constitutes another department, called (6) *palæozoölogy.*

Finally, the animals inhabiting different parts of the earth are very different from one another. The causes of these differences and their laws constitute another absorbingly interesting department, for which no universally accepted name has yet been proposed. It has been called *chorology*, but is usually spoken of as *geographical distribution of animals*, or (7) *geographical zoölogy.*

Thus, then, the main departments of zoölogy are:

1. Comparative anatomy or morphology.
2. Comparative physiology.
3. Comparative embryology.
4. Taxonomy, or classification } systematic.
5. Descriptive zoölogy }
6. Palæozoölogy.
7. Geographical zoölogy.

Each one of these departments constitutes a field of study sufficient to occupy the lifetime of any one. It is evident, then, that we can not take up all these with equal fullness. Instruction spread over so wide a field must be far too meager. We select, then, as our central subject the second one, *comparative physiology of animals.* For this, which deals with the phenomena of animal life, is certainly the department to which all others are tributary. But it is impossible to understand function without a knowledge of structure, with which it is associated. Therefore our subject will be physiology, and so much anatomy or morphology as is necessary to explain the physiology, and often something more when the morphology has an important bearing on classification, and especially when it has an important bearing on the question of *evolution.* Embryology we will touch on only when it bears in an important way on the same two subjects. Classification we shall not touch at all except in the indirect way explained above. Some scheme of classification, however, we must, of course, assume as the necessary condition of study, for we can deal with animals only *in groups.* But this we put off until we must have it. Lastly, if we find time we will devote some pages to the laws of geographical distribution of animals, as this has a most important bearing on the question of evolution.

So much to define the scope and limits of our course. It is limited (1) to the science of life, *biology;* (2) to the science of animal life, *zoölogy;* (3) in zoölogy it is limited to *comparative physiology* mainly, but not entirely, for function is indissolubly united with structure and form. It may therefore be called *comparative physiology and morphology.*

SECTION III.

GENERAL STRUCTURE OF ANIMALS.

We have already said that all organisms are composed of living cells. A living cell consists of three parts, viz., (1) a mass of semiliquid protoplasm, usually granulated, (2) a nucleus of more solid matter, and (3) a thin delimiting membrane (Fig. 3). Cellular structure is coextensive with life, but the cells of animals differ considerably from those of plants, and are far less distinct for the following reasons:

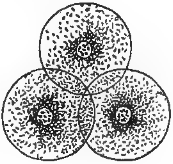

FIG. 3.—Cells.

1. **Size.**—Cells are nearly always microscopic in size, but are far more minute in animals than in plants.

2. **Softness.**—In plants each cell is incased in a firm shell of cellulose, so that in thin sections, such as are used in microscopic examination, they retain their form perfectly; while in animals, unless specially prepared, they collapse and lose their cellular appearance.

3. **Transparency.**—The cells of animals, unless specially prepared by staining, are so transparent that their outlines are often detectable with difficulty. This is far less true in plants.

4. **More highly Differentiated.**—But with proper care all these difficulties may be overcome. The real greatest difficulty is the differentiation of cell form, which is much greater in animals than in plants. Cells take on different forms in order to perform different functions. Therefore as functions increase in number and become more perfect the cells take on more numerous forms, and the forms differ more and more from one another, and all from simple undifferentiated cells. Now functions are more numerous and higher in animals than in plants, and therefore the structure of animals, especially the higher animals, differs greatly from simple cellular structure; so that in the mature condition of the higher animals the simple cellular structure may be entirely lost. The universal cellular structure of animals therefore is best seen in the lowest animals and in the embryonic condition of the higher.

TISSUES.

A tissue may be defined as an aggregate of cells of the *same form* and having the *same function*, but differing in form and function from the cells of other aggregations; different tissues therefore are different *styles of cell structure*, each adapted to a peculiar function. The animal body is made up of cells as completely as a brick building is made up of bricks; but as we may have different kinds of brickwork adapted for various purposes, so we have various kinds of cell work, and these constitute the different tissues. The kinds of tissues are more numerous and more varied as the functions are more numerous and higher, and consequently as we rise in the scale of organization. Therefore they are more numerous and varied in animals than in plants, and in the higher than in the lower animals. It would be useless and confusing to speak of all the kinds of tissues treated in special works on histology. We shall treat of six general kinds, although some of these will be subdivided.

1. **Connective.** — This consists of transparent white interlaced fibers or bands of fibers running in all directions, forming sometimes a loose mesh, sometimes a closely felted structure, in which are found scattered spindle-shaped nucleated cells with continuing branching fibers (Fig. 4). It is called connective because it penetrates and supports—it connects, and yet separates, all the other tissues and organs of the body, forming a sort of universal warp in which all other tissues are woven as a woof determining the pattern of the fabric; so that if all other tissues could be picked out and removed and this one only remained, the whole form of the body with all its organs would be retained in the connective tissue.

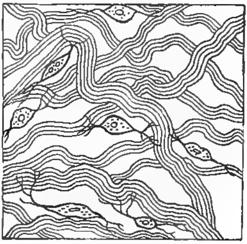
FIG. 4.—Connective tissue.

Examples.—In skinning the dead body of an animal, as we pull the skin from the underlying flesh we observe a white shining mesh connecting them. This is divided with the knife in the act of skinning. This is the subcutaneous connective. It is so loose a mesh that water or air may be pumped in so as to swell up the whole body. General dropsy, in fact, arises from accumulation of water in this tissue. When the skin is removed we may dissect between and separate the several muscles. In doing so we cut the connective *between* the muscles. The same tissue in a denser form constitutes the investing membrane of the muscle. If we cut into the muscle we find that every fiber is invested by the membranous form, and separated from its neighbor fiber by the mesh form of the same. In brief, we may say that this tissue in its denser form invests every fiber, and in its loose form separates and yet connects the fibers; then it emerges on the surface of the muscle in denser form, investing and individuating it; and finally in loose form lies between the muscles, separating and yet connecting them. The same is true of all the organs of the body.

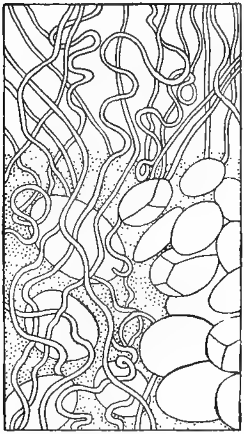

FIG. 5.—Connective tissue with fat cells.

Varieties.—The loose, meshlike form is called *areolar tissue*, or sometimes cellular tissue. The denser form is called *fibrous tissue.* By a little stretch of our definition, the skin, which consists of closely felted, interlacing fibers, may be regarded as an extreme variety of connective. It is called *dermoid* tissue. Scattered about among the interlacing fibers, especially of the areolar variety, are found *nucleated, spindle-shaped cells* with branching fibers—*connective-tissue cells.* Also, the same variety is usually the place of deposit of so-called fat cells, which accumulate often in large quantities (Fig. 5). This is sometimes spoken of as *adipose tissue*, but it is not properly a tissue at all.

2. **Cartilage.**—This will be easily recognized under its popular name, *gristle.* Its *firmness* and yet *elasticity*, its white translucency, its smooth homogeneous surface when cut, are familiar and characteristic properties. If a thin section be placed under the microscope, it is at once seen to consist of innumerable nucleated cells lying in a structureless, semitransparent, hyaline mass (Fig. 6). The cells are in clusters, evidently formed by cell division.

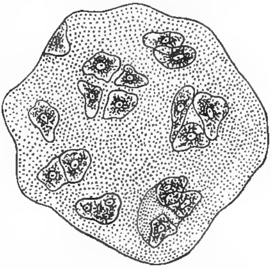

FIG. 6.—Structure of cartilage.

Cartilage is the tissue used in the animal body whenever a moderate degree of firmness combined with elasticity is required. It therefore caps the ends of the bones at the joints. The anterior portions of the ribs are cartilage, so as to yield to respiratory motions. The external ear consists of cartilage, so as to retain its form and yet to be not liable to break. The tip of the nose is of the same substance, and for the same reason.

Varieties.—In higher animals there are two varieties, viz., permanent cartilage, such as all those already mentioned, and temporary cartilage, which afterward becomes bone. Hence cartilage is very abundant in young animals. But the difference between these varieties is too unimportant to detain us.

3. **Bony Tissue.**—Bone is the hardest tissue in the body and is used wherever rigidity is required. It is therefore in higher animals the material of the skeleton. It consists of an organic tissue, a kind of connective, hardened by a deposit in it of mineral matter, chiefly

lime phosphate. These two parts may be easily separated. If bone be thoroughly burned, the organic matter is consumed and the white lime phosphate remains, retaining the form, the structure, and the stiffness of the bone. On the other hand, if a bone be immersed in a weak acid—HCl—for several days, the lime phosphate will be dissolved, leaving the organic tissue, also retaining the form and structure but not the stiffness of the bone. It may now be tied in a knot.

Structure.—Looking closely on the surface of bone one can see with the naked eye long channels, and on cross-section pores like those seen in wood. In this respect it differs from ivory, which has no such pores. These are the *Haversian canals* (Fig. 7, *h*). They are, in fact, blood vessels of the bone. This is as much as can be seen with the naked eye. Under the microscope, in addition, we see that the bony matter is arranged in concentric circles or cylinders about the canals, and that

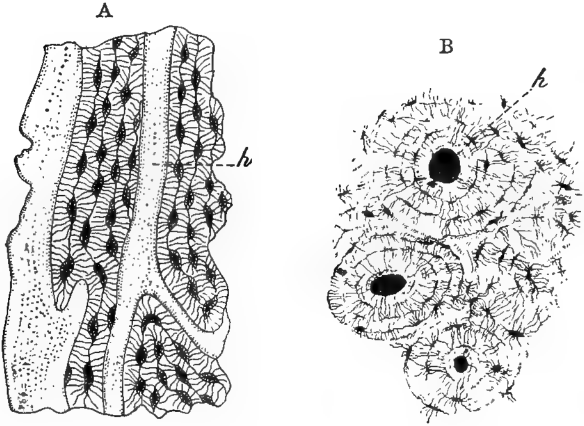

FIG. 7.—Structure of bone: A, longitudinal; B, cross-section; *h*, Haversian canals.

scattered numerously through the bony matter are black cavities. These are the *lacunæ.* Running from these in all directions, like the legs of an insect, are very slender tubes connecting the lacunæ with one another and with the canals. These are the canalicles (canaliculi). The red blood circulates freely through the canals, but the blood globules are too large to pass the canalicles. Therefore only colorless blood plasma reaches the lacunæ.

As already said, bone is the material of the skeleton of higher vertebrates, but as we pass backward in the embryonic series, or down in the animal series, cartilage replaces bone. In other words, cartilage is the embryonic or imperfect form of bone.

Origin.—Bone comes usually from cartilage by deposit of mineral matter; but bone may also be formed by deposit of mineral matter in other tissues, as in fibrous membranes and in skin. So we have cartilage bones, membrane bones, and skin bones.

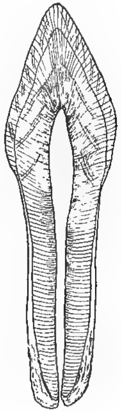
FIG. 8.
Section of tooth.

Varieties.—Dentine is a denser kind of bone in which the canals are wanting. This is the principal material of teeth. Ivory is the finest example. Enamel is a still denser variety of bone which covers the teeth of higher vertebrates (Fig. 8).

We must bear in mind the distinction between *a* bone as an organ and *bone* as a tissue or material of which the organ is composed.

4. **Muscle Tissue.**—We must also distinguish here between a muscle as an organ and muscle as a tissue. A muscle is an organ consisting of several tissues—for example, connective, nervous tissue, etc.—but its charac-

teristic tissue is the muscular. The characteristic property of this tissue is contractility under stimulus of any kind, but, normally, under the stimulus of nerve force.

Structure.—To the naked eye muscle tissue consists of bundles or fascicles of fibers lying parallel to one another; but under the microscope each fascicle is seen to be composed of a multitude of cylindrical fibers transversely striated, and under favorable conditions these again are separable into still finer fibrillæ. Each fiber is invested with a thin membrane of connective tissue (Fig. 9). When a muscle contracts the fibers are observed to *shorten* and *thicken* (Fig. 9, A, B, C).

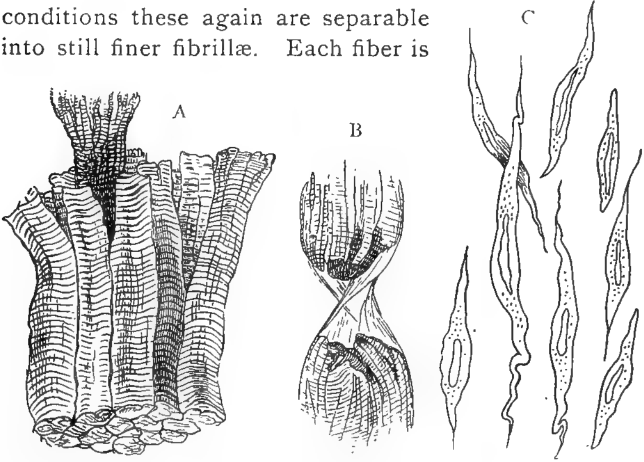

FIG. 9.—A, muscular fibers of voluntary muscle; B, one fiber broken to show its investing sheath; C, cells of involuntary muscle.

Varieties.—There are two kinds of muscle, voluntary and involuntary. The fibers of the one are transversely striated or minutely wrinkled; the fibers of the other are not thus wrinkled (Fig. 9, C).

Of all tissues, muscle is that one in which the original cell structure is most obscured by modification for function. In perfectly formed striated muscle there is no appearance of cell structure visible; but its essential cell structure is seen in the embryonic development of muscle. Fig. 10 shows the fibers of the muscle of the embryonic heart of a monkey. The formation of fibers by fusion of nucleated cells is evident. We shall discuss this again in connection with the physiology of muscle as an organ.


FIG. 10.—Muscular fibers of the heart of the embryo monkey. After Kent.

5. **Nerve Tissue.**—This is the highest and most wonderful tissue of the animal body; not, however, so much in structure (for it is perhaps less specialized than muscle), but in its function. With it, in some way imperfectly understood, is connected the transmission of impressions from the external world to the consciousness, and from the will back again to the external world. With it also is connected sensation, consciousness, will, thought, and all the higher faculties of the mind.

Varieties.—There are, again, two kinds of tissue in nerve tissue, viz., *gray granular* and *white fibrous.* The gray granular consists of nucleated cells of different forms and sizes, apparently connected with one another by interlacing fibers (Fig. 11). The white fibrous consists of very slender parallel fibers, of great length, connected with gray-matter cells. The characteristic function of the gray granular matter is the origination of nerve force; the function of the white fibrous matter is the transmission of the same. The one may be compared to battery cells generating, the other to the wires transmitting, electric energy. The one is found only in the *nerve centers*, such as the brain, the spinal cord, etc.; the other also and most characteristically in the nerves proper. We will discuss this more fully in connection with the physiology of the nervous system.

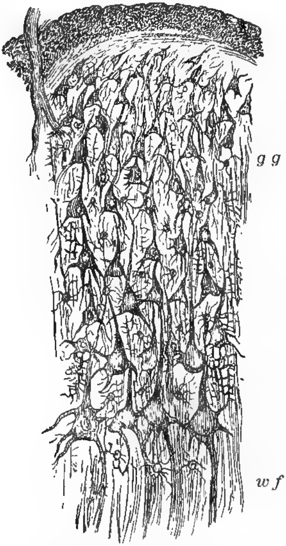

FIG. 11.—Vertical section of a convolution of the brain, showing the cells of the gray granular matter (*g g*) giving out fibers which go to form the white fibrous matter (*w f*) below. After Luys.

6. **Epithelial Tissue.**—The whole surface of the animal body, both external and internal, is covered with a pavement of *living nucleated cells*. These are called epithelial cells. In the higher vertebrates those on the outer surface dry up, become more or less indurated, and are called epidermal. Those on the interior surfaces or mucous membranes always retain their soft, active condition. They are constantly dying, dissolving and passing away as mucus of the mucous surfaces, and as constantly being born and the pavement renewed. It is the least modified of all the tissues.

Function.—Their function is perhaps the most important in the body, viz., the absorption of matter (food) from the external world into the interior of the body, and the elimination of waste matter from the body into the external world. In other words, the whole exchange of matter between the exterior and interior is carried on through this tissue.

Varieties.—This pavement of living cells may be of different patterns; most usually the cells are somewhat rounded (cobble-stone pavement). Sometimes they are flat, polygonal, and fitted together, like a tesselated pavement. Sometimes they are elongated and set on end (columnar epithelium), like wooden block pavements. Sometimes these living cells are provided with ciliæ, which are in continual waving motion and determine currents on the surface in definite directions (ciliated epithelium) (Fig. 12, A, B, C, D).

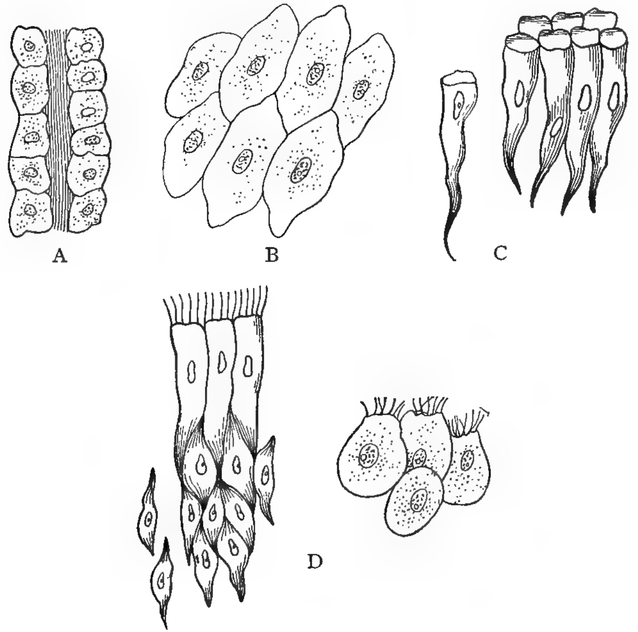

FIG. 12.—Different forms of epithelial cells: A, rounded; B, flat tesselated; C, columnar; D, ciliated.

For convenience of reference we give a schedule of the principal kinds and their varieties:

1. Connective	Areolar. Fibrous. Dermoid.
2. Cartilage	Permanent. Temporary.
3. Bone	Bone proper. Dentine. Enamel.
4. Muscle	Striated. Nonstriated.
5. Nerve	Gray granular. White fibrous.
6. Epithelium	Rounded. Tesselated. Columnar. Ciliated.

Thus, then, there are composing the animal body six different kinds of tissues with their varieties, each with a different function, and all co-operating to produce one end, viz., the conservation of the life and happiness of the organism. This is the type and expression of organization, but it is realized only in the higher animals. As we go down the scale either in the animal series or in the embryonic series, one tissue after another disappears, first bone, then cartilage, then muscle, then nerve, until only unmodified cell aggregate remains, and still lower only a single unmodified cell remains. The corresponding functions merge into one another, and at the same time become less and less perfect, until every part performs, but very imperfectly, *all* the functions of life. Or, taking the reverse order, which is the order of evolution: first there is only *one* cell performing all the necessary functions of life, but very imperfectly; next an aggregate of unmodified and therefore similar cells all performing similar, i. e., all the functions, but imperfectly. Then the process of differentiation commences and proceeds. Some cells take on a special form adapted to the performance of a special function, say contraction, and aggregate to form a tissue, muscle. Other cells take other forms and aggregate to form other tissues adapted to perform other characteristic functions, until finally in the mature condition of the highest animals each kind of cell performs but *one function*, but performs it very perfectly. Thus a muscular fiber can do nothing else but contract. A nerve cell gives no other sign of life but feeling, etc. This whole process of modification of form and limitation and perfecting of function, or division of labor, is called the *law of differentiation*. It is the most fundamental and universal law of evolution.

Observe here—and the same is true of all differentiations—two ideas which must be kept distinct in the mind, viz., (1) identity of plan or *community of origin*—in this case cellular structure—and (2) *adaptive modification* for various functions.

So much for tissues. But physiology is concerned with *functions*, and functions are usually and properly treated in connection with *organs*, such as muscle, brain, gland, etc. The body consists primarily of organs. Thus cells aggregate to form tissues, tissues aggregate to form organs, and organs aggregated form the animal body.

SECTION IV.

ORGANS AND FUNCTIONS OF THE ANIMAL BODY.

Classification of Functions.—The functions of the animal body are of two general kinds, viz., functions of *animal life* and functions of vegetative or *organic life*, or, more briefly, animal functions and organic functions. The animal functions are those which are distinctive of animals. The organic functions are those which are possessed in common by animals and plants, and are therefore coextensive with life. Thus an animal may be regarded as a plant with certain higher and distinctive functions superadded. So also man may be regarded as an animal with certain higher and distinctive functions or faculties superadded. As the idea of animal life is realized in proportion as the distinctive animal functions predominate over the organic, so also the idea of human life is realized only in proportion as the distinctive human faculties predominate and control the animal.

Now these superadded distinctive animal functions are all concerned with conscious action and reaction between the external world and the organism. They are therefore divisible into sensation and consciousness (action) on the one hand, and will and voluntary motion (reaction) on the other. These are, however, very closely related, being both connected with the nervous system. The organic functions—viz., those common to all life—are subdivided into two more widely separated groups, viz., the *nutritive* and *reproductive.* The *nutritive* functions are all that assemblage of functions which co-operate for the conservation of the life of the individual; the *reproductive*, all that assemblage of functions which co-operate for the conservation of the *kind*, even though the individual must die.

Functions	Animal....	Sensation and consciousness.
		Will and voluntary motion.
	Organic...	Nutritive functions.
		Reproductive functions.

Order of Treatment.—Of these groups we shall take up animal functions first, because in the higher animals these functions dominate the others. These will form the subject of Part I. In Part II we shall treat the first subdivision of the organic functions, viz., the nutritive functions, or those which have to do with the conservation of individual life. There ought to be a Part III, treating of all that assemblage of organs and functions concerned with the conservation of the race or species; but this is so vast a subject that it would require a separate treatise.

PART I.

ORGANS AND FUNCTIONS OF ANIMAL LIFE.

THESE must be treated under four groups or *systems* of organs, viz.: 1. Nervous system. 2. Sense organs. 3. Muscular system. 4. Skeletal system. These are closely connected in the performance of the functions of animal life. The general way in which they co-operate is shown in the diagram (Fig. 13).

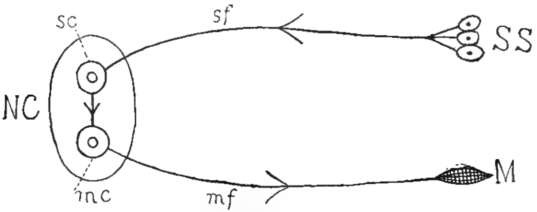

FIG. 13.—Diagram showing essential parts of an apparatus of exchange between the external world and consciousness: *NC*, nerve center; *sc*, sensory cell; *sf*, sensory fiber; *SS*, sensory surface; *mc*, motor cell; *mf*, motor fiber; *M*, muscle. Arrowheads show the direction of transmission.

We have (1) an impression on a sense organ, *SS*; (2) a transmission *inward* along a sensory fiber to a nerve center *N.C.*, say the brain; (3) a change of some kind in a sensory cell, *s.c.*, which awakens conscious sensation; (4) an influence of some kind transferred by a connecting fiber to a motor cell, *m.c.*; (5) an impulse transmitted *outward* along a motor fiber, *m.f.*, to a muscle, *M*, and determining (6) muscular contraction and motion and changes in the external world. The skeleton acts as levers to make the motion more rapid, precise, and effective. Thus the sense organs may be regarded as *receptive* organs of *sensation* and *consciousness*, and the muscles and skeleton as executive organs of the *will*, and the whole as an instrument of action and reaction between the external and the internal world.

Therefore the necessary parts of an instrument of communication between the outer and the inner world are (1) two kinds of cells in the nerve center, viz., a sensory cell and a motor cell with connecting fiber between; (2) two kinds of transmitting fibers, the one sensory, transmitting inward, the other motor, transmitting outward; and (3) two kinds of nerve-fiber *endings*, one in a sensitive surface or a sense organ, the other in a contractile tissue or muscle. Each cell, sensory or motor, with its fiber and its ending is called a *neurone* or *neurocyte*. The connection between a sensory and a motor neurone, until recently, was supposed to be continuous and permanent, as represented in the figure; but now it is believed to be by *contact* of branching processes, and perhaps only during stimulation. This will be explained more fully hereafter.

Of the four systems mentioned as concerned in animal functions, viz., nervous system, sense organs, muscles, and skeleton, the fundamental one is the nervous. The others may be regarded as appendages of this one. We therefore take this first.

Order of Treatment.—There are two modes or orders of taking up the subject of comparative physiology and morphology. We may begin with the lowest and go up the scale; this is the order of evolution. Or we may begin with man and pass down the scale. If our subject were mainly morphology the former might possibly be the best, although even then, it is perhaps doubtful; but in physiology there can be no doubt that the latter is best. It is so for two reasons: first, because we take hold at once of the interest of the student, and, second, because *functions* are fully separated and declared and therefore intelligible only in the higher animals. As we go down the scale functions are more and more merged into one another, and therefore more and more indistinct, until in the lowest animals each part performs all the functions, but in so imperfect a way that it is impossible to understand them unless we have already studied them in their separated and perfect form in the higher animals. "In higher animals the functions rise to the surface; in lower animals they are deeply buried. We grope in vain unless we find the key by the study of the higher animals." *

Our plan, then, will be to take up each system of organs first in man; then, running down the scale of *vertebrates*, show the modifications and simplifications which we find there. Then we shall take the other departments of the animal kingdom and treat them in the same way, but much more cursorily.

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* Foster, Nature, vol. lvi, p. 437, 1897.

CHAPTER I.

THE NERVOUS SYSTEM OF MAN.

THE nervous system of man, and indeed of all vertebrates, may be divided into two subsystems, viz., the *cerebro-spinal* and the *ganglionic*. Their relations to one another are shown in a subsequent figure (Fig. 38, page 68). We put aside for the present the ganglionic system.

THE CEREBRO-SPINAL SYSTEM.

General Plan.—The general plan of structure of this system in man, and indeed in all vertebrates, is simply expressed as a continuous tract or axis of gray matter extending nearly the whole length of the body, from which run off in pairs bundles of fibers (nerves) going to every part of the body, as shown in the diagram (Fig. 14). In the lower vertebrates there is very little more than this, but in the higher vertebrates, and especially in man, this simple plan is obscured by the enormous development of the anterior part as a brain, as shown in the dotted outline. This continuous tract is called the *cerebro-spinal axis*.

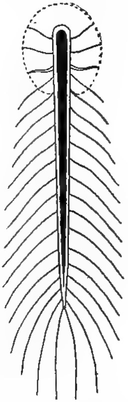

FIG. 14.—Diagram showing the general plan of structure of the vertebrate nervous system.

The cerebro-spinal axis may be again subdivided into the *brain* and the *spinal cord*; so that the subject of the cerebro-spinal system may be treated under three heads of (1) the *brain*, (2) the *spinal cord*, and (3) the *nerves*. The brain and spinal cord are *centers*, the nerves are conductors. The first two contain gray matter as well as white, the last white matter alone. The first two are generators of nerve energy, the fibers of the third are transmitters only. The former may be likened to battery cells, the latter to conducting wires.

SECTION I.

Brain of Man.

We can give only such general description as is necessary to explain physiology.

Skull.—The brain is inclosed in a bony box consisting of many pieces fitted together by sutures with interlocking teeth. The growth of the skull to accommodate the growing brain takes place along these sutures. The sutures finally consolidate and the brain can grow no more. The age of consolidation is later in the higher races, and is probably also later in educated men.*

Membranes.—Take off the skull, and beneath we see the brain still enveloped by its membranes. These are (1) the *dura mater*, a thick, strong, fibrous membrane. This invests the brain and dips in and separates all the great divisions of the brain, but not the convolutions. It carries also the large blood vessels of the brain. Beneath and more closely investing the brain, passing between not only the larger but also the smaller divisions, and even dipping down between the convolutions of the surface and carrying the smaller blood vessels which penetrate the substance of the brain itself, there

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* Galton, Nature, vol. xxxviii, p. 14, 1888,

is seen (2) a more delicate membrane called the *pia mater*. Between these and uniting them is still a third membrane (3) the arachnoid. It is inflammation of these membranes rather than of the brain itself that constitutes the more acute forms of brain disease attended with violent delirium.

Main Parts of the Brain. 1. **Cerebrum.**—Take out the brain from the skull and place it on the table and remove the membranes.* Looking down on it from above we see nothing but a great hemispherical irregularly convoluted mass—the cerebrum—divided along the middle into two equal halves. These are the right

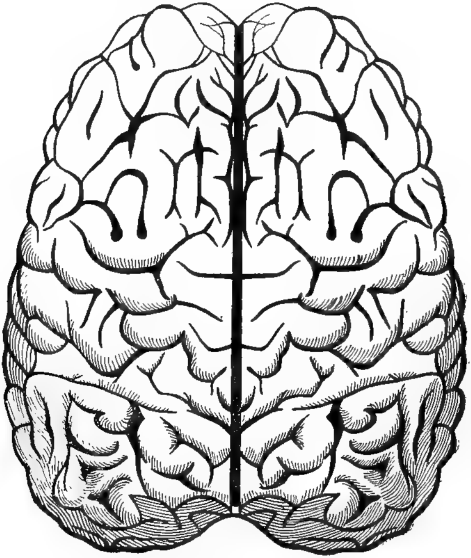

FIG. 15.—Cerebrum seen from above.

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* In the absence of brain an Auzoux model will serve an excellent purpose.

and left cerebral hemispheres (Fig. 15). The trench that divides them is about two inches deep and occupied by an extension of the membranes. The two hemispheres are connected below by a band about half an inch thick —the corpus callosum. The cerebrum constitutes about four fifths of the whole brain.

2. **Cerebellum.**—Lifting the cerebrum from behind, the next most important part brought into view immediately beneath the hinder part of the cerebrum is the *cerebellum*. This is also a double organ like the cerebrum, but the two halves are not so deeply divided by the membranes. The peculiar leaflike arrangement of the convolutions will be observed. A side view of the brain (Fig. 16) shows the cerebellum beneath the under part of the cerebrum.

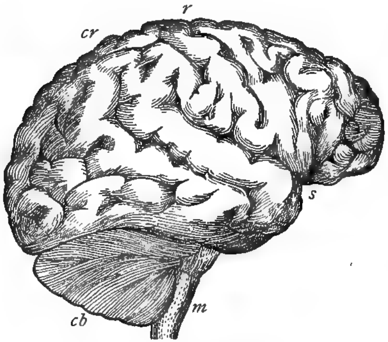

FIG. 16.—Side view of the brain: *cr*, cerebrum; *cb*, cerebellum; *m*, medulla; *s*, fissure of Sylvius; *r*, fissure of Rolando.

3. **Medulla and Pons.**—Lying beneath the cerebellum, as if this latter had grown out of it, is an enlarged continuation of the spinal cord within the skull. This is called the medulla. Beneath this again, with fibers running across the medulla and connecting the two sides of the cerebellum, is the *pons Varolii* (bridge of Varolius). This can only be seen, however, by turning the brain over so as to see the under side (Fig. 17).

4. **Optic Lobes.**—Lifting the cerebrum from behind still higher and looking farther forward, the optic lobes are brought into view in front of the cerebellum. In

human anatomy these are called the corpora quadrigemina, because they consist of two pairs of rounded eminences, but in comparative anatomy they are called the optic lobes, because connected with the sense of sight. They are small and inconspicuous in the human brain, but in the lower vertebrates they may be larger even than the cerebrum.

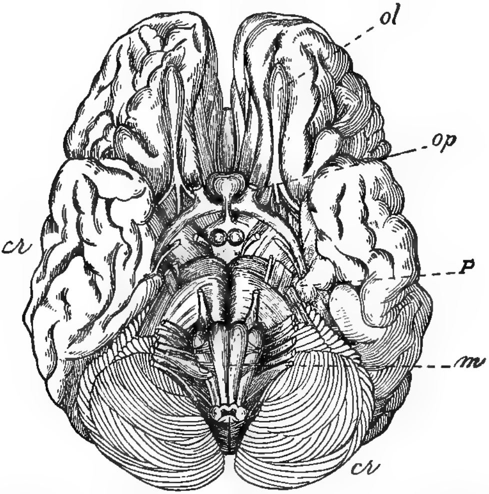

FIG. 17.—View of brain from below: *cr*, cerebrum; *cb*, cerebellum; *m*, medulla; *p*, pons, showing the origins of the nerves; *ol*, olfactory, and *op*, the optic nerves.

5. **Thalamus.**—Lifting the hinder part of the cerebrum still higher and looking as far forward as possible, we see two pairs of much larger rounded masses. These are the thalamus (the first pair) and the corpus striatum (the second pair). We shall often speak of these together as the *thalamus* (Fig. 18).

It would appear, then, but will become far more evident presently, that the spinal cord enters the skull and runs along its base, forming successive swellings and outgrowths in its course forward. First the medulla with its outgrowth, the cerebellum, then the optic lobes with their four swellings atop, then the thalamus with its four swellings, and lastly the cerebrum; but this last has grown backward and covered all the other parts and thus obscured the real structure of the brain. This will come out more clearly presently.

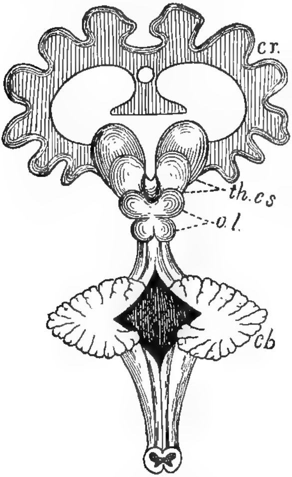

FIG. 18.—A cross-section of the lifted cerebrum: Longitudinal section of the cerebellum, showing optic lobes, *ol*; thalamus and corpora striata, *th*. After Dalton.

Convolutions of the Brain.—The surface of the cerebrum is diversified with irregular folds (convolutions) with deep trenches between. Into the trenches enter the pia mater, but not the dura mater. There are a few larger trenches called fissures dividing the cerebral hemispheres into *lobes*. The most conspicuous of these is the fissure of Sylvius (Fig. 16, *s*). It commences well forward, runs backward and upward, separating the *posterior* lobe from the rest of the cerebrum. Another is the fissure of Rolando (Fig. 16, *r*), which separates the rest of the cerebrum into two parts. By these two fissures the cerebrum is divided into three lobes—anterior, middle, and posterior, or frontal, parietal, and occipital.

The cerebellum is convoluted also, but in a more regular way, being deeply separated into parallel laminæ or leaves. *All the other parts are smooth.*

Interior Structure.—So much may be seen without cutting, but on making section we find at once in all parts the two kinds of nerve matter already spoken of (page 19), viz., the gray granular and the white fibrous; but the relative positions of these two kinds are different in the different parts. In the two largest parts, viz., the cerebrum and cerebellum, the gray matter is on the *outside* and the white fibrous matter on the *inside*. In these the surface gray matter follows all the inequalities of the surface convolutions—in fact, it is evident that the convolutions are a device to increase the quantity of gray matter. In the case of the cerebellum the complexity of the infoldings of the surface gray matter is so great as to give rise on section to the peculiar appearance called *arbor vitæ* (Fig. 19).

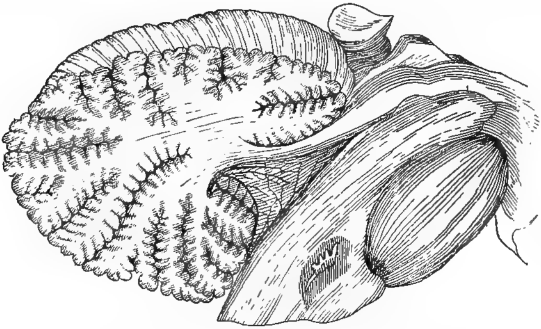

FIG. 19.—Section of cerebellum showing arbor vitæ.

In all the other parts mentioned, viz., the medulla, the optic lobes, and the thalamus, the gray matter is in the *center* and the white matter on the outside.

Microscopic Structure.—As already explained (pages 19 and 27), the gray matter consists of cells of various sizes and shapes, giving out fibers, some connecting with other cells, and some going to form the white fibrous matter (Fig. 20). The white fibrous matter seems to be made up wholly of slender fibers which come from the cells of the gray matter. We may imagine these fibers coming from the surface gray-matter cells, converging to form the white matter of the brain, and then passing out of the skull to form the spinal cord, to be distributed everywhere. Or, conversely, we may conceive fibers of the spinal cord coming into the brain and diverging to end in the cells of the surface gray matter. Then, last of all, these gray-matter cells send out each of them fibers which connect with those of other gray-matter cells. Now it is probable that such a cell with all its fibers, both those connecting with other cells and the long fiber (axis cylinder) connecting with other parts of the body, together constitute one individual cell. Such an individual element of nerve matter is called a *neurone*. On this view the brain, and indeed the whole nerve system, may be regarded as naught else than a collection of neurones intricately connected. The fibers connecting neurones are not simple, but branching (dendrites), and the connection is not continuous, but by contact. They do not unite, but only touch fingers or interlace dendrites (Fig. 21).*

FIG. 20.—Vertical section of a convolution of the brain, showing the cells of the gray granular matter (*g g*) giving out fibers which go to form the white fibrous matter (*w f*) below. After Luys.

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* Professor Turner, British Association Address, 1897. Mathias–Duval, Rev. Sci., vol. ix, p. 321, 1898.

Embryonic Development of Brain.—The fundamental fact that the brain may be regarded as an intercranial continuation of the spinal cord, with swellings and outgrowths atop, is made evident by its embryonic development. The following figures give the stages of this development. In the very early stages the brain is a direct continuation of the spinal cord and consists of three hollow swellings or vesicles. These are what afterward become medulla (1), optic lobes (2), and thalamus (3).

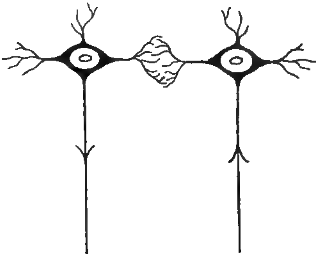

FIG. 21.—Diagram showing the interlacing of dendrites of neurones.

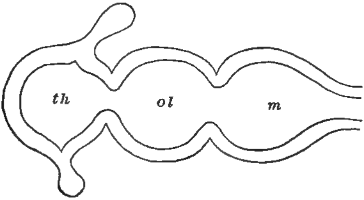

FIG. 22.

We shall call these the *hindbrain*, the *midbrain*, and the *forebrain* (Fig. 22). The next step is the outgrowth of the cerebrum (*cr*) and olfactory lobes (*of*) from the fore-

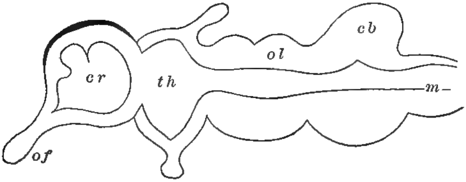

FIG. 23.

brain (No. 3), the cerebellum (*cb*) from the hindbrain (No. 1), and from the midbrain (No. 2) the formation

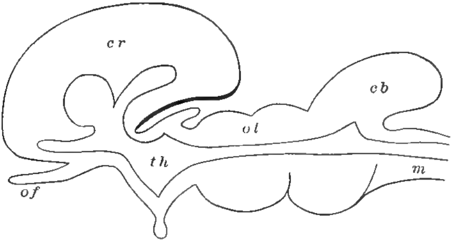

FIG. 24.

or outgrowth of the swellings characteristic of the optic lobes (Fig. 23). The next step is that the outgrowths from 1 and 3—i. e., the cerebellum and cerebrum—increase enormously. This is especially true of the cerebrum, which, commencing as the foremost in the series, grows forward, sidewise, and especially backward, covering first the thalamus (Fig. 24), then the optic lobes (Fig. 25), and finally the cerebellum, and thus masks the

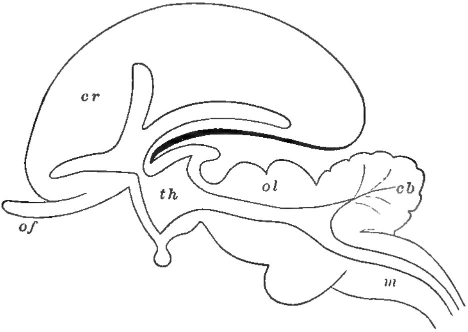

FIG. 25.

true structure of the brain (Fig. 26). The following schedule gives the parts as brought out by embryology.

The italicized are the basic parts, the others being outgrowths.

Forebrain	Olfactory lobes. Cerebrum. *Thalamus.*
Midbrain	*Optic lobes.*
Hindbrain	*Medulla.* Cerebellum. Pons.

See also the strange upward and downward growths from the thalamus. These are the pituitary (*pt*) and the pineal (*pn*) glands. We shall speak of these again.

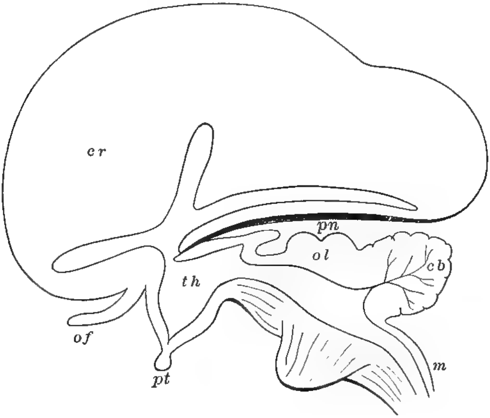

FIG. 26.

The Distinctive Functions of these Parts.—We determine the functions of these several parts partly by observation of injury or disease affecting them in case of man, but mainly by removal of them in case of the lower animals.

Cerebrum.—For example, if the cerebrum be removed from the brain of pigeons, the bird continues to live, but remains in deep, comatose sleep, unconscious and incapable of initiating any movement whatsoever. It stands; if pushed, it will recover itself; if thrown into the air, will fly a little way and alight, but lapses again into coma. If food be put into the mouth, it swallows and digests it, but does not voluntarily take it. Indeed, it will starve in the presence of abundant food. From these experiments it is believed that the cerebrum is the seat of consciousness and conscious sensation, of volition and voluntary motion, and *a fortiori* of all the still higher functions, such as intelligence, etc.

Cerebellum.—If the cerebellum alone be removed, the animal seems to be perfectly conscious, and tries to make its usual movements of standing, walking, flying, etc., but can not do so successfully. It can not stand or walk *steadily.* It flutters, but can not fly. All its movements are voluntary, but uncertain and staggering. It is concluded, therefore, that the function of the cerebellum is the *co-ordination of muscular contraction.* "It is the reflex organ of equilibration." * In the acts of standing, walking, flying, etc., very many muscles are used. The contraction of these is initiated by the will, whose seat is in the cerebrum, but they must be perfectly co-ordinated in order to accomplish any complex act successfully. This is done by the cerebellum. The staggering of drunkenness is the partial paralysis of the cerebellum.

Medulla.—This is the connecting link between the other parts of the brain and the spinal cord, and through the cord with the rest of the body. For this reason, then, its importance is supreme. Again, the nerves controlling the most vital functions of the body, such as those of the lungs and the heart, originate in the gray matter

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* Rev. Sci., vol. viii, p. 503, 1897.

of this part. It is therefore the part most immediately necessary to life. The gray matter of the medulla is the center controlling *automatically* the most vital processes of the body. Removal of this produces immediate death.

Optic Lobe.—This is probably the immediate controller of the sense of sight; its destruction, therefore, destroys that sense. The optic nerve, coming from the eye, sends one root to the optic lobes and another to the thalamus. The latter sends an influence to the visual area of the cerebrum. We will explain this more fully later.

Thalamus and Corpus Striatum.—These ganglia are undoubtedly very important and very necessary to life. Their function is still obscure, but from their connection with the cerebrum on the one hand, and the rest of the body on the other, they seem to be an intermediary between these two. Sense impressions from surfaces and sense organs, on their way to the cerebrum, seem to pass through the thalamus and receive impulse from that organ; and impulses or mandates from the cerebrum on their way outward to the muscles seem to pass through the corpus striatum and receive fresh impulse there. They are relay batteries in the course of communication between brain and body (Fig. 27). They are, moreover and especially, *centers* of *semiautomatic or habitual movements.* There are

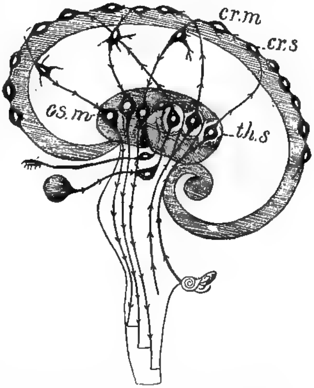

FIG. 27.—Diagram showing supposed function of thalamus and corpus striatum in relation to the cerebrum: *cs*, cerebral sensory; *cm*, motor; *csm*, corpus striatum; *ths*, sensory thalamus.

three kinds of movements in the animal body, viz., voluntary, semivoluntary, and reflex. The cerebrum presides over the first—viz., the distinctly and consciously voluntary actions—such as movements undertaken for the first time and requiring full attention and distinct effort. On the other hand, the medulla and spinal cord preside over the purely automatic or reflex movements—movements wholly withdrawn from consciousness and will, like those of *respiration* and of the *heart*. The thalamus seems to preside over intermediate movements—i.e., semiautomatic or habitual, like those of standing, walking, flying, writing, speaking, playing on a musical instrument, etc. All these are acquired with some difficulty, the cerebrum presiding, but gradually become easier and easier until they require only the most *general* superintendence of consciousness and will. If anything goes wrong, the cerebrum takes control for a while and sets things right, and again the movements lapse into semiautomatism. It is *as if* the cerebrum gradually taught these under-agents or employees—the thalamus and corpus striatum—to do the work themselves, but under general supervision. To compare to an electric apparatus, it is *as if* the sense impulse goes up to the cerebrum through a sensory cell of the thalamus and comes back from the cerebrum through a motor cell of the corpus to the muscle, but a part of the current *short circuits* from the

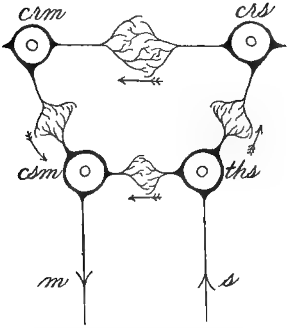

FIG. 28.—Illustrating function of thalamus: *s*, sensory fiber; *m*, motor fiber; *ths*, sensory cell of thalamus; *csm*, motor cell of corpus striatum; *crs* and *crm*, sensory and motor cells of cerebrum.

thalamus to the corpus and downward to the muscle. This short circuiting becomes more and more perfect until only a little overflow goes to the cerebrum, and thus keeps it aware of what is going on. This view is illustrated by the diagram (Fig. 28), in which *s* and *m* = sensory and motor fibers, *ths* and *csm* = sensory and motor cells of thalamus and corpus striatum, and *crs* and *crm* = similar cells in the cerebrum. The arrows show the direction of the nerve current.

Localization of Cerebral Functions.—The cerebrum is the highest ganglion of the brain, and therefore we ought to expect there the greatest degree of differentiation and localization of functions. The old phrenology attempted to localize the faculties of the mind; but recently there has arisen a new and more scientific though far less ambitious attempt to localize *not* indeed the *faculties of the mind*, but the *functions of the cerebrum*—i. e., the areas of the cerebrum receiving and appreciating sense impressions from, and the areas determining and controlling the motions of, various parts of the body. The conclusions arrived at in these investigations are based almost wholly on experiments on the lower animals, especially the monkey, although some of them have been confirmed by observations on man in cases of injury or diseases of the brain.

These investigations are as yet very imperfect, but some reliable results have been attained. Fig. 29 gives the best established areas. It must be remembered that many of our movements are automatic or semiautomatic. These are presided over by the lower ganglia, such as the thalamus, the optic lobes, or the medulla. Take the sense of sight, for example. Many of our sight impressions do not rise into distinct consciousness, and yet appropriate actions may take place. These are probably determined by the thalamus and optic lobes, into which the optic roots are seen to enter. But in many cases we consciously observe and remember the impressions of sight—form mental images of objects seen. In such cases the impression is sent on from the thalamus to the cerebrum. The area to which these impressions are sent—visual area—is situated in the posterior lobes and marked *v*. Similarly, auditory areas are marked *a.a*, general sensation areas by *s*, general motor areas by *m*, and olfactory areas by *olf*.

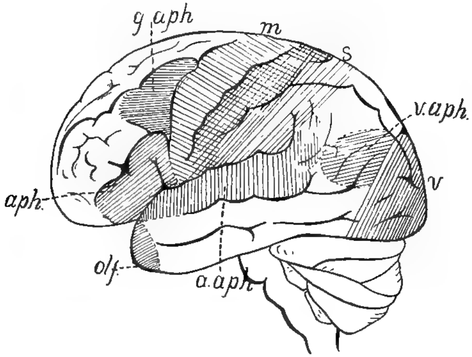

FIG. 29.—Functional areas of the cerebrum: *m*, motor of the body; *s*, sensory of the body; *v*, visual; *olf*, olfactory areas; *aph*, motor aphasia (speech; *a.aph*, auditory aphasia; *v.aph*, visual aphasia (reading); *g.aph*, graphic aphasia (writing).

One of the most curious and interesting of these discoveries is that of the *speech area*, *aph*. This, of course, was discovered by observation on man—not experiments on animals. It has been long observed that there are cases in which a patient is perfectly intelligent and knows what he wants to say, but can not say it. Such an affection is called *aphasia*. In such cases it is invariably found by post mortem that there is a lesion of a particular convolution of the frontal lobe, especially of the left side.

There are, however, many kinds of aphasia. The one above mentioned is *motor* aphasia. But there is also an auditory aphasia (*a.aph*), in which the patient can speak but can not understand spoken words; a *visual* aphasia (*v.aph*), in which the patient can not read; and, finally, a *graphic* aphasia (*g.aph*), in which the patient can not write. These are situated in different parts of the brain and shown on Fig. 29.*

The higher operations of the mind, such as self-consciousness, thought, moral sentiment, etc., which the older phrenology sought to locate, are possibly not localized at all, but involve the co-operative activity of the whole brain, and such co-operative activity is probably controlled by special *centers of association* yet unknown.†

Dextrality.—We have said that aphasia is an affection of a certain convolution of the frontal lobe, especially on the *left* side. This naturally leads one to draw attention to the fact that the cerebral hemispheres control each the opposite side of the body. The fibers from the gray matter of the cortex coming down cross over to the other side. It would seem, therefore, that the greater dexterity of the right side—right-sidedness—is the result of the higher development of the left cerebral hemisphere—left-brainedness. Dexterity is a more perfect co-ordination of muscular motion. Now, there is nothing in which this is more conspicuous than in speech.

SECTION II.

Spinal Cord.

We have already said that the basal part of the brain may be regarded as an intercranial continuation of the

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* Duval, Rev. Sci., vol. xl, p. 769, 1887.

† Turner, Brit. Assoc. Address, Nature, vol. lvi, p. 525, 1897.

spinal cord, or, conversely, the spinal cord as an extracranial continuation of the basal part of the brain. But this extracranial part is so important that it must be treated separately.

Envelopes.—Like the brain, it is incased and protected by a bony cover; but in this case the bony cover must be flexible, and is therefore jointed. This is the jointed backbone so characteristic of vertebrate animals, and giving name to the department. Like the brain, also, it is invested by membranes—an outer tough fibrous and a thin vascular one. As in the brain, too, it is the inflammation of the membranes which gives rise to the acuter forms of disease, such as cerebro-spinal meningitis.

Description.—The spinal cord is a nearly cylindrical white cord, about half an inch in diameter and eighteen inches long. Like the brain, it is a double organ, divided almost into two semicylinders by a cleft down the dorsal and the ventral side. Thus it consists of two semicylinders joined along the axis. Therefore, viewed from the ventral side, we have two *anterior columns*, and, from the dorsal side, two *posterior columns.* The posterior columns carry *sensory fibers*; the anterior, *motor fibers.*

Spinal Nerves.—From the spinal cord proper there go off thirty-one pairs of nerves; from the intercranial continuation of the same there go off, in addition, twelve pairs—making, in all, forty-three pairs of axial nerves. The spinal or extracranial (but not the intercranial) nerves have each two roots, which quickly unite to form one nerve. One of these roots is connected with the posterior or sensory column, and one with the anterior or motor column of the cord. The posterior root has on it a knot or ganglion (Fig. 30, *a*, *b*, and *c*). These nerves pass out between the joints of the backbone and go to be distributed to all parts of the body. This is the case until we reach nearly to the sacrum, where the cord splits up at once into nerves, but still in pairs, to form the *cauda equinæ*—horsetail (Fig. 30, *d*).

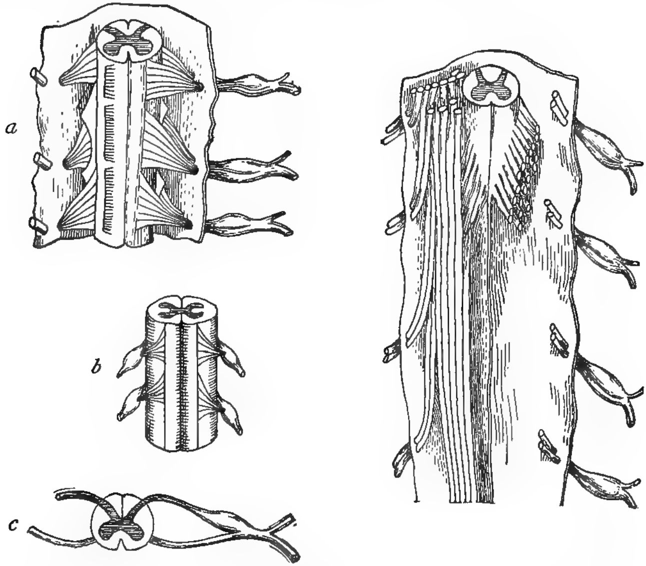

FIG. 30.—Spinal cord: *a*, showing the membrane; *b*, the two roots; *c*, transverse section showing the two roots; *d*, cauda equinæ.

Section.—On making a transverse section (Fig. 30, *b*), it is at once seen that the two kinds of nerve matter are found here also. But here, as in the intercranial basal continuation (but not in the cerebrum and cerebellum), the gray matter is within, and the white matter on the outside inclosing it. We see also that the gray matter has a peculiar form, found also in the medulla—viz., that of a semicircle on each side and a connecting band between (Fig. 30, *b*). As this is only a section view, it is evident that the gray matter on each side is in the form of a plate scrolled outward and connected by a flat transverse plate. Tracing the fibers from the nerves, we find that those from the posterior roots are seen to enter the posterior horn of the gray matter; and those of the anterior roots, into the anterior horn of the gray matter (Fig. 31). The former enter, each, a sensory cell, and through it communicates with a fiber going up the posterior column toward the brain, and even, perhaps, to the cerebral gray matter; the latter similarly through a motor cell and upward perhaps to the cerebrum. This is shown in section (Fig. 32).

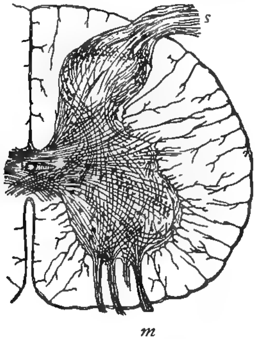

Fig. 31.—Cross section of half the spinal cord, showing how sensory fibers, *s*, and motor fibers, *m*, enter the gray matter.

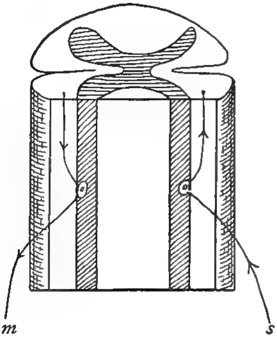

Fig. 32.—Cross and longitudinal section, showing how sensory fibers, *s*, and motor fibers, *m*, communicate with cells of gray matter and pass on. Arrows show direction of transmission.

General Function.—The general function of the cord, therefore, is twofold: *first*, it is a cable—the biggest cable—of conducting fibers from the gray matter of the brain to all parts of the body; and, *second*, it is also a center of gray matter from which issue fibers to all parts. As a center, its distinctive function is reflex or automatic. It is called reflex because an impression coming from a sensitive surface to this center is reflected back, like a bounding ball, to the appropriate muscle without rising into consciousness at all. To it is assigned the control of all those wholly unconscious and involuntary movements—such as those of the heart, the stomach, and the intestines—so necessary to the continuance of bodily life.

The gray matter of the cord is continuous with the gray matter of the basal part of the brain, especially of the medulla, but entirely separated from the exterior gray matter of the cerebrum and cerebellum. The function of the gray matter of the medulla, like that of the spinal cord, is wholly reflex or automatic; that of the thalamus, semiautomatic. Thus, speaking generally, as we go headward and cerebrumward the function of gray matter becomes higher, less automatic, more distinctly conscious, and voluntary.

SECTION III.

Nerves.

We have already said that there are forty-three pairs of axial nerves—i. e., twelve intercranial and thirty-one extracranial or spinal.

Cranial Nerves.—These all come from the intercranial continuation of the axis at the base of the brain, and not from the great outgrowths of the cerebrum and cerebellum, unless we except one, the olfactory, coming from the cerebrum. They all pass through holes in the base of the skull, and are distributed, with two exceptions, to the head and face. Several of them are nerves of special sense. The cranial nerves, on account of their higher and more differentiated functions, have all of them, in addition to their ordinal, also *special* names. In the order of their position, beginning in front, they are:

First pair.—Olfactory = Special sense of smell.

Second pair.—Optic = Special sense of sight.

Third, fourth, and sixth pairs.—Motors of the eye.

Fifth pair.—Trigemini = Common sensory of the face.

Seventh pair.—Facial = Common motor of the face.

Eighth pair.—Auditory = Special sense of hearing.

Ninth pair.—Glosso-pharyngeal (gustatory) = Special sense of taste.

Tenth pair.—Vagus or pneumogastric = Sensory and motor of the heart, lungs, and stomach.

Eleventh pair.—Recurrens = Motor.

Twelfth pair.—Hypoglossal = Motor of the tongue.

In Fig. 33 we give a diagram showing general distribution of these nerves. The origins, as seen in Fig. 17, page 33, are near together. In this Fig. 33 the base of the brain, and especially the medulla, are drawn out so as to separate these origins. In Fig. 34 the medulla is a little drawn out. Fig. 17, page 33, shows their natural position.

Description.—1. The olfactory nerve, the only one which comes from the cerebrum, is observed to pass forward beneath the frontal lobe (Fig. 17), on the base of the skull, until it reaches just above the nasal cavity and on each side of the crista galli. There it throws out a great number of small branches (Fig. 33, 1) through the cribriform (colandered) plate, to be distributed to the mucous membrane of the upper cavities of the nostrils. Its function is to respond to the impression of odoriferous vapors.

Even in man it is seen to swell a little at the end. As we pass down the vertebrate scale, by the increasing size of this swelling it loses entirely its character as a nerve and becomes a great lobe—the olfactory lobe of the brain.

2. *Optic Nerve.*—As already said (page 41), this arises

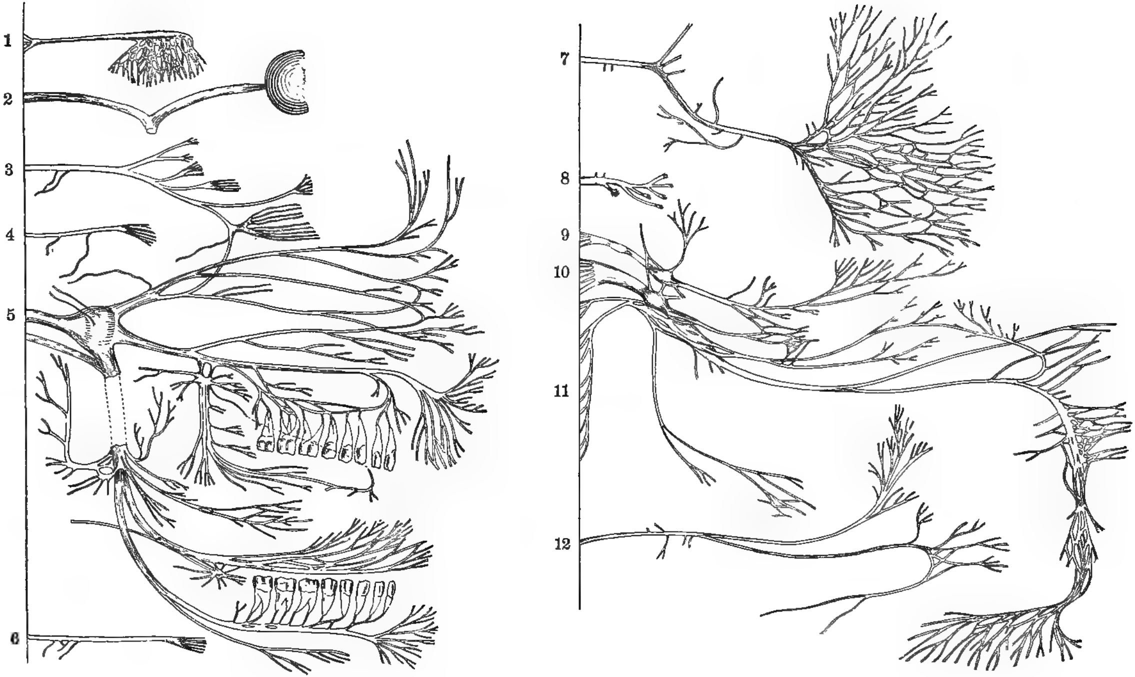

FIG. 33.—Diagram showing the distribution of the cranial nerves. Their origins are shown in Fig. 17, page 33, and more clearly in Fig. 34.

by two roots on each side, one from the optic lobe and one from the thalamus. These quickly unite to form one root on each side, and these join to form the optic chiasm, which lies on the sella turcica (Turkish seat). This is all within the skull (see Figs. 17 and 33). The chiasm immediately separates again into two large nerves, the optic nerves proper, which, piercing the skull at the bottom of the eye sockets, pass forward to enter the eyeball, and there form the retina. Its function is, of course, to respond to impressions of light.

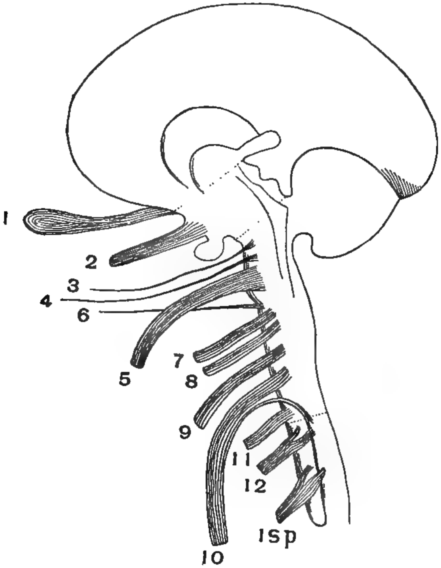

FIG. 34.—Diagram showing side view of brain and medulla somewhat drawn out to separate the origin of the nerves. The last one (1 *sp*) is the first spinal.

3, 4, and 6. *Oculi Motores.*—These we take together because they all have a somewhat similar function, viz., the movements of the eyeball. They come out from the anterior part of the medulla, and are distributed to the ocular muscles (Figs. 33 and 34).

5. *Trigeminal.*—This comes from the anterior portion of the medulla, pierces the skull, and comes out on the face on each side, just in front of the ear. It forms there a ganglion or knob, and then divides into three branches and is distributed to all parts of the face to form the nerves of *sensation of the face.* It is a morbid condition of this nerve which constitutes neuralgia of the face, or *tic douloureux.* Fig. 34 shows how a branch of this nerve goes to each tooth. Toothache also is a painful affection of this nerve.

7. *Facial.*—This, also originating from the medulla, comes out on the face near the ear and ramifies over the whole face and head. It is the general motor nerve of the face. It controls all the facial muscles, and therefore gives emotional expression. Paralysis of the face is an affection of this nerve.

8. *Auditive.*—Coming also from the medulla in close connection with the last, this does not come out on the face at all, but passes immediately into the inner ear, to be distributed there as the nerve of hearing.

9. *Glossopharyngeal* (*Gustatory*).—It is not quite certain what nerve is the gustatory, but the distribution of this one to the back part of the tongue and adjacent parts of the throat, where the gustatory sense chiefly resides, makes it probable that this is it. The distribution is shown in Fig. 33, page 51.

10. *Vagus or Pneumogastric.*—This large nerve comes from the medulla, passes through the base of the skull and down into the thoracic and abdominal cavities, and is distributed to the lungs, the heart, and the stomach. It reports their condition and wants and determines their movements. It is therefore both sensory and motor.

11. *Spinal Recurrent.*—So called because, arising from the spinal cord outside of the cranium, it passes upward within the backbone, enters the skull, and again comes out to be distributed to the muscles of the shoulder. It is a *motor* nerve.

12. *Hypoglossal.*—Arising from the medulla, low down, just before it becomes the cord, it passes out to be distributed to the tongue and to become its motor nerve. It therefore controls articulation.

General Observations on Cranial Nerves.—Observe (1) they all except No. 1 come from the base of the brain or intercranial continuation of the axis; (2) all except 1 and 2 come from the medulla; (3) all the special senses are to be found here; (4) in most cases the sensory and motor fibers are embodied in *separate* nerves, in this regard differing from the spinal nerves, which have each two roots, a sensory and a motor.

Spinal Nerves.—As already said, there are of these thirty-one pairs, each with its two roots. Their distinctive functions are not so different as in the case of the cranial, and they do not therefore need distinct names. They are divided into four groups: cervical, dorsal, lumbar, and sacral. There are eight cervical, twelve dorsal, five lumbar, and six sacral. Those of each group are numbered first, second, third, etc. (Fig. 35).

Distribution.—Most of these are distributed to adjacent parts of the body, but in the upper and lower portion of the series several are united to form the great limb nerves. Thus the fifth, sixth, seventh, and eighth cervical and first dorsal form a plexus from which go the nerves of the arm and hand, while the two last lumbars and four of the sacrals form the plexus from which go the great nerves which supply the leg and foot. In all cases by division and subdivision the branches become smaller and smaller until they pass beyond the power

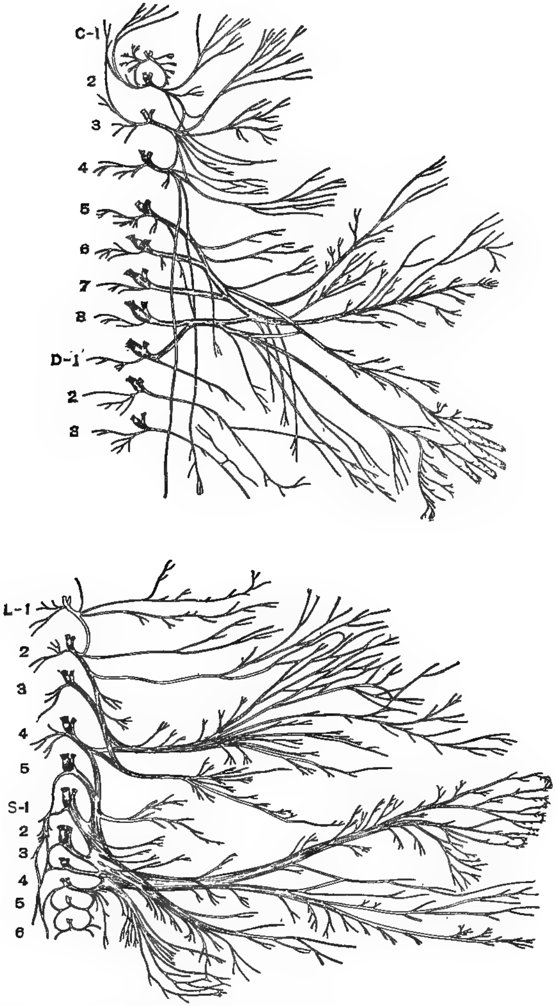

FIG. 35.—Diagram showing spinal nerves and their distribution: *c*, 1, 2, 3, etc., cervical; *d*, 1, 2, 3, etc., dorsal; *l*, 1, 2, 3, etc., lumbar; *s*, 1, 2, 3, etc., sacral. After Flower.

of naked-eye vision, and finally terminate mainly in two ways, viz., some in *muscular* tissues and some in *sensitive surfaces* and *sense organs.*

Structure of Nerves.—A nerve is a bundle of slender fibers of extreme fineness lying parallel and invested by a membrane of fibrous tissue—neurolemma. The size of the fibers varies from $\frac{1}{1500}$ to $\frac{1}{10000}$ of an inch, or even less. The coarsest are the motor fibers and the finest the sensory fibers of the optic nerve. The number in a nerve of $\frac{1}{10}$ inch in diameter may be a million or more. Each fiber consists of a central medullary part and an investing sheath. Each fiber may be continuous from a cell in the central gray matter to its termination in the tissue, but this is probably not true of all. The cerebral cells connect with the surface only through a chain of several cells in the thalamus, the medulla, and the spinal column. A branch of a nerve therefore consists of a number of fibers separated and invested as before, but without branching of the fibers themselves, except at the extreme end where they may form *dendrites.* Thus we may regard each fiber as continuous, one end terminating in a central cell, the other in a tissue.

Function of Nerves.—Nerve fibers are of two kinds, sensory and motor. The one transmits external *impressions inward* to the nerve center (afferent), and may or may not awaken consciousness; the other transmits internal *impulses outward* (efferent), and determines muscular contraction. These two kinds may lie side by side in the same nerve undistinguishable from one another except that the motor is usually larger. The terminations of the one are *centrally* in a *sensory* cell of the central gray matter, and *peripherally* by a peculiar ending in a *sensitive surface* or a sense organ; the terminations of the others are *centrally* in a *motor* cell of the central gray matter, and peripherally in a *muscular* fiber.

Every mechanism for action and reaction between the organism and the external world must consist of two kinds of central cells (a sensory and a motor), two kinds of transmitting fibers (afferent and efferent), and two kinds of peripheral terminations (a sensitive surface or sense organ and a muscular or contractile tissue). Fig. 36, repeated from page 26, is a diagram illustrating this action and reaction. The manner in which the whole acts is briefly as follows: Impression on a sensitive surface or sense organ (S) is transmitted centripetally along a sensory fiber to the nerve center, awakens response, which is transmitted centrifugally along a motor fiber, and determines muscular contraction, which produces motion.

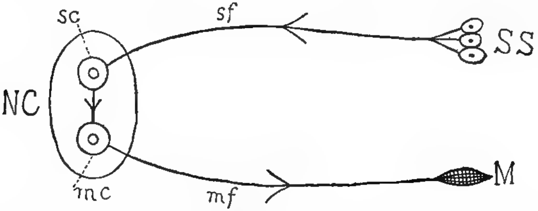

FIG. 36.—Diagram showing essential parts of an apparatus of exchange between the external world and consciousness: *NC*, nerve center; *sc*, sensory cell; *sf*, sensory fiber; *SS*, sensory surface; *mc*, motor cell; *mf*, motor fiber; *M*, muscle. Arrowheads show the direction of transmission.

Both these kinds of fibers are inclosed in the same sheath in the case of spinal nerves, but are usually separated and found in different nerves in the case of the cranial nerves. Thus in the case of the cranial series we speak of sensory and motor *nerves*, but in the spinal series we can only speak of sensory and motor *fibers*.

The Two Subsystems.—The cerebro-spinal system may be conveniently subdivided into two subsystems. By function they may be called the *conscio-voluntary* and the *reflex*; by center they may be called *cerebral* and spinal or *axial*, for it includes the medulla as well as the cord. The center of the one is the *surface* gray matter of the *cerebrum*; the center of the other the *central* gray matter of the *cord* and its continuation in the skull. Each subsystem has its sensory or afferent and its motor or efferent fibers, but the two subsystems are so closely connected that they may act as one. The *spinal* nerves carry both kinds of fibers, which may act as belonging to *both* systems. The cranial nerves usually carry but one kind—i. e., either sensory or motor, acting for both systems.

Course and Termination of Fibers.—A sensory fiber of the cerebral system, beginning in a sensory cell of the cerebral cortex, passes down a posterior column of the cord, communicates with a sensory cell of a posterior cornu, and, continuing, becomes a sensory fiber of the reflex system as well as the cerebral system, and then goes out by a posterior root of a spinal nerve to terminate in a sensitive surface or a sense organ. A motor fiber of the same system goes from a motor cell of the cerebral cortex, down an anterior column of the cord, communicates with a motor cell of the anterior cornu, and continues as a motor fiber of both systems, to terminate in a muscle. The sensory and motor cells, both of the cerebrum and of the spinal cord, connect with one another, so as to complete the circuit, of the cerebral system in the one case, and of the spinal system in the other.

Or, more explicitly, and tracing each impulse in the direction of its transmission: A sensory fiber of the cerebral system, commencing in a terminal on a sensitive surface or in a sense organ, passes up a spinal nerve, through a posterior root into a posterior cornu, communicates there with a spinal sensory cell, then goes up a posterior column to the thalamus, communicating with a sensory cell of that ganglion, and thence onward to a sensory cell of the cerebral cortex, awakening consciousness there; then the impression is transferred to a motor cell of the cerebral cortex, which sends it on in the form of will down through a motor cell of the corpus striatum, then down a fiber of an anterior column of the cord, and, after communicating with a spinal motor cell, out by an anterior root and a spinal nerve, to terminate in a muscle and cause contraction there.

In the reflex system the course is the same, except that the impression carried up by the sensory fiber "*short circuits*" across from the spinal sensory cell to the spinal motor cell without going up to the cerebrum to awaken consciousness there. The course is shown in the diagram (Fig. 37).

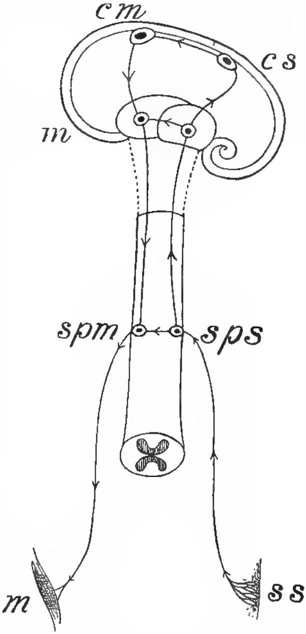

FIG. 37.—Diagram of brain, thalamus-corpus, and a portion of spinal cord, representing course of transmission of nerve influence: *cs*, cerebral sensory, and *cm*, cerebral motor cells; *sps*, spinal sensory, and *spm*, spinal motor cells; *ss*, sensitive surface; *m*, muscle. The arrows show the direction of transmission.

General Mode of Action of the Whole.—Suppose each sensory fiber to have its own terminal, its own spinal sensory cell, and its own cerebral sensory cell, and each motor fiber to have its own muscular fiber terminal, its own spinal motor cell and cerebral motor cell, and the sensory cells in the cerebrum and in the cord to communicate each with its corresponding motor cell. Thus, every cerebral sensory cell would have its corresponding terminal on the body surface, with a connecting fiber between, passing through a corresponding spinal sensory cell; and every cerebral motor cell its corresponding spinal motor cell and muscular terminal with a connecting fiber between. Now touch a point on the body surface, and a wave or current of influence is carried along a sensory fiber through the cord, as already explained, to a cerebral sensory cell, awakening consciousness there. Immediately, or perhaps only after deliberation, the influence is transferred by a connecting fiber to a cerebral motor cell, awakening will, and by it down the spinal cord by a motor fiber, and out to a muscle determining appropriate motion.

See, then, all the phenomena in a case of simple response to external impression: (1) Impression; (2) transmission inward; (3) change in a sensory cell—*conscious sensation*; (4) transmission to a motor cell; (5) change in the motor cell—*will*; (6) transmission outward along a motor fiber; (7) contraction of a muscle. Metaphorically we might say that we have here a complex instrument of communication between the external world and the conscious self, with the self playing on brain cells or interior nerve terminals at one end, and the external world playing on exterior nerve terminals at the other end.

In *Reflex Action.*—If the impression is on an interior surface in a normal condition, the current of influence on reaching the spinal sensory cell is transferred across by short circuit to the corresponding spinal motor cell and *reflected* immediately back along a corresponding motor fiber to the appropriate muscle, without rising at all into consciousness. Such is the case in impressions on the stomach, heart, etc. In other cases, as in swallowing, sneezing, coughing, breathing, etc., the current short circuits, indeed, and appropriate motion takes place immediately by reflex, but sufficient overflow reaches the cerebrum to produce consciousness. In ordinary cases of impression on an external consciously sensitive surface or sense organ, as already seen, the current passes on without short circuit directly to the cerebrum, and consciousness takes charge of the response; but if the impression be *painful*, then the current short circuits without waiting for the slower action of the cerebral system.

For simplicity's sake we have represented the connection throughout as physical and continuous; but, as already explained (Fig. 21, page 37, Fig. 28, page 42), the connection between neurones is probably by touching fingers or interlacing dendrites. It has been suggested that the fingerlike extensions are like pseudopods of amœbæ—that by extension and contraction they *make* and *break contact* with one another. In the active waking state they elongate and make contact; in unconsciousness, in coma, and in sleep they contract and break contact. On this view disconnection of neurones is the physical cause of sleep.*

Illustration by Telegraphy.—To enforce these principles still further and make them still clearer we make a somewhat elaborate comparison with a system of telegraphy.

Suppose, then, the Capitol at Washington represents the *head.* In it there is a great rotunda; this represents the *cerebrum.* Suppose all about the walls a series of alcoves; these shall be the *convolutions.* These are, say, full of battery cells; these are the sensory and motor

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* Mathias Duval, Rev. Sci., ix, 321, 1898.

cells of the cerebrum. From these battery cells there go wires, converging to the hallway and forming there a great cable of wires going out of the door; these are the white fibers converging and forming the *medulla*, and going out of the skull as the *cord.* Before going out, however, certain wires are sent out from the cable to all the offices in the building; these are the *cranial nerves* going to the head and face, and especially to the sense organs. The cable starts out now to communicate with the whole country, but protected by an archway; this is the cord protected by the *vertebral column.* As it goes, the cable gives out wires to adjacent and even distant regions; these are the *spinal nerves.* These must go to every State, county, and city, and terminate in intelligence offices and in executive or police offices; these are the sense organs and the muscles. Suppose also the alcoves are all named as States and the batteries all numbered.

Now, suppose anything to occur in any place. The intelligence office reports the fact to the head center. The State, county, city, neighborhood, is at once known, and the command immediately goes out to the executive office and determines appropriate action.

Application.—Let us now apply this idea and show how it explains the phenomena:

1. Cut the cord high up in the neck. The whole body is paralyzed to both consciousness and volition, but not to reflex function, for that is in the gray matter of the cord, which we are not now considering. Prick the foot and it will jerk, but the prick is unfelt and the jerk is involuntary. Meanwhile all the parts of the face are unparalyzed. The patient sees and speaks as usual, because the nerves controlling these come out from the medulla.

2. Cut the cord in the middle of the back. Now the upper parts of the body, including the arms, etc., feel

consciously and may be moved voluntarily; but the whole lower portion, including the legs, is paralyzed both to conscious sensation and to voluntary motion, because these parts are cut off from the cerebral center. But reflex movements remain.

3. Cut the posterior root of a spinal nerve. Now all that part to which this nerve is distributed is paralyzed to sensation, but may be voluntarily moved. If, on the contrary, the anterior root is cut instead of the posterior, then the part is paralyzed to motion, though not to sensation. If, finally, the nerve is cut below the junction of the two roots, then the part to which the nerve is distributed is paralyzed to both sensation and motion.

4. Irritate a nerve in its course—say, by pinching it. For example, pinch or strike the ulnar nerve, lying between the elbow joint and the inner condyle. We are all familiar with the fact that we *feel pain in the little and ring fingers, where this nerve is distributed.* If it were not for the skin covering the nerve, and which of course has its own nerves of sensation—if the skin were cut away so as to bare the nerve and the nerve alone was pinched, the *only* sensation we should feel would be in the little and ring fingers and that side of the hand. Why? Because the nerves are distributed there. The intelligence offices are there. Therefore *at the head center the painful intelligence seems to be reported from there.* How could it be otherwise?

5. Cut a nerve, perhaps high up in the arm or leg. Expose the ends. Pinch the end below the cut; you feel nothing. But pinch the end above the cut; you feel pain—but where? Not at the place pinched, but in the fingers or toes where the cut nerve is distributed —i. e., where the nerve terminals, the intelligence offices, are. In any telegraphic system, if a wire is cut and a

message sent from the cut end, the head office at Washington could not but refer it to the place where this wire ought to go.

Law of Peripheral Reference.—Thus we have the law *that an impulse received by the brain through a nerve fiber is of necessity referred by the consciousness to the peripheral extremity.* . This explains the fact that in the case of an amputated limb the patient still has a sense of the presence of a foot or hand; and if the nerve of the stump should become diseased, he will often feel intense pain in foot or hand.

Nerve Force versus Electricity.—I have used this comparison with a telegraphic system in order to make the mode of action of the nervous system clear. But we must not conclude, therefore, as many do, that *nerve force*, and indeed life itself, is nothing but *electricity.* It becomes necessary, therefore, that we should draw attention to some fundamental differences between these two forms of energy:

1. Wires lying in contact with one another in the same bundle will not conduct true unless insulated. Nerve fibers, on the contrary, conduct true although lying in contact in the same sheath—in a moist condition, and therefore uninsulated.

2. Cut a wire and press the fresh-cut ends together—they still conduct well. But a cut nerve pressed together utterly fails to conduct nerve influence.

3. In the case of an electric current there must be a *closed* circuit. This is fundamental. If the circuit is open anywhere there is no current and can not be. Not so in the case of a nerve current. There is indeed a sensory current and a return motor current. They are connected, too, at the cerebral end, but certainly not at the peripheral ends. Besides, there is often current only one way—i. e., sensation without corre-

sponding motion, or motion initiated without inciting sensation.

4. The velocity of electricity is always, like all ethereal vibrations, inconceivably great; but the velocity of a nerve current has been measured and found to be very moderate—only about one hundred feet a second. In fact, the phenomena of transmission of nerve influence would suggest an analogy with propagated chemical change, such as combustion of a train of gunpowder rather than electric current.

But it will be answered that "seeing is believing." The electric organ of certain fishes, as the electric eel, discharges powerful currents—sufficient, indeed, to kill a man. These organs are connected with the brain by very large nerves. The discharge of electricity is certainly under the control of the will. It is an act of volition. The fish is exhausted by it as by any powerful effort.

At first sight this seems, indeed, demonstrative; but not so. All the forces of Nature, nerve force and life force among the number, are correlated—i. e., are convertible one into another. Now, the electric organ of a fish constitutes an arrangement for converting nerve force into electricity, precisely as a muscle is an arrangement for converting nerve force into mechanical power. We might as well say that nerve force is identical with mechanical power as to say that it is naught else than electricity.

The fact is, there are many different *forms* of force in Nature, each producing a peculiar group of phenomena, the study of which gives rise to a peculiar department of science. Now the phenomena of nerve force are so different from those of electricity that these two are rightly called different *forms* of the universal energy, although, indeed, they are transmutable into one another.

Function of the Spinal or Reflex System.—As already said, the function of this system is to preside over and control all the routine work of the body—work so constantly necessary that it can not be left to the conscio-voluntary system, which is occupied with other and higher work. Thus the beating of the heart, the play of the respiratory muscles, the movements of the stomach and intestines, are under the control of this system, which never sleeps night or day. The conscio-voluntary system alone sleeps. The passage of control from one system to the other is well seen in the act of swallowing. The food is chewed, then gathered by the tongue, then pressed back into the throat; so much is under control of the voluntary system. As soon as it touches the throat it is seized by the involuntary system and hurried on to the stomach. Nevertheless, there are all gradations between reflex and conscio-voluntary movements. The movements of stomach, intestines, and heart are not only involuntary, but also, in health, unconscious; the acts of swallowing, sneezing, coughing, are involuntary, but not unconscious; the act of breathing is not only conscious, but also partly controlled by volition.

When the conscio-voluntary system is in full activity it takes possession of the consciously sensitive surfaces and the voluntary muscles, so that the reflex system is in abeyance except under conditions of extreme stimulation or pain, in which case the reflex takes hold because the conscio-voluntary is too slow. But when the conscio-voluntary control is withdrawn, as in sleep, or paralyzed, as in section of the cord or of a nerve, then the reflex is far more active, as shown by the unconscious, involuntary movements of hand or foot on the least irritation.

Illustration by Telegraphy.—The system of telegraphy already used to illustrate the action of the conscio-voluntary system may be made to illustrate this also by adding battery cells all along the *cable within the archway*, and these also sending out wires to intelligence offices and executive offices in every part of the country and controlling all necessary routine business without troubling the head center except in case of extreme emergency. By some stretch of the imagination they may be compared to state government.

SECTION IV.

Ganglionic System.

It will be remembered that we divided the whole nervous system of vertebrates into two subsystems, viz., the cerebro-spinal and the ganglionic. The latter we put aside for the time. We now take it up, but very briefly, because it is very imperfectly understood.

Definition.—Nerves are cylindrical bundles of fibers. Every *knot* or *swelling* on these cylindrical strings contains gray matter with cells and gives out the two kinds of fibers terminating in the tissues. In a word, they are little centers of force and are called ganglia. Now the ganglionic system is so called because it consists entirely of such small ganglia scattered about in the body and connected by nerve strings.

Description.—The system consists (1) of a series of ganglia on each side of the spinal column (not in the canal) the whole way from the base of the skull to the end of the sacrum, one opposite each joint of the column (see Fig. 38, *g g*). (2) This series of ganglia is connected throughout on each side by a nerve cord. The two knotted cords thus formed are called the sympathetic nerves (Fig. 38, *n n*). (3) From each spinal nerve there goes off a small branch which connects with the sympathetic nerve on each side, and thus the two sys-

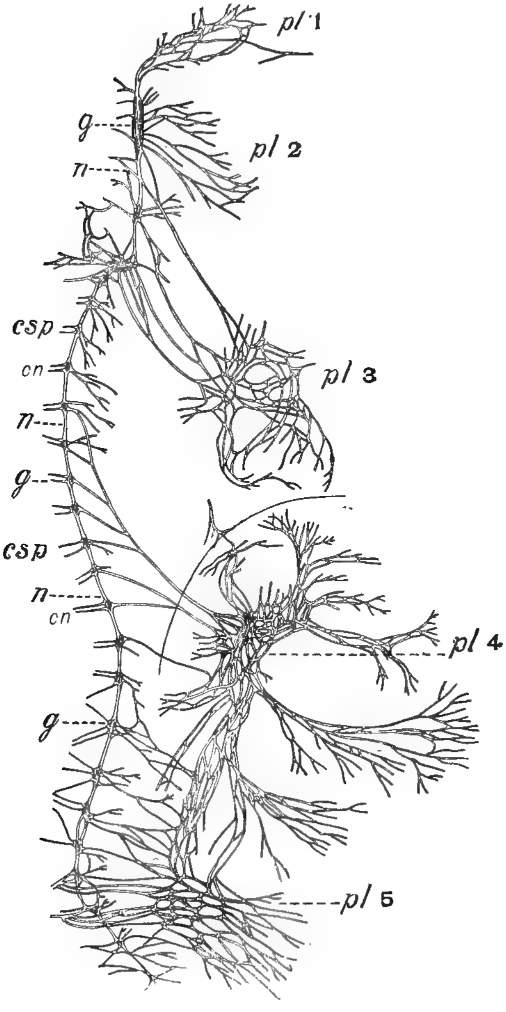

FIG. 38.—Diagram showing distribution of the ganglionic system : *g*, ganglions ; *n*, sympathetic nerve ; *csp*, connecting spinal branch ; *pl*, 1, 2, 3, etc., plexuses.

tems, the axial and the ganglionic, are brought into relation with one another (Fig. 38, *cn cn*). (4) From the sympathetic ganglia on each side there go nerves to the visceral region, where are performed the most important functions. There the nerves from each side unite to form *plexuses* or networks—i. e., the nerves cross one another in every direction, uniting at the crossings and forming ganglia there, and from these again come smaller branches going to all the important viscera and controlling their functions (Fig. 38, *pl*).

The Plexuses.—Beginning above and going downward, the principal plexuses are (1) the carotid and (2) the pharyngeal, small plexuses with their ganglia controlling the throat viscera (Fig. 38, *pl* 1 and 2); (3) the cardiac (plexus in the thorax) with its ganglia, controlling the action of the heart (Fig. 38, *pl* 3); (4) in the stomach region the epigastric or solar plexus with its ganglia, controlling the action of the stomach, spleen, and liver (Fig. 38, *pl* 4); (5) the hypogastric plexus and its ganglia, controlling the functions of the pelvic viscera (Fig. 38, *pl* 5). Into the cardiac and epigastric plexus enter the branches of the pneumogastric nerve from the medulla, and play an important part in the control of the heart, lungs, and stomach.

Function.—The function of this system is obscure, but certainly largely connected with the processes of nutrition, secretion, etc., or organic functions. Its function is doubtless also reflex, so far as the organs to which its nerves are distributed are concerned, but whether by its own fibers or by means of fibers derived from the axial system is more doubtful. It seems to control nutrition and secretion by controlling the blood supply; and this is done by means of certain fibers—vasomotor fibers—distributed to the capillary blood vessels—*vasomotor nerves.* Cutting the vasomotor nerves seems to paralyze the smaller blood vessels, which then enlarge, become gorged with blood, and the part becomes finally hot and inflamed. Stimulation of these nerves, on the contrary, produces contraction of these blood vessels and coolness and paleness of the part. Blushing, on the one hand, and the paleness of terror, on the other, are supposed to arise from opposite conditions of the vasomotor nerves.

Illustration by Telegraphy.—If we must push the telegraphic illustration to include this system also, then it may be compared to a municipal government controlling local affairs.

SECTION V.

COMPARATIVE PHYSIOLOGY AND MORPHOLOGY OF THE NERVOUS SYSTEM.

Introductory—Outline of the Classification of Animals.

About to enter now on the comparative morphology and physiology of the nervous system, it becomes necessary to have in mind some scheme of classification of the animal kingdom. A true classification is a compendious expression of perfect knowledge, and would seem therefore to come last of all. But some provisional classification is a necessary condition of increase of knowledge, because it is impossible to deal scientifically with animals except in *groups*. Therefore our plan will be to give a simple outline of such a classification and to verify it or modify it as we proceed. There are a great variety of classifications which have been proposed, almost as many as the proposers. We select one which is probably as good as any, and has, moreover, the additional advantage of comparative simplicity, for our main object is to be able to handle the material.

The whole animal kingdom may be primarily divided into seven groups called *subkingdoms* or *departments* or *phyla*. These are again each subdivided into *classes*, and these latter into *orders*, *families*, *genera*, *species*, etc. In the schedule given below we go no further than *classes*. *Orders* will be referred to sometimes, but not often. Even some classes are not used.

METAZOA.						PROTOZOA.
	ARTICULATA.			RADIATA.		
Vertebrata.	Arthropoda.	Annelida.	Mollusca.	Echinodermata.	Cœlenterata.	Protozoa.
Mammals	Insects :	Annelids	Cephalopods	Echinoids	Acalephæ	Infusoria
Birds	Arachnids		Gasteropods	Asteroids	Polyps	
Reptiles	Myriapods		Acephala	Crinoids		Rhizopods
Amphibia	Crustacea		Brachiopods	Holothurioids		
Fishes						

These groups are not of equal value or significance, as shown above. The whole animal kingdom may be divided into two prime groups, viz., protozoa, or simplest animals consisting of *one cell only*, and metazoa, or animals consisting of an aggregate of more or less differentiated cells. The metazoa, being higher, are more differentiated, and therefore are divided into many great departments. Again, I have linked together the echinoderms and cœlenterates under the name radiata, as having a common radiated plan of structure; also the arthropods and annelids, or segmented worms, under the name articulata, as having a common jointed or ringed plan of structure. We shall use these terms in connection with the general laws of animal structure. I take for granted that the student already has some general knowledge of zoölogy. I give only such classifications and such names as I shall use in the comparison that follows.

COMPARATIVE MORPHOLOGY AND PHYSIOLOGY OF THE VERTEBRATE NERVOUS SYSTEM.

The *general* plan of the nervous system is so precisely the same in all vertebrates that only the most general statements are necessary in regard to this. In all vertebrates, but in no other animals, we have both an axial and a ganglionic system. In all vertebrates the axial system consists of a continuous tract of gray matter inclosed in white matter lying along the dorsal aspect of the body, enlarged at the anterior end to form a brain, and giving off nerves in pairs from one end to the other (Fig. 14, page 29). In different vertebrates the number of these pairs vary, being least in frogs and toads, where there are only eighteen or twenty, and greatest in some fishes, as the eels, where they may be two hundred or more. Therefore the only part where the differences are important enough to arrest our attention in this rapid sketch is the *brain.*

THE BRAIN OF VERTEBRATES.

In running down the vertebrate scale there are three important changes which take place in the brain: 1. *In size*, both absolute and relative. 2. In relative amount of gray matter compared with white, as shown by the complexity of the convolutions. 3. In the relative size of the cerebrum as compared with the other ganglia of the brain. Perhaps I may add: 4. In the relative size of the frontal lobe compared with the other lobes of the cerebrum, as shown by the position of the fissure of Rolando. In all these respects the brain of man stands pre-eminent.

1. **Size** (*a*) *Absolute.*—The brain of man weighs about three pounds (forty-eight to fifty ounces). The heaviest which have been weighed—viz., that of Cuvier, the great

comparative anatomist, and that of Turgenief, the great novelist—were about four pounds. It varies slightly in different races, being greater in the superior races, but not so much greater as might have been expected. There are only two animals that have larger brains than man, viz., the elephant, whose brain is about eight pounds, and the whale, whose brain is about five pounds. The enormous size of these animals is sufficient reason.

(*b*) *Size relative to the Body or to Rest of the Nervous System.*—This is far more significant than the last. The brain of the highest animal of like size, viz., the gorilla is only about one third that of man, viz., fifteen ounces. Below this there is a constant decrease of relative size. This is shown in the following table. Of course we only take averages of these various classes.

CLASSES.	Brain to body.	Brain to nervous system.
Fishes	1 : 1,000	1 : 7 = $\frac{1}{7}$
Reptiles	1 : 1,000	1 : 5 = $\frac{1}{6}$
Birds	1 : 100	5 : 1 = 5 times.
Mammals	1 : 200	3 : 1 = 3 times.
Man	1 : 50	30 : 1 = 30 times.

There are some things in this table which require explanation. First, it is seen that there is no superiority in reptiles over fishes in brain to body weight, but there is in the relation to the rest of the nervous system. Again, it is seen that birds are apparently superior to mammals. The reason of this is that, as a law, small animals have larger brains proportionately than large animals. Now birds, as a rule, are smaller animals than mammals. Indeed, some of the smallest birds, such as the humming bird and the kinglet, have actually larger brains proportionately than man. The same is true of the smallest mammals, such as the mouse. But there are other things spoken of later, viz., fineness of organization, which determine intellect quite as much as or more than size. Perhaps it might be well to say here, for the comfort of those who wear small-sized hats, that brain power does not depend on size alone, any more than bodily strength depends on weight alone. In both cases it is a product of two factors, viz., size and fineness of organization, and the latter is the more important factor.

Brains of Extinct Species.—It is a curious and significant fact that in each of these classes extinct species are remarkable for the smallness of their brains. There has been a gradual increase in the size of the brains of animals in each of these classes from their first introduction until now. To give one example, the extinct Cretaceous bird Ichthyornis was about the size of a tern, but its brain was hardly one quarter as large (Fig. 39).

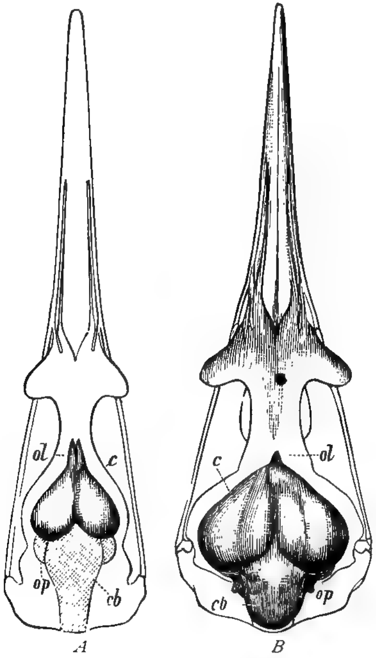

FIG. 39.—*A*, outline of the skull and brain cavity of Ichthyornis victor (after Marsh), seen from above. (Five sixths natural size.) *B*, outline of the skull and brain cavity of Sterna cantiaca (after Gmelin), same view. (Natural size.) *ol*, olfactory lobes; *c*, cerebral hemispheres; *op*, optic lobes; *cb*, cerebellum.

2. **Relative Amount of Gray Matter.**—The gray matter is the *generator*, the white fibers only *transmitters* of

nerve force. The former, therefore, is the higher. The organization of the brain is tested by the relative amount of gray matter. Comparing again to electricity, the electro-motive force varies as the gray matter. Further, this relative amount, other things being equal, is expressed by the number and depth of the convolutions. Now, of all animals the number and depth of the convolutions of the cerebrum is by far greatest in man. In higher mammals, especially anthropoid apes, the convolutions are well marked, but they become less and less so as we go down the mammalian scale, until they entirely disappear *before we reach the lowest mammals* (Fig. 40). Therefore all below mammals—i. e., *all birds, reptiles, and fishes—have smooth brains.*

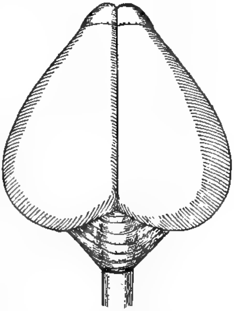
FIG. 40.—Brain of Ornithorhynchus. (Natural size.) (After Parker.)

There is, however, a modifying cause here which must not be neglected; it is, that the brains of small animals tend to smoothness irrespective of deficiency of gray matter. The reason is that *bulk* varies as the *cube*, while *surface* only as the *square* of the diameter, and therefore a small sphere has proportionately a greater surface than a large sphere. It follows from this that the brain of a small animal, though smooth, may have as much gray matter proportionately as the highly convoluted brain of a large animal. Thus all small mammals have smooth brains, while large mammals have all convoluted brains. The brain of an elephant, or even of a whale, is wonderfully convoluted, almost as much so as that of man.

As we go back in the *embryonic* series the brains of mammals and of man become less and less convoluted, until they become entirely smooth. The same is true as we go back in the evolution series. Extinct mammals have less and less convoluted brains as we go back in time. All the earliest mammals had smooth brains.

3. **Relative Size of Cerebrum.**—The cerebrum is confessedly the highest part of the brain. The relative size of this is the best of all tests of position in the scale of organization. Observe, then, that there are four lobes used in this comparison, viz., the cerebellum, the optic lobes, the cerebrum, and the olfactory lobes; for this last is an important lobe in all lower vertebrates.

Now in man, as already seen, the cerebrum, growing out from the thalamus, spreads forward, covering entirely the olfactory lobes, and backward, covering first the optic lobes, then the cerebellum, until looking down upon the brain we see nothing else. It covers and dominates all. In monkeys, by a less backward prolongation, the cerebellum begins to peep out behind In the average mammals, such as the lion or the dog, the olfactory lobes are exposed in front, and nearly the whole of the cerebellum is uncovered behind (Fig. 41). Still lower among mammals the cerebellum is wholly uncovered and the optic lobes begin to appear, and all the four lobes are seen in a series (Fig. 42). The brains of extinct mammals are all of this low type.

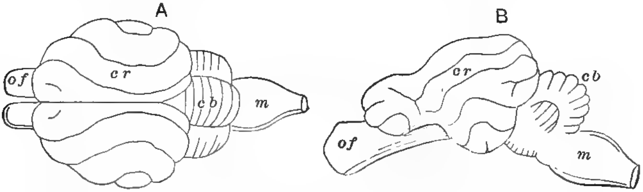

FIG. 41.—Mammal brain. A, top view; B, side view of the brain of a cat.

Owen's Classification of Mammals.—Professor Owen classified mammals by this test into four groups: 1. *Archencephala*, or ruling brain. In this subclass he placed man alone. 2. *Gyrencephala*, or convoluted brains. In this he placed all the larger mammals. 3. *Lissencephala*, or smooth brains. In this he placed all the rodents and some other small mammals. 4. *Lyencephala*, or separated brains. The lowest mammals, such as insectivores and marsupials, he placed in this. This attempt is interesting, but the classification can not be regarded as natural, for the earliest animals of all these subclasses, except one—man—have smooth brains.

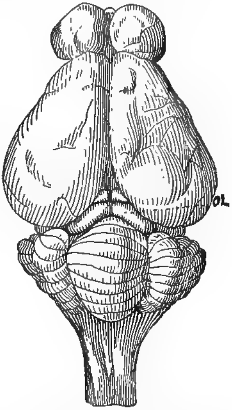

FIG. 42.—Brain of Dasyurus ursinus, showing exposure of the optic lobes, *ol*. (From Owen.)

In the average *bird* (Fig. 43) not only is the olfactory lobe wholly uncovered in front and the cerebellum behind, but also the optic lobes are at least half uncovered.

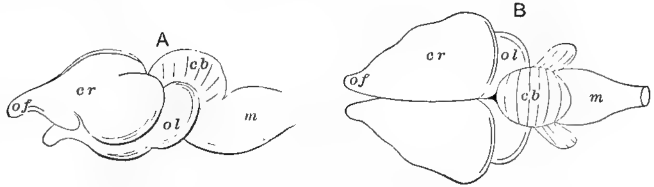

FIG. 43.—Bird brain: A, side view; B, top view.*

In the *reptile* (Fig. 44) all the lobes are fully exposed, and the brain becomes a succession of lobes in a

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* In all these figures to 54: *m*, medulla; *cb*, cerebellum; *ol*, optic lobes; *cr*, cerebrum; *of*, olfactory lobes.

linear series, but the cerebrum still maintains its pre-eminence as the largest of the series.

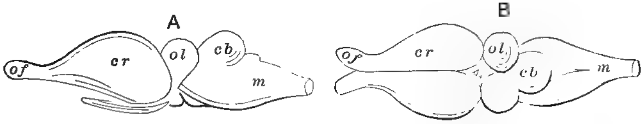

FIG. 44.—Reptile brain: A, side view; B, top view.

Finally, in *fishes* (Fig. 45) this pre-eminence of the cerebrum is lost and the optic lobes are the largest. In the very lowest fishes, such as the lampreys (*Petromyzon*), there is scarcely any enlargement at the anterior end, and in the lancelet (*Amphioxus*, Fig. 46) the cord is continued into the head with no perceptible enlargement at all.

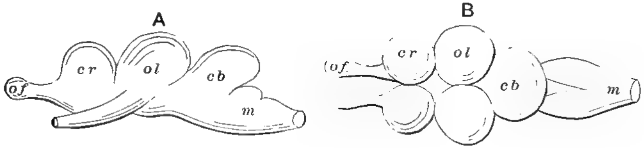

FIG. 45.—Fish brain: A, side view; B, top view.

In all these gradual changes by which the brain is reduced finally to a linear series of swellings, it is remarkable to see how persistent are two little organs, the functions of which are still doubtful, one below and one

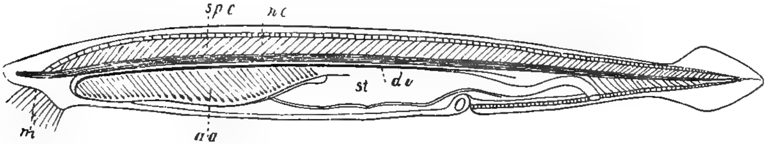

FIG. 46.—Amphioxus: *spc*, spinal cord.

above the thalamus, viz., the pituitary gland and the pineal gland. These are seen in Figs. 48–53. The use of the former, if any, is unknown. The latter seems to be a useless remnant of a once useful eye in the top of the head. In some lizards it still retains the structure of an eye (Fig. 47).

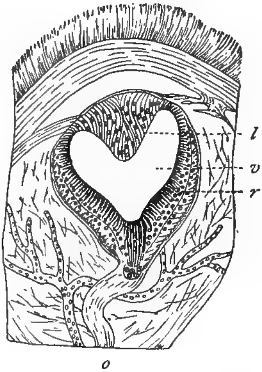

FIG. 47.—Parietal eye of Hatteria (after Spencer): *l*, lens; *v*, vitreous humor; *r*, retina; *o*, optic nerve.

Embryonic compared with the Taxonomic Series.—It is a most significant fact that the brain of the embryo of man passes through all these stages: (1) The earliest condition of the human brain is seen in Fig. 48. This can be compared with the brain of only the very lowest fishes. It may therefore be called the *subfish stage.* It does not yet contain a cerebrum. (2) Then the cerebrum grows out of the thalamus, but is yet inferior in size to the optic lobes (Fig. 49). This may be called the average *fish stage.* (3) Then the cerebrum grows until it is the largest of the series, but covers nothing as yet (Fig. 50). This may be called the *reptile stage.* (4) Then it begins to cover the optic lobes (Fig. 51). This corresponds to the *bird stage.* (5) Then it covers the whole of the optic lobe and encroaches on the olfactory lobe

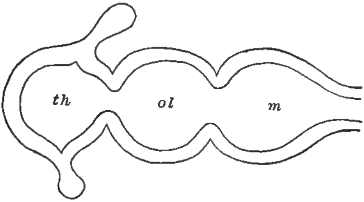

FIG. 48.—Sub-fish stage: *th*, thalamus; *ol*, optic lobe; *m*, medulla.

in front and the cerebellum behind (Fig. 52). This corresponds to the condition of the average mammal, and may be called the *mammal stage.* (6) Finally, it grows forward, wholly covering the olfactory lobe, and backward, wholly covering the cerebellum, and we have the *human stage* (Fig. 53).

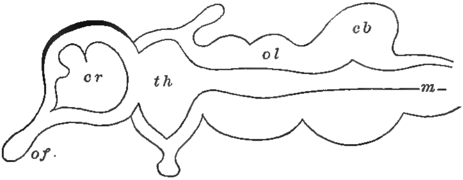

FIG. 49.—Fish stage.

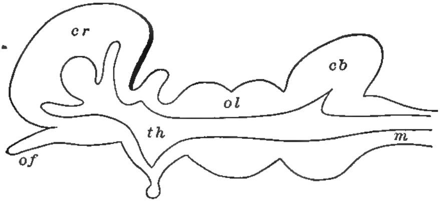

FIG. 50.—Reptile stage.

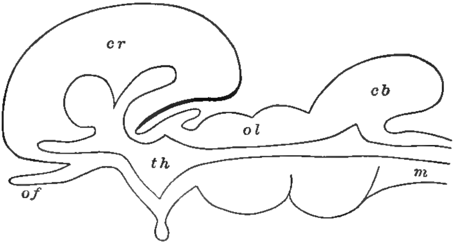

FIG. 51.—Bird stage.

Meanwhile several other changes are in progress: (1) In proportion as the head is raised nearer and nearer to a vertical position, the base of the brain, which was at first in direct line with the cord, begins to bend more and more until it is at right angles in man; (2) the cerebellum has been increasing in relative size; and (3) the convolutions of both the cerebellum and the cerebrum have been becoming more and more complex. All these changes are combined and represented in Fig. 54.

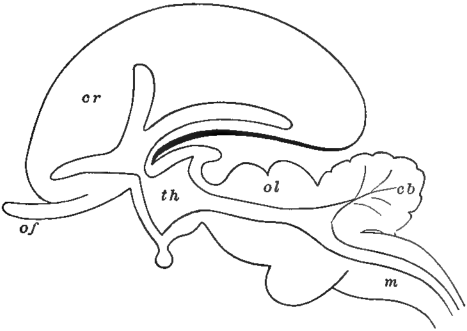

FIG. 52.—Mammalian stage.

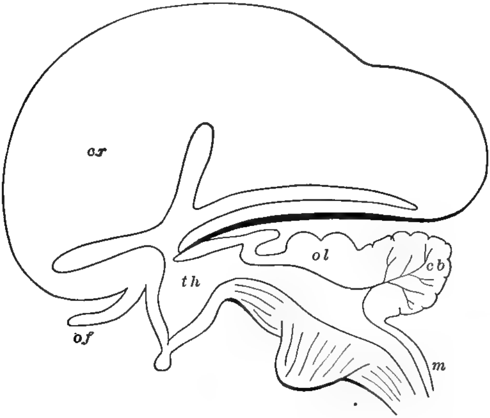

FIG. 53.—Human stage.

4. **Relative Size of Frontal Lobe.**—The highest functions of the intellect are connected with the *frontal lobe* of the cerebrum. This is marked off by the fissure of Rolando. In man the portion anterior to this fissure is large. In monkeys the fissure is plain, but the anterior lobe is much smaller, and increasingly so as we go down the scale of monkeys. The fissure is not certainly discernible at all below monkeys.

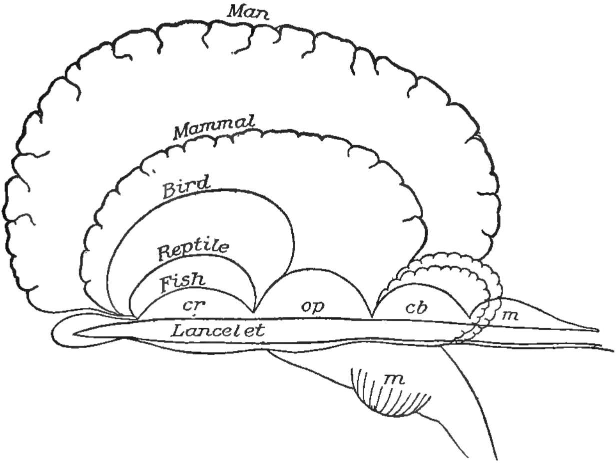

FIG. 54.—Diagram showing all the stages in one.

CEPHALIZATION.

This may be defined as *headward development.* Introduced by Dana to express the gradual transfer of functions headward by the modification of homologous organs as we go up the scale of crustacea (see page 268), we here use it in a similar but a wider sense as the gradual increasing dominance of higher over lower functions in the process of evolution and usually accompanied with transfer headward.

In the process of development, whether in the evolution series, or in the taxonomic series, or in the embryonic series, we observe the same order. Organisms are at first unmodified cell-aggregates. From such aggregates tissues performing different functions are differentiated. From this time onward cephalization begins. Among the tissues there is a gradually increasing dominance of the highest, the controlling tissue, viz., the *nervous tissue*. Then *in the nervous tissue* a gradually increasing dominance of the highest part, viz., the *brain*. Then *in the brain* a gradually increasing dominance of the highest ganglion, viz., the *cerebrum*. Then *in the cerebrum* a gradually increasing dominance of the highest substance, the surface *gray matter*, as shown by the complexity of the convolutions. And, lastly, *among the convolutions* a gradually increasing dominance of the highest, viz., those in the frontal lobe, as shown by the position of the fissure of Rolando. In all there is an increasing dominance of the higher over the lower, and of the highest over all. This is everywhere the law of evolution.

Shall it stop here? Shall it not be carried forward on a higher plane by the conscious effort of man? Is not all civilization, all culture, all education a *voluntary* process of cephalization? Here, also, there must prevail the same law of progressive domination of the higher over the lower, of the distinctively *human* over the animal, of mind over body; and, in the mind, of the higher faculties over the lower, the reflective over the perceptive, and of the moral character over all. In all your culture be sure that you strive to follow this law of evolution.

SECTION VI.

Nervous System of Invertebrates.

The departments below the vertebrates we group together under the general term *invertebrates*, not because they are more nearly related to one another than they are to vertebrates, for this is not true, but because we must treat them far more cursorily.

1. **Articulata.** *Arthropods and Annelids.*—The plan of structure of these is widely different from that of vertebrates. In these (1) the skeleton is on the *outside*, the muscles acting from *within* to produce motion and locomotion; instead of being within, and muscles working on the outside for the same purpose, as in the vertebrates. (2) Of all departments these animals are the most distinctly and most numerously jointed, and therefore they are called *articulata*. (3) The skeleton being on the outside, it forms a hollow tube or cavity inclosing all the viscera and organs of the body (Fig. 55),

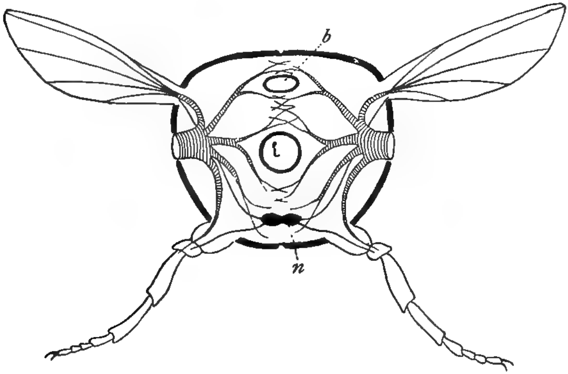

FIG. 55.—Diagram of section across an arthropod: *b*, blood system; *n*, nervous system; *i*, intestines.

while in vertebrates there is a separate cavity inclosing and protecting the nervous centers (Fig. 56). (4) In the vertebrates, as we have seen, the nerve center consists of a continuous tract of gray matter lying along the *dorsal* aspect of the body, above the visceral canal. In the articulata, on the contrary, the nerve center is a continuous chain lying along the *ventral* aspect of the body, below the visceral canal. (5) In the case of vertebrates, as already seen, the nerve system is subdivided into two subsystems, the axial and the ganglionic. In the case of the articulata there is but one system, which probably performs the functions of both, these subsystems not having yet been differentiated.

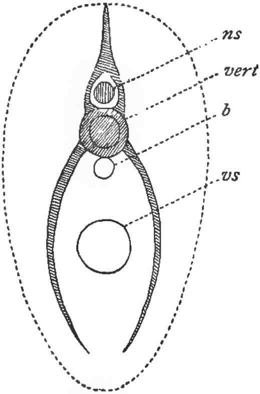

FIG. 56.—Cross section through a fish: *vs*, visceral system; *vert*, vertebra; *b*, blood system; *ns*, nervous system.

It is difficult, indeed impossible, to conceive how the vertebrate nervous system could have been evolved out of that of the articulates. If vertebrates came as a branch from the articulates, as many think, they must have come off so low down that the distinctive plan of neither was yet declared.

In treating of the plan of the nervous system we shall take all the articulata together, as the plan is the same in all, although most distinct in the arthropods.

General Plan of Articulate Nervous System.—To bring this out clearly it is best to take an example from about the middle of the series—as, for instance, a leech, or a crayfish. In Fig. 57 we give a side view of the nervous system of one of the lower crustacea, and in Figs. 58 and

59 a back view of that of a leech and of a crayfish. It may be most simply described as consisting of a chain of ganglia strung along the whole ventral aspect of the body and below the alimentary canal, one to each joint, connected by a single or double thread, and the most anterior one—the *œsophageal ganglion*—being connected with a large ganglion in the head, above the gullet—*cephalic ganglion*—by two threads, one on each side of the gullet, to form the *œsophageal collar*. It is a remarkable fact that an œsophageal collar is found in nearly all invertebrates.

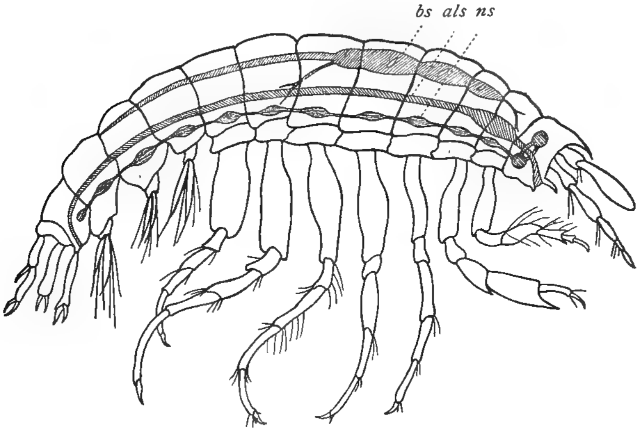

FIG. 57.—Diagram of a crustacean (*Vibilia*): *bs*, blood system; *als*, alimentary system; *ns*, nervous system.

Functions of the Several Ganglia.—The cephalic ganglion seems to preside over the higher senses, viz., the *eyes* and the *antennæ*. It is also the seat of consciousness and volition and of whatever instinct or intelligence the creature is possessed of, and, through its connections with other ganglia, it dominates the whole body. In a word, it corresponds in function to the cerebrum of vertebrates. The œsophageal ganglion presides over the gathering and mastication of food, and, judging from experiments on crustaceans, it seems also to coördinate the motions of the whole body. It may be said to correspond in function to the cerebellum of vertebrates. The other ganglia preside each over its own body-segment and corresponding limbs automatically, but all under the conscio-voluntary control of the œsophageal collar, and especially of the cephalic ganglion.

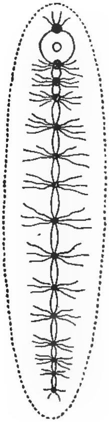

FIG. 58.—Diagram of nervous system of a leech, seen from above.

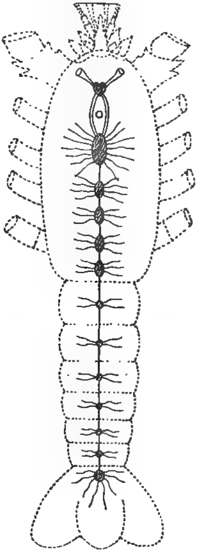

FIG. 59.—Nervous system of a crayfish, seen from above.

Modifications going down and up the Scale.—Taking the above as the type, as we go down the scale of articulates, the cephalic ganglion becomes smaller in comparison with the others, and loses more and more its dominance over them. The other ganglia become more and more independent, and the movements more and more automatic or reflex, until finally, in the lowest worms, the different segments become almost wholly independent, and indeed almost like separate animals.

In going *up* the scale, on the contrary, we find opposite changes of two kinds, viz., *centralization* and *cephalization. Centralization* reaches its highest degree in crabs and spiders, where all the ganglia except the cephalic are consolidated into one in the center of the cephalothorax, and therefore in the vicinity of the stomach and locomotive organs (Fig. 60). The *cephalization* reaches its highest degree in the high insects, as bees, flies, beetles, etc. (Fig. 61).

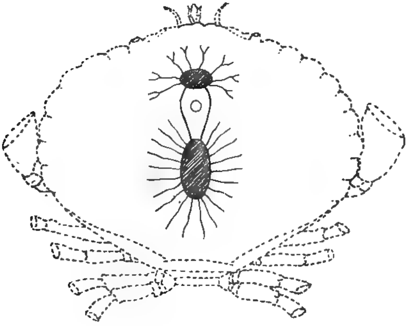

FIG. 60.—Nervous system of a crab.

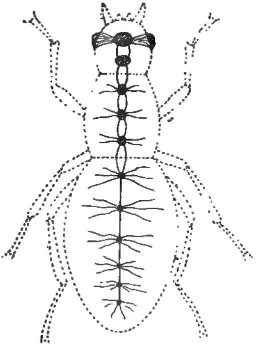

FIG. 61.—Diagram of nervous system of a beetle.

Embryonic History of the Nervous System.—The same changes are gone through in the embryonic history of one of the higher insects, such as the butterfly. In the caterpillar all the ganglia are separate, one to each segment. In the chrysalis the cephalic ganglion increases in size, and three or four of the anterior body ganglia are drawing closer together. In the butterfly the cephalic ganglion is still larger, and four of the ventral ganglia, together with the œsophageal, have united into a great thoracic ganglion to control the powerful muscles moving the wings and legs, as well as to preside over the stomach, etc. (Fig. 62). It is well to observe that the consolidation

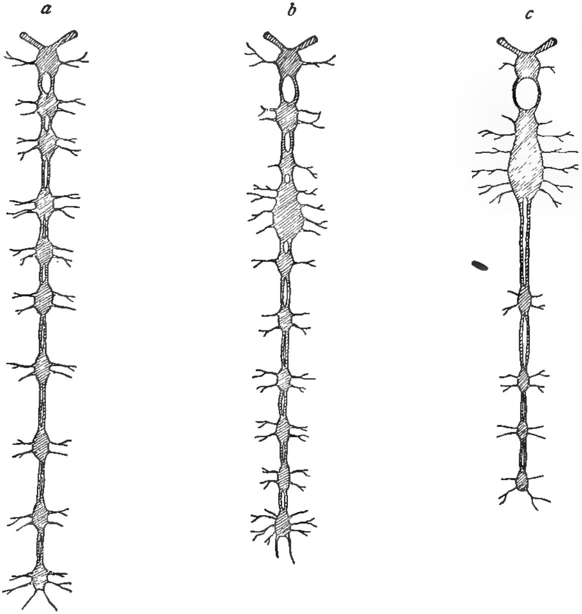

FIG. 62.—Diagram showing the embryonic development of a lepidopter: *a*, caterpillar; *b*, chrysalis; *c*, the perfect butterfly.

of the segments of the skeleton follows the same course —goes hand in hand with that of the nervous system.

2. **Mollusca.** *Comparison with Other Departments.*— The whole plan of structure of these is again different. The vertebrates and arthropods both have a true locomotive skeleton, the one *interior*, the other *exterior*. In both, also, but especially the latter, the skeleton consists of segments repeated in a linear series. The mollusks have no locomotive skeleton, but only a protective shell. The mollusks also have no segmented

structure, no repetition of similar parts in a linear series. Now it is probable that the nervous system controls the general structure of the body. Thus while the nervous system of vertebrates is a continuous axis, and that of arthropods and worms a string of ganglia running through the body, in mollusks there is no axial arrangement as in vertebrates, nor a linear series of ganglion as in arthropods.

FIG. 63.—Nervous system of a clam: *cg*, cephalic ganglion; *pg*, pedal ganglion; *vg*, visceral ganglion.

General Plan of the Nervous System.—In these animals the nervous system consists (1) of an *œsophageal* collar, and (2) of ganglia irregularly placed wherever important functions, either nutritive or locomotive, are situated.

Examples.—1. In bivalves (acephala), such as clams, for instance, we have (Fig. 63): (1) The œsophageal collar, which presides over the mouth and head functions (e. g., gathering of food and whatever beginnings of intelligence the creature may possess), and also has general presidence over conscious voluntary movements, and therefore over other ganglia; (2) a large visceral ganglion in the region of nutritive and respiratory organs, to preside over these; and (3) a locomotive or foot ganglion to control locomotion. This is all. In the oyster the nervous system is

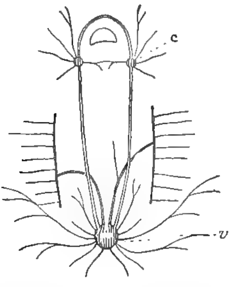

FIG. 64.—Nervous system of an oyster: *c*, cephalic ganglion; *v*, the visceral ganglion.

still simpler, since it lacks the locomotive ganglion (Fig. 64).

2. In gastropods, as the *snails* (Fig. 65), we find, (1) as usual, the cephalic ganglia and œsophageal collar in which are lodged all the higher functions—consciousness and volition, control of voluntary movements, etc.; (2) in the foot or crawling disk a ganglion to preside over locomotion; (3) visceral ganglia in the visceral region, appropriately placed. All are, of course, connected with the cephalic ganglion and dominated by it. In the figure, however, only the œsophageal collar is represented.

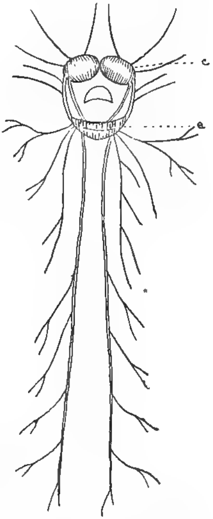

FIG. 65.—Nervous system of a gastropod: *c*, cephalic ganglion; *e*, œsophageal ganglion.

3. In cephalopods (squids, cuttlefish, etc.) (Fig. 66) we have (1) a large ganglion in the head completely and closely encircling the gullet, and forming a very perfect close-fitting œsophageal collar. This is doubtless a combination of cephalic and œsophageal ganglia. It controls the movements of the jaws and arms, and it presides over the higher senses of sight and hearing, which are well developed in these animals. It is the seat of conscious voluntary motion and of whatever higher faculties the creature may possess. (2) Besides this there are a pair of locomotive ganglia in the muscular mantle to control its contraction. (3) A large visceral ganglion presiding over nutrition and respiration. All of these are, of course, connected with the head ganglion.

3. **Radiata.**—We include in these the echinoderms and the cœlenterates, as having the same general plan of nervous system. Here again we have the whole plan of structure of the animal different. We have again segments of the body, not, however, repeated in a linear series, but *in a circle* about the stomach, like the segments of an orange about the pit or the spokes of a wheel about the hub. Therefore we find that the nervous system follows the same plan (Fig. 67).

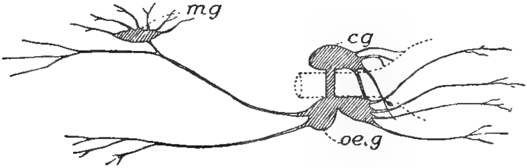

FIG. 66.—Diagram of nervous system of a squid: *cg*, cephalic ganglion; *oeg*, œsophageal ganglion; *mg*, mantle ganglion.

General Plan.—Take a *starfish* as an example. There is a ganglion at the base of each arm, and therefore five surrounding the mouth, connected into a perfect œsophageal collar. From these ganglia there go nerves, one to each arm, giving branches to the arm and terminating at the extremity in an eye spot.

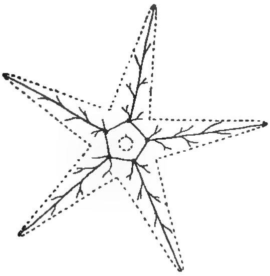

FIG. 67.—Diagram of the nervous system of a starfish.

In the medusæ we have the same perfect radiated structure, but the nervous system has as yet *no general center.* From the several eye spots on the margin of the disk there go nerve cords a little way toward the center of radiation, but they do not meet one another in a common center. It is difficult to see how such an animal can have a *common* consciousness (Fig. 68).

4. **Protozoa.**—As these consist of a single cell and not even a cell aggregate, and therefore can have no tissue of any kind, they have no nervous system. Yet there is a general sensibility or response to stimulus even in these little spherules of protoplasm. All functions are performed, though imperfectly, by these living drops of jelly. This is the starting point from which by evolution have been differentiated all the tissues and organs and functions found in higher departments.

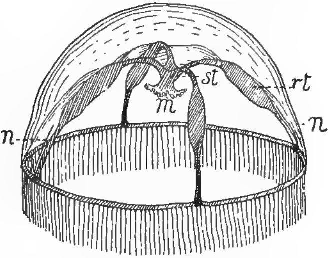

FIG. 68.—Diagram of a medusa : *n n*, nerve ; *m*, mouth ; *st*, stomach ; *rt*, radiating tubes.

CHAPTER II.

SENSE ORGANS.

SECTION I.

Introductory.

A NERVOUS system, as seen, consists essentially of a center and two kinds of fibers, one carrying impressions from the external world to the center and producing changes in consciousness, which we call sensation, the other carrying impulses back from the center to the external world and producing changes of phenomena there. But to make these exchanges more efficient there must be special receptive organs of sensation (these are the *sense organs*) and special executive organs of the will (these are the *muscles*). We have now to do only with the sense organs. We shall speak of the muscles later.

Relation of Special Sense to General Sensibility.—The sensory fibers of the conscio-voluntary system terminate peripherally in external sensitive surfaces, and in the lowest animals everywhere *alike*—i. e., in the skin. This gives only the *existence* of an external world, but not its *properties.* This is the case in all the lowest animals, and nothing more. But as we go up the animal scale certain fibers are specialized to give knowledge of certain properties, and certain other fibers to give knowledge of other properties. Thus, for example, the fibers of the first pair of cranial nerves are specialized to give us cognizance of odors, and *nothing else*, and any kind of stimulation of this nerve will produce a perception of odor. The fibers of the second pair of cranial nerves are specialized in such wise as to respond to impressions of light, and nothing else, and any stimulation of this nerve, whether by pricking or by electricity or otherwise, gives rise to a flash of light. The eighth pair is so specialized as to respond to vibrations of the air, and any stimulation of this nerve gives rise to a sensation of sound. Similarly the ninth pair is so specialized as to produce the peculiar sensation which we call taste, and nothing else, and hence stimulation of this nerve in any way will produce this peculiar sensation. This is only one example of the universal law of differentiation, but so admirable a one that we stop a moment to dwell upon it.

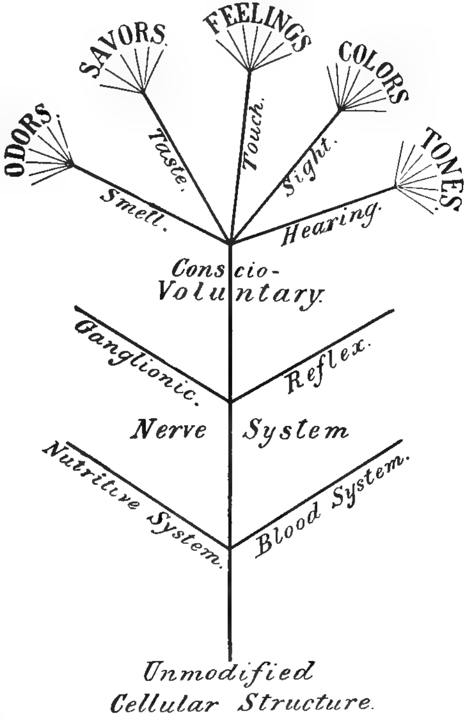

FIG. 69.

Commencing with the lowest animals—protozoa—or with the earliest embryonic condition of the higher, we have first a single cell, and then an unmodified *cell aggregate.* As we pass upward three fundamental systems separate, having each a characteristic fundamental function, viz., the epithelial or nutritive system, the blood system, and the nervous system (Fig. 69). The function of the first is the exchange of matter with the external world—foreign commerce; of the second, exchange of matter between different parts of the body—internal carrying trade; of the third, the exchange of intelligence, both foreign and interior. Putting aside the other two (which, however, are also differentiated), we take only the nervous system. In vertebrates this again is differentiated into three subsystems, viz., the conscio-voluntary, the reflex, and the ganglionic. Putting aside again all but the conscio-voluntary, and taking here only the sensory fibers, these are again differentiated into five kinds, viz., the five special senses. Even these are probably further differentiated—i. e., different kinds of colors, tones, feelings, etc.—and perceived by different fibers differently specialized.

Now as different as these kinds of sensation are from one another, so different that they can not be conceived the one in terms of another, yet they are all probably but modifications of one another and all refinements of the lowest—viz., feeling. It will be interesting, then, to trace the gradations between them in several respects.

1. **Vibrations.**—Coarse vibrations are perceived by the nerves of common sensation. We call them *jars* or *tremors*. If these increase in number and decrease in size until they lose their separateness—i. e., until there are sixteen in a second, then they appear in consciousness in another and entirely different form—as *sound*—and we have a special nerve adapted to perceive these more rapid vibrations. As the vibrations become more and more rapid they are perceived as higher and higher musical pitch, until they reach some thirty thousand to forty thousand in a second, which is the acutest sound

we can hear. Beyond this the vibrations exist, but we have no nerve specialized to perceive them. After a long interval vibrations again appear in consciousness, but in a new form—as *light.* This only takes place when they reach a rapidity which can be taken on only by the ethereal medium, viz., four hundred million millions in a second. As they become still more rapid they appear as different colors until they reach about eight hundred million millions, when they again disappear from consciousness. We know that they are there, for they show themselves in other ways—e. g., by photography—but we have no nerve specialized to perceive them.

2. **Kind of Contact.**—*Feeling* takes cognizance of any kind of direct material contact, but especially of *solid* contact. Taste must have *liquid* contact, and unless a substance is soluble it can not be tasted. In the case of smell the contact must be more refined; it must be *gaseous*, and unless a substance is volatile it can not be smelled. In the case of hearing and sight there is no direct contact at all of the sensible body, the impression being made by vibrations of a medium, the air in case of hearing and the universal ether in case of sight. All other senses are *terrestrial;* sight alone is *cosmical.*

3. **Objectiveness.**—In the three so-called lower senses, viz., feeling, taste, and smell, we are conscious that the sensation is in *us*—i. e., *subjective*—although in smell we already refer the sensible body to a distance. In hearing, the thing perceived no longer seems to be in *us*, but in the sensible body—in *yonder bell*—though there may be still a remnant of the subjective element. Finally, in sight there is not a remnant of perception of anything in *us.* The sensation, say of redness or blackness, is completely externalized, objectified, referred outward to the sensible body. To the untrained mind there is not a suspicion of any change in the eye.

Higher and Lower Senses.—The lower senses are those in which contact is *direct*—viz., *feeling*, *taste*, and *smell*. The higher senses are those in which the impression is through the vibrations of a medium, viz., *hearing* and *sight*. When the impression is indirect—i. e. through a medium—besides the specialized nerve there is also a mechanical instrument—acoustic in the case of the ear and optic in the case of the eye—placed in front of the specialized nerve in order to make the impression stronger and more definite. The specialized nerve, together with the mechanical instrument, constitute the *sense organ*. On these two higher senses, therefore, are founded all our fine art and nearly all our science.

SENSE OF SIGHT AND ITS ORGAN, THE EYE.

The most specialized of all sensory fibers are those of the *optic nerve ;* the most refined of all instruments is the *eye ;* the highest of all the senses is the *sense of sight*. And yet we are apt to greatly overestimate what is really given by this sense. The direct gifts of sight are *light*, its *intensity*, its *color*, and its *direction*, nothing more. All else, as *size*, *distance*, *relief-form*, etc., are judgments. This will be explained hereafter.

Again, we must distinguish between light *objective* and light *subjective*. The one consists of vibrations of the ether and exist independent of *us ;* the other is the peculiar sensation produced in us or in some other percipient by these vibrations. The one belongs to physics, the other to physiology, or perhaps, some may claim, to psychology. We are here concerned mainly with light as *sensation ;* but since this is produced by vibrations, we shall be compelled to say something of the physics of the subject also.

Primary Divisions of the Subject.—The phenomena of vision may be divided into two primary groups: *monocular* and *binocular*. Monocular vision includes all those phenomena which are essential and universal; binocular vision only certain additional phenomena which are the result of the use of *two* eyes as *one* instrument. We take up, first, the general phenomena characterizing all vision—i. e., monocular vision. And as it is impossible to understand these without a knowledge of the structure of the eye, this must be our first subject.

SECTION II.

The Eye of Man—General Structure.

Shape, Setting, etc.—The eye is a nearly globular organ, about one inch in diameter, a little more protuberant in front. Set in a deep conical socket, it occupies only the anterior part; the posterior is filled with a cushion of fat on which it rests and rolls easily in all directions. The exposed part may be covered by the lids, which protect and at the same time wipe and keep it clean and bright. There is really no interruption of the skin here; on the contrary, the skin passes over the lid, then over its edge, then under the lid as mucous membrane, then much short of the equator of the ball it is reflected on to the ball (*a*) (Fig. 70), then over the white of the eye, then over the clear part (but here it is very closely adherent and is transparent), and so on to be again reflected on to the lower lid (at *a*′) and out on to the face. By nice dissection it is possible to separate it continuously, so as to leave the ball behind the skin. Now all this tender portion lining the lids and covering the front part of the ball is called the *conjunctiva.* Ordinary inflammation of the eye is an inflammation of this membrane. Inflammation of the

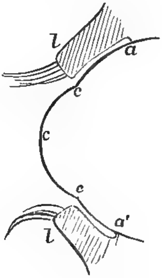

FIG. 70.

eyeball itself is a much more serious affair. From this arrangement it is evident that motes in the eye can not go beyond easy removal, as it can not go beyond *a a'*, Fig. 70.

Muscles.—The nimble movements of the eye are effected by six muscles in each eye. Four of these, the straight muscles (*recti*), arise near together at the bottom of the conical socket (Fig. 71), come forward diverging, and are attached to the ball a little in front of the equator, one above (superior rectus), one below (inferior rectus), one on the outside (exterior rectus), and one on the inside (interior rectus). The functions of these are obvious. Each turns the ball in the direction of its pull. When we look upward the two superior recti pull; when we look downward, the two inferior recti. When we look to the right, the external rectus of the right eye and internal rectus of the left eye pull, and *vice versa* when we look to the left. When we look at a very near object, then the two interior recti pull so as to converge the eyes on the object looked at. But we can not contract the two exterior recti so as to turn both eyes outward, nor can we turn one eye upward and the other downward, because these movements can not serve any useful purpose, and therefore have never been learned.

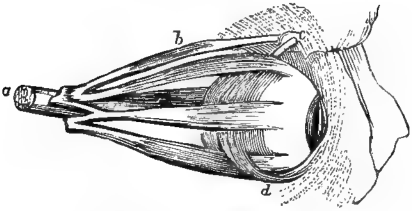

FIG. 71.—Muscles of the eyeball: *a*, optic nerve; *b*, superior oblique muscle; *c*, pulley; *d*, inferior oblique. The other four are the recti.

There are two other muscles—the *oblique*. The superior oblique arises along with the recti at the bottom of the socket, passes forward to the opening of the orbit, then through a loop on the inside which acts like a pulley, then back obliquely over the upper side of the ball, to attach itself on the outside a little behind the equator. Its pull being from the loop, it turns the eye downward and outward and rotates it on its axis *inward.* The *inferior oblique* arises from the lower part of the inside of the orbital opening, runs under the eye obliquely backward and outward across the equator, to attach itself on the outside of the ball a little behind the equator. Its action, therefore, is to turn the eye outward and upward and rotate it on its axis outward.

The use of these oblique muscles is much more obscure; their full explanation would carry us too far. For this we would refer the reader to the author's book on Sight (pages 11 and 12 and page 210).

In the normal condition, looking forward, the axes of the eyes are either parallel or *equally* convergent, so as to bring their axes together on the object looked at. Any deviation from this position is quickly detected by an observer as a squint or a cast. These malpositions of the eyes are often, but not always, caused by too great action of some one of the muscles, and are corrected by cutting the muscle and allowing it to attach itself to a new point on the ball.

Coats of the Ball.—Take the ball out of the socket. Dissect away the muscles. The ball, except the front part, is seen to be invested with a strong white coat of fibrous tissue. This is the *sclerotic.* It gives form to the eye and serves as attachment of the muscles. The front or more protuberant part is covered with an equally strong but perfectly transparent coat, apparently continuous with the sclerotic. This is the cornea. Its function is to retain the form of this part of the eye, and at the same time to freely admit the light. Looking through the transparent cornea, we see a little way behind it a flat colored screen, the iris, in the center of which is a round hole, the pupil, which in the living eye is seen to expand or contract, according to the intensity of the light (Fig. 72). The color of the eye is the color of the iris. The pupil is black, as any hole opening in a dark room is black.

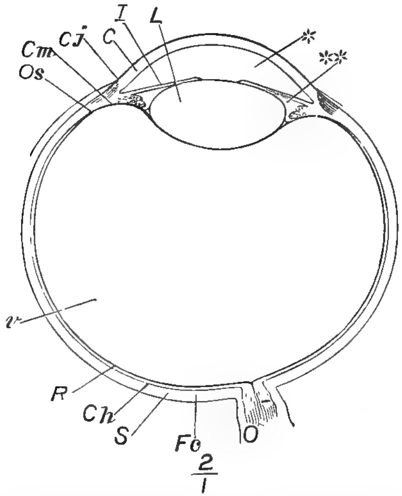

FIG. 72.—Section of the eye: *O*, optic nerve; *S*, sclerotic; *Ch*, choroid; *R*, retina; *v*, vitreous body; *Cm*, ciliary muscle; *Cj*, conjunctiva; *C*, cornea; *I*, iris; *L*, lens; *, aqueous humor; **, ciliary body or zonule of Zinn.

Linings. — For further examination dissection is necessary. We thus find that the sclerotic part is lined with two membranes. In direct contact with the sclerotic is a dark brown, almost black, and very vascular coat, the *choroid*. Its function is to absorb the light as soon as it strikes. The choroid lines the whole sclerotic as far forward as the outer margin of the cornea. It is there split into two layers, the anterior one, as it were, drawn together and thickened, forms the *iris*. The posterior one, also drawn together and plaited, forms the ciliary processes radiating about the back portion of the lens. The innermost lining coat is the *retina*, the most important of all. This is a deep cup-shaped expansion of the optic nerve. This nerve enters the eye socket at the bottom, comes forward through the middle of the fatty cushion, pierces the sclerotic and choroid, and then spreads as a thin translucent membrane nearly, but not quite, as far forward as the choroid.

Contents.—The hollow globe thus described is filled with materials as clear as finest glass. These are the humors or lenses of the eye. They are three in number. The *crystalline*, or lens proper, is a clear, glassy, double convex lens, one third of an inch in diameter and one sixth of an inch in thickness, and somewhat firm and elastic to the touch. It is placed just behind the iris and in light contact with it. It is invested with a transparent membrane, the *capsule*, which continues from its margin outward as a *curtain* to attach itself all around to the sclerotic a little behind the iris, and thus serves to hold the lens in its place. The lens and the lens curtain divides the interior of the eye into two unequal parts. The smaller anterior part is filled with the *aqueous* humor, the larger posterior part with the *vitreous* humor. The aqueous humor is as liquid as water, the vitreous humor about the consistence of soft jelly. All of these may be regarded as lenses. The crystalline, with its double convexity, is the lens *par excellence*; the aqueous, with its corneal surface, is also a powerful convex lens; while the vitreous, on its anterior surface, is a concave lens.

As already said, all of these are normally clear. Opacity of the crystalline, which often comes with age, constitutes what is called *cataract*, and produces blindness.

FORMATION OF THE IMAGE.

Now the whole of what has been described is an elaborate instrument to form an image on the sensitive retina. If we ask, "Why an image?" the answer is, Without an image we would perceive light, but not an object. Moreover, the image must be an exact facsimile of the object, because what we see will be a facsimile of the actual image. See, then, the two very distinct parts of the eye, viz., the specialized nerve (retina) and the optic instrument for making an image. The one is necessary for the perception of *light*, the other for the perception of *objects*.

In order to bring out more clearly the distinctness of these two parts I will use an illustration. Suppose we eviscerate the eyeball—i. e., remove all its contents—leaving only a deep cup-shaped cavity lined with the retina, as can be, and indeed has been, done. Suppose, further, that the retina could retain its healthy condition, which, of course, is impossible but supposable. Then I would undertake to have made a glass eye which, fitted into the cup-shaped cavity, would see just as well as the natural eye, and perhaps even a little better.

The Necessity of Lenses.—The image must be a perfect facsimile of the object, because what we see will be a perfect facsimile of the retinal image. If there is *no* image we will see no object. If the image is blurred the object will seem blurred. If the image is clear and sharp the object will be seen sharp in outline and clear in all surface details. Now light passing through a small hole will make an image (pinhole image), and therefore a very small pupil would make an image on the retina. But such an image is very imperfect. To make a perfect image we must have a *lens*. The manner in which a lens acts in producing an image is shown in Fig. 73. It is seen that all the rays coming from a point (a) of the object are bent (refracted) in such wise as to meet one another at a point (a') of the image, all the rays from the point b are gathered to one point b', and all from c to c', and similarly for all other points of the object. Thus for every *radiant* point of the object there is a corresponding *focal* point in the image, and therefore the image will be a perfect facsimile of the object.

Observe, then, (1) the image is inverted. All images made by lenses (dioptric images) are inverted. They must be, because the central ray of the pencil from each radiant passes straight through the lens without bending, and therefore these central rays all *cross* one another at a certain point in the lens called the *nodal point*. Observe again (2) that in order to have a sharp image the receiving screen must be exactly at the focus of rays; for nearer than this the rays have not yet come together to a focal *point;* farther than this they have already crossed and spread out again. Observe (3) that the *size* of the image will be to that of the object in the exact proportion to their relative distances from the *nodal point*. (4) Again, as the object comes nearer the lens the image will be thrown farther back, while if the object recedes from the lens the image will approach the lens. (5) It is not every lens that will make a perfect image. It must have a proper shape, and, moreover, it is found that a system of several lenses is better than a single lens.

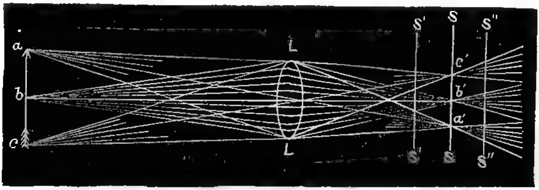

FIG. 73.

Application of these Principles to the Eye.— Now the eye is an instrument consisting of a system of lenses. The eye therefore forms its images of all objects presented to it. In Fig. 74 rays from the two points *A* and *B* of an object *A B* are brought to focus on the retina at *a′ b′*, and so of all intermediate points. If the retina is properly placed the image will be perfect. If the retina be too far back or, what is the same, if the lenses are too refractive, the image will fall short of the retina *a′ b′* and will be blurred. This is the case in the nearsighted. The object must be brought nearer, so as to throw the image a little farther back. If the retina be too near the lens or, which is the same, the lenses too little refractive, the image will fall behind the retina *a″ b″* and will also be blurred. This is the case in the old-sighted for near objects. The refraction must be supplemented by glasses. These defects, however, will be explained later.

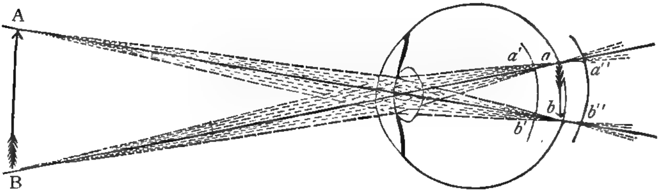

FIG. 74.—Diagram illustrating the formation of an image on the retina.

The fundamental fact that the images of all external objects are really formed on the retina may be shown in many ways. (1) Take the dead eye of an ox. Remove the coats on the back part of the ball, and replace them by a mica plate—an inverted image of the landscape is seen. (2) The eyeball of a white rabbit shows it without mutilation, because in these albinos the sclerotic is more transparent and the black pigment of the choroid is wanting. (3) The image may be seen in the living eye by the use of the ophthalmoscope.

It is seen (Fig. 74) that the central rays of the pencils cross one another at the nodal point. In the eye the nodal point is a little behind the center of the lens.

The distance of this point from the retina is about six tenths of an inch. Now when we remember that the relative size of the object and image is exactly proportioned to their relative distances from the nodal point, we at once see how extremely minute the retinal images of objects must be.

COMPARISON OF THE EYE AND CAMERA.

The purely instrumental character of the eye and its mechanical perfection may be clearly brought out by a comparison with the photographic camera. Take, then, the *dead* eye and the dead camera—i. e., with only the ground-glass plate in place. They are both optic instruments for making an image. Look in at the back of the camera and see the inverted image on the ground-glass plate. Look in at the back of the eyeball and see also the inverted images. Both are dark chambers, with a lens in front to admit the light and make an image by refraction; both are lined within with black pigment, to absorb the light and prevent reflection from side to side, and so the spoiling of the image. But it is not every lens that will make a perfect image. There are certain defects in common lenses which must be corrected to produce the best effects. These are corrected in the best cameras and in all good eyes.

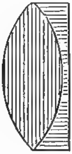

FIG. 75.

1. **Chromatism.**—In all simple lenses we find that the images are bordered with colored fringes—blue or orange. These mar the sharpness of the image. This defect is corrected in optic instruments by a combination of lenses of different curvatures and different refractive and dispersive powers. In a fine telescope, for instance, a double convex lens is combined with a plano-concave lens. The one is crown glass, the other flint glass (Fig. 75). Such a com-

bination is achromatic. Now the eye also is corrected for chromatism, otherwise all objects would appear fringed with colors. The mode of correction also is the same, for the eye also consists of several lenses differing in curvature and in material. In fact, the structure of the eye gave the first hint as to the proper mode of correcting lenses—i. e., by combination.

2. **Aberration.**—In ordinary lenses (i. e., those with spherical curvature) it is found that the marginal rays are refracted too much for the central rays, and therefore all the rays are not brought together to the same focus. This may be partly remedied by cutting off the marginal rays by a diaphragm, but, of course, with great loss of light. But it can be completely remedied only by making the central part of the lens more refractive. This can be done either by graduating the density of the matter of the lens from the margin to the center, or else by graduating the curvature from margin to center. The first method art has found impossible to accomplish, and therefore it adopts the second method. Instead of a spherical curvature, it makes an elliptical curvature, the axis of the ellipse being the axis of the lens. In this way the best lenses are corrected for aberration.

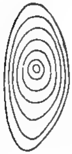

FIG. 76.—Section showing the structure of the lens.

Now the eye also is corrected, for otherwise it could not sharply define the objects it looks at. How is it corrected? It is probable that it uses *both methods*. The crystalline lens consists of concentric layers, becoming denser and denser to the center (Fig. 76). Also the curvature of the corneal surface is elliptical instead of spherical.

3. **Adjustment for Distance.** *Focal Adjustment. Accommodation.*—We have seen that in order to have a good image the receiving screen must be at the exactly

proper place. Now if the images of all objects at all distances were thrown to the same place, we might find that place and fix the screen permanently there. But we have already seen (page 105) that as the object is farther away the image comes nearer the lens, and as the object approaches the image recedes. Now there are two ways of adjusting this: if the lens retains its form then the screen must be moved back and forth to the proper place, or else, if the screen be fixed, the lens must change its form so as to throw the image on the fixed screen—i. e., it must become more refractive as the object comes nearer. The former is the method of the camera and of nearly all optic instruments, such as the opera glass, the field glass, etc. In these the tube is drawn out so as to carry the screen back for near objects, and is pushed in so as to carry the screen nearer the lens for distant objects. The microscope is an exception. Usually, when the object is brought near (as in magnifying greatly) the lens is changed and the image is thrown to the same place.

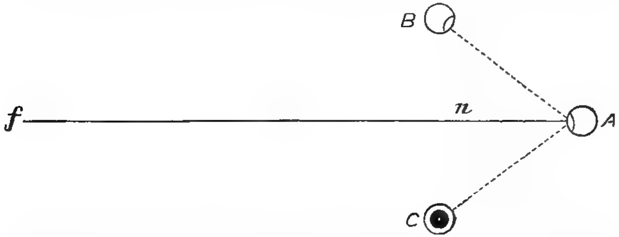

FIG. 77.—*A*, eye observed; *B*, eye of observer; *C*, section of candle flame; *f*, a distant point of sight, and *n*, a near point of sight. (After Helmholtz.)

Now in the eye the adjustment for distance is perfect, for objects at all distances from five or six inches to infinite distance; for the moon or sun is seen perfectly defined. How is it done? It is done by *changing the*

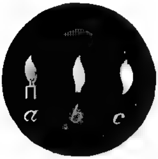

FIG. 78.

form of the lens. For the complete proof of this we are indebted to Helmholtz. The experiment is shown in Fig. 77, in which *A* is the eye of the patient observed, *B* the eye of the observer, and *C* a candle. In looking into the eye *A* with an ophthalmoscope three images of the candle are distinctly seen (Fig. 78). One of these—the first (*a*)—is the reflection from the corneal surface. The second (*b*), much fainter and smaller, is from the anterior convex surface of the lens. Both of these are upright. The third (*c*), still fainter and smaller, is *inverted*, because it is reflected from the posterior surface of the crystalline, which is *concave*. All this is observed while the patient gazes at a distant point (*f*, Fig. 77). Now tell the patient to look at a very near point (*n*), perhaps six inches from the eye. Immediately the image (*b*, Fig. 78) is seen to change. It becomes smaller, and changes its place in such wise as to show that the anterior surface of the lens has become more convex, has bulged out, and even pushed the iris out a little (see Fig. 79). Thus it seems certain that in accommodation of the eye to near vision the lens thickens and becomes more refractive. But the question still remains, How does it do this? We are distinctly conscious of a muscular strain. What muscle?

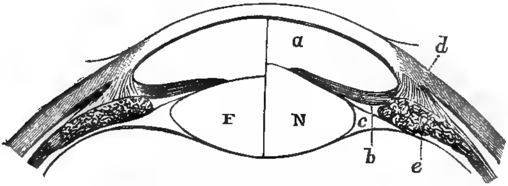

FIG. 79.—*F*, lens adjusted to distant objects; *N*, to near objects; *a*, aqueous humor; *d*, ciliary muscle; *e*, ciliary process.

This is not definitely settled, but we are again indebted to Helmholtz for the most probable view, viz., that it is done by *contraction of the ciliary muscle.* We have already mentioned (page 103) the lens capsule, its continuation as a curtain outward all around, and its attachment to the sclerotic a little behind the iris. Now this curtain is taut, and therefore the capsule presses gently on the elastic lens and flattens it. This is the passive condition of the eye when it is accommodated to distant objects. Now there is a muscular collar about the iris, on the inside of the sclerotic, the fibers of which, arising from the outer margin of the iris, radiate outward and backward, and, taking hold of the outer margin of the lens curtain where it is attached to the sclerotic, pulls it forward to where the circumference is less, and therefore slackens its tautness and allows the elastic lens to bulge. The amount of bulging is in proportion to the slackening, which will be in proportion to the contraction, and this in proportion to the nearness of the object.

See, then: the eye is more like the microscope, in that it changes the lens rather than removes the screen. But how much more perfect! The microscope has its four-inch lens, its two-inch lens, its one-inch, its half-inch, its tenth-inch lens, and changes one for another as the object is nearer. The eye has but one lens, but it changes the form of its one lens so as to make it a six-inch lens, a foot lens, a twenty-foot lens, a mile lens, or a million-mile lens, for at all these distances it makes a perfect image.

4. **Adjustment for Light.**—In both the camera and the eye some contrivance is wanted to regulate the amount of light admitted. In both, too, this is done by diaphragms with holes of varying size. In the eye the iris is the diaphragm and the pupil the hole. But in this

case the diaphragm is contractile and the pupil self-regulating.

Structure of the Iris.—The iris, as already seen, is a continuation of the choroid, which lines the sclerotic as far forward as a little in front of the lens curtain, and then is drawn together transversely to form the iris. This part is thickened with muscular fibers. These are of two kinds, circular and radiating, as shown in the figure (Fig. 80). The circular fibers, by contracting, draw the pupil together and make it small; the radiating fibers take hold on the margin of the pupil and pull it outward in every direction and enlarge it. Or, perhaps better, regard the circular fibers as sensitive and actively contractile and the radiating fibers as elastic and passively contractile. When the circular fibers contract they draw up the pupil, stretching the radiating fibers. When they relax, the radiating fibers elastically contract and enlarge the pupil. Now, the circular fibers are in sympathetic relation with the retina in such wise that stimulation of the retina by strong light reflexly causes the pupil to contract. As the light decreases, the pupil expands to take in more until, in the dark or in case of paralysis of the retina, the pupil expands until the iris becomes a slender ring.

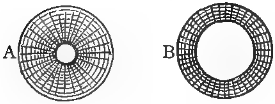

FIG. 80.—Showing structure of the iris.

The hint has been taken here also by the instrument maker. The iris diaphragm of the microscope is made of thin overlapping plates of steel, which, by turning a thumbscrew, slide toward or away from one another, contracting or enlarging the opening between. It is a beautiful contrivance, but far inferior to the living iris.

DEFECTS OF THE EYE AS AN INSTRUMENT.

We have shown the beauty of the eye as an instrument by comparing it with the photographic camera. But all eyes are not perfect. The defects of the eye are indeed quite common, and apparently becoming more and more common through abuse of this delicate organ, especially in the schoolroom. In order to understand these defects it is necessary to define the normal eye.

Normal Sight—Emmetropy.—The normal eye in a *passive* state is prearranged for a perfect image of a distant object. The focus of *parallel* rays is on the retina. For all nearer distances it accommodates itself by action of the ciliary muscles until the object is as near as five or six inches. Nearer than this it can not accommodate itself to make a perfect image. Its range of distinct vision, therefore, is from six inches to infinite distance. This is the standard. Any considerable deviation from this is a defect. The most common defects are *myopy*, *hyperopy*, *presbyopy*, and *astigmatism.*

Myopy, Brachyopy—Nearsightedness.—This is perhaps the most common of all defects of the eye, especially in large cities and in most advanced communities. In the myopic eye the refractive power of the lenses of the eye is too great for the position of the retina. The focus of parallel rays when the eye is passive is not on the retina, but in front of it. The rays must be divergent to make a perfect image on the retina. Therefore distant objects can not be seen distinctly. The object must be brought near to a certain limit before it can be seen well. But within that limit it accommodates itself like the normal eye. In the normal eye the range of distinct vision is from infinite distance to six inches; in the myopic eye the range is from a yard to four inches, or a foot to three inches, or six inches to two inches, according to the degree of myopy. The fault being too great refraction, the remedy is, of course, to diminish the refraction by the use of *concave* glasses. If these be so chosen that the focus of parallel rays is on the retina when the eye is passive, so that distant objects are seen distinctly; then the eye accommodates itself to all nearer objects, and behaves in all respects like a normal eye.

Hyperopy—Oversightedness.—This is the opposite of myopy. In the passive state the focus of parallel rays is *behind* the retina. In this defect the refractive power of the lenses is too small for the position of the retina. The defect is far more common than generally supposed. It often exists unknown to the patient or his friends. Distant objects are seen perfectly well, because a slight accommodation brings the focus on the retina. But the eye is *never passive* unless in sleep. For this reason it is often a distressing defect, producing headaches and the like. Since the defect is a deficiency in refractive power, the obvious remedy is the use of slightly convex glasses suited to the degree of deficiency. The eye then functions exactly like a normal eye.

Presbyopy—Old-sightedness.—Both the preceding are *structural* defects; this is a *functional* defect. The eye may be structurally normal—i. e., in a passive state the focus of parallel rays is on the retina—but it has lost the power of accommodating itself to divergent rays. The patient sees well distant objects, but can not see near objects well. In order to see near objects well the eye must be re-enforced by convex glasses. But the use of glasses can not make the eye normal, as in the other two defects, because it has lost the accommodating power. Therefore the glasses are not worn habitually, as in the other two defects, but only in looking at near objects—not in walking, but only in reading.

The term longsightedness or farsightedness is sometimes used to express this defect. It is a misnomer. No eye can be longer-sighted than the young normal eye. It can define perfectly the edge of the moon or of the setting sun. Moreover, all eyes—the myopic and hyperopic, as well as the normal—undergo the presbyopic change with age; but the myopic eye does not thereby become normal, as many suppose.

Astigmatism—Dim-sightedness.—All other eyes see distinctly at *some* distance, but the astigmatic eye does not see distinctly at *any* distance. Hence the term dim-sightedness. In all other eyes *all* the rays of light issuing from a radiant point are brought to a focal *point;* in this one they are brought together to a focal *line*, or rather to two focal lines, one farther than the other. Hence the term astigmatism.* In all other eyes the curve of the lenses, and therefore their refraction, is equal in all directions. In this one the curve and the refractive power *up and down* is greater or less, usually greater, than from *side to side*. The remedy is, of course, the use of glasses which correct the unequal refraction. For example, suppose the curve and the refractive power from side to side is normal, but the curve and refractive power up and down is too great, then the glasses should have no curve horizontally, but should be concave vertically—i. e., should be cylindrical concave glasses, with the axes of cylinder horizontal.

The usual test for astigmatism is a large rectangular cross, thus +. At a certain distance the astigmatic eye sees the vertical line distinctly, but the horizontal line is blurred. At a certain other distance the horizontal line is distinct, but the vertical blurred. But at no distance are they both distinct.

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* Not *a point.*

SECTION III.

The Retina and its Functions.

Thus far, as much as possible, we have confined ourselves to the eye as an instrument for making an image, and have compared it with the camera in order to show the beauty of its adaptation for that purpose. But in both the camera and the eye the image is only a *means* to accomplish an end—to make a photogram in one case and accomplish vision in the other. In both cases there must be a sensitive screen to receive the image—the iodized plate in the one, and the living retina in the other. In both cases, too, the most wonderful changes take place in these sensitive screens. Before we can un-

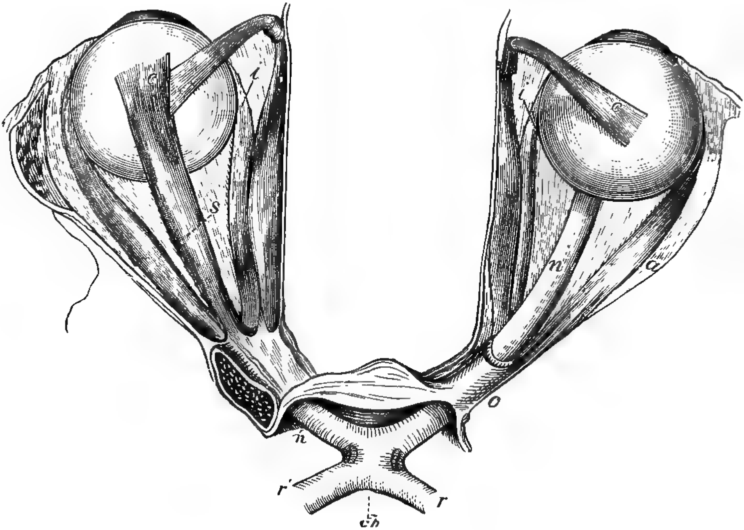

FIG. 81.—A view of the two eyes, with optic nerves: *ch*, optic chiasm; *r r*, nerve roots; *n* and *n'*, right and left optic nerves. (After Helmholtz.)

derstand the phenomena of vision we must know something of the general structure and function of the retina.

Structure of the Retina.—The second pair of cranial nerves, as already seen, arise by fibers partly from the optic lobes and partly from the thalamus. These fibers unite to form the optic roots (*r*, Fig. 81), which converge and unite to form the chiasm (*ch*). From the chiasm there go out diverging the two optic nerves (*n*), which enter the eye sockets near the conical point, pass forward through the fatty cushion and between the recti muscles, enter the eyeballs a little to the interior or nasal side of the axis or south pole, pierce the sclerotic and choroid, and spread to form the innermost lining coat directly in contact with the vitreous humor. As a thin, translucent coat it passes forward almost to the attachment of the lens curtain, forming thus a deep cup-shaped receptive plate (Fig. 33, p. 51). Its greatest thickness at the bottom of the cup is one quarter millimetre or one one-hundredth inch, and thence thins out to a feather edge on the forward margin of the cup.

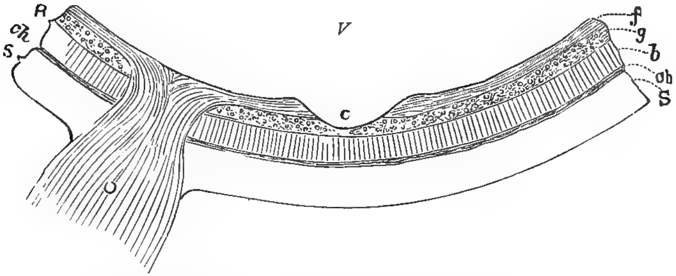

FIG. 82.—Generalized section of retina, etc.: *O*, optic nerve; *S*, sclerotic; *ch*, choroid; *R*, retina; *b*, bacillary layer; *g*, granular and nuclear layer; *f*, fibrous layer; *V*, vitreous humor; *c*, central spot.

Although so thin, its structure is very complex. In a cross section under a low power of the microscope, it is seen to consist of three layers (Fig. 82): (1) an *inner* or *fibrous layer* in contact with the vitreous body, consisting wholly of interlacing fibers of the optic nerve; (2) of an *outermost* layer—*bacillary layer*—composed entirely of rodlike bodies set on end and in contact with the choroid; and (3) between these a middle layer, consisting of granules and larger nucleated cells, and therefore called the *granular* and *nuclear layer*.

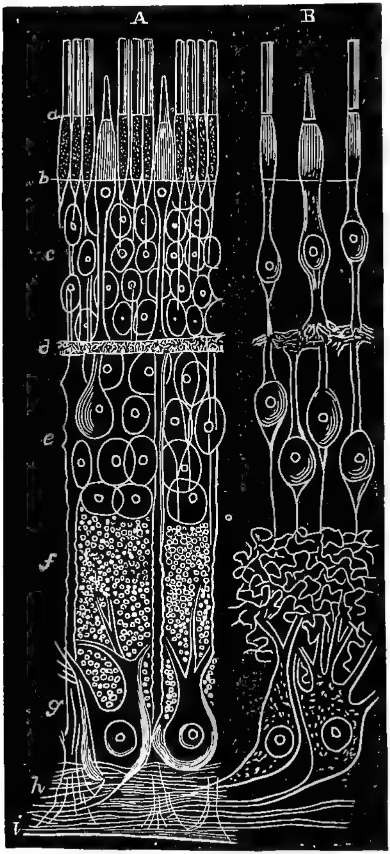

FIG. 83.—Enlarged section of retina (after Schultze): *A*, general view; *B*, nervous elements; *a*, bacillary layer; *b*, interior limit of this layer; *c*, external nuclear layer; *d*, external granular layer; *e*, internal nuclear layer; *f*, internal granular layer; *g*, ganglionic layer; *h*, fibrous layer, consisting of fibers of optic nerve.

All three layers exist in all parts of the retina except in two small spots: (1) where the optic nerve enters there can be, of course, only the fibrous layer; (2) in the center of the bottom of the cup and in the very axis of the ball there is a small depression in which the fibrous layer is entirely, and the granular and nuclear layer nearly entirely wanting. This is called the *central spot* on account of its position, and the *fovea* on account of its depression.

But the importance of the retina is so great that it must be studied more carefully under a higher magnification. Fig. 83 is a highly magnified section. Concerning the inner or fibrous layer nothing more is revealed. The middle layer is seen to be very complex, consisting of several granular layers and several layers of nucleated cells and one layer of very large ganglionic cells. The functions of these various layers are not certainly known. The bacillary layer is now seen to contain two kinds of elements—the one slenderer, longer, and more *rodlike*, the other shorter, stouter, and more *conelike.* The rods are about one fourteen-thousandth of an inch (one five-hundred-and-sixtieth millimetre), and the cones about one five-thousandth of an inch (one two-hundredth millimetre) in diameter. The rods are usually most numerous. Fig. 84 is a view of the outer surface, showing the larger cones surrounded by the more numerous rods. But the relative number of these is not the same in all parts.

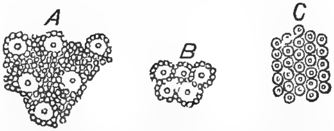

FIG. 84.—Bacillary layer, viewed from the outside surface: A, appearance of usual surface; B, appearance of surface of the raised margin of central spot; C, surface of central spot.

Distribution of the Rods and Cones.—On the anterior margin of the retina there are no cones, but only rods. As we approach the bottom of the retinal cup the cones become more and more numerous, and at the same time smaller until in the central spot or fovea there are no rods, but only cones, and these have become very small, only about one ten-thousandth of an inch (one four-hundredth millimetre) in diameter (Fig. 84). Further, it must be observed that the fibers of the fibrous layer—i. e., of the optic nerve—turn back through the granular and nuclear layer and terminate in the rods and cones (see Fig. 83). These, therefore, must be regarded as *fiber terminals of the optic nerve.* It is probable that the connection between the nuclear cells and the rods and cones is by means of dendrites; and, furthermore, that the dendrites of a nuclear cell touch those of *several* rods, while the cells corresponding to the cones, especially those of the fovea, communicate with much fewer, perhaps with *only one* cone, as seen in the accompanying figure (Fig. 85). The importance of this will be seen hereafter (page 131).

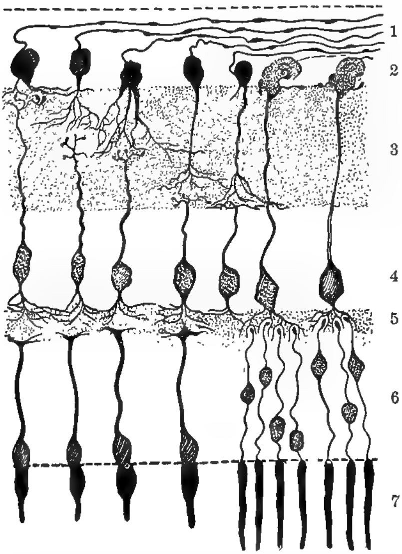

FIG. 85.—Diagram showing the mode of connection between nucleated cells and the rods and cones: 1, fibrous layer; 2, ganglionic layer; 3, first granular layer; 4, first nuclear layer; 5, second granular layer; 6, second nuclear layer; 7, bacillary layer.

The Distinctive Function of the Layers.—The function of the fibrous layer is wholly transmissive. It is made up of sensory fibers, which transmit impressions on the retina to the brain. The function of the middle layer is doubtless intermediary between the elements of the bacillary layer and the fibers of the optic nerve. The true receptive layer is the bacillary. This is proved (1) by the fact that there is only one spot where this layer is wanting—viz., where the optic nerve enters—and *this spot is blind;* and (2) by the fact that the central spot or fovea is the most sensitive spot in the retina, and there the fibrous layer is entirely, and the middle layer almost entirely, wanting. In this spot the bacillary layer is almost directly exposed to the impression of light. Thus, then, the fovea is the most highly organized spot of the retina. It differs from other parts in three particulars: 1. The bacillary layer there consists only of cones. 2. The cones there are much smaller than elsewhere. 3. The bacillary layer is there almost directly exposed to the influence of light.

The distinctive functions of the rods and the cones will come up for discussion hereafter. Suffice it to say now that the perception of *color* seems to reside in the cones alone.

Visual Purple.—There has recently been found in the outer or terminal ends of the rods, but not the cones, a purplish red substance, which probably has an important but imperfectly understood function in vision, and is therefore called *visual purple.* It is bleached by light, and again restored by darkness. Photographic images (optograms) of objects may be taken on the purple retina and by appropriate means may be fixed.* The discovery of this substance naturally excited hopes that its study would solve the mystery of sensation by reducing it to a chemical process; but these hopes have not been realized, for it is now known that the visual purple is not present in all animals, nor does it exist in the cones, and therefore is not present in the fovea, which is, nevertheless, the most sensitive spot in the retina both to *form* and *color*, though not to simple faint light. The visual purple, therefore, is certainly not essential to the perception of either light or color.

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* Foster's Physiology, p. 1254.

There are, however, some facts concerning the occurrence of visual purple which throw light on its function.* It is wanting in night-blind animals, such as snakes and most birds, and is abundant in nocturnal animals, such as most ruminants and all cats, and in owls among birds. Its probable function is to give greater sensitiveness to the impression of simple *faint*, *diffused* light, but not to form and color, and is therefore found in the rods, but not in the cones. It is easily destroyed by light and re-formed in darkness, and is therefore specially adapted to feeble light. Hence in very faint light, but not in full light, at night, but not by day, we detect the *presence* of an object (though not its form and color) by *indirect* better than by *direct* vision. Direct vision is by the cones only (because the image is then on the fovea); indirect vision is by rods mostly, and these are made specially sensitive by the presence of the visual purple. This explains also the temporary night blindness of one coming out from a brilliantly lighted room into the night. The restoration of the night vision is the result of the re-formation of the visual purple destroyed by the brilliant light.

SECTION IV.

Perception of Space and of Objects in Space.

There is a certain fundamental property of the retina, optic nerve, and associated brain apparatus which must now be explained, for it lies at the very basis of visual phenomena.

The First Law of Vision. The Law of External Reference of Retinal Impressions.—An image is formed on the retina, but we do not see the retinal image. We do not see anything in the eye, but some-

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* Parinaud, Rev. Scientifique, vol. iv, 134, 1895.

thing—the object—outside in space. The object, however, is the facsimile of the image. It is *as if* the retinal image were projected outward into space and appeared there as an external image, which we interpret as an object. I said *as if*. Really the retinal image is the sign of the definiteness of the impression. For the molecular changes in the retina are *graduated in degree and kind* exactly as the light is graduated. The light image is a sign of an invisible molecular image. It is this perfectly definite impression, this invisible molecular image, which, by the brain or by the mind, is referred outward into space and interpreted as an object.

This law is so fundamental that we stop a moment to show that it is no new law specially enacted for the sense of sight, but only an extreme modification of a general law of sense-perception.

Comparison with Other Senses.—We have already seen that stimulation of any sensory nerve in its course is referred by the brain to the *peripheral* extremity. If the ulnar or the sciatic nerve is pinched anywhere in its course, pain is felt not at the place, but in the fingers or toes where the nerve is distributed. In the case of an amputated leg, pinching the end of the nerve in the stump causes pain in the toes where the nerve is naturally distributed, even though there be no longer any foot at all. In ordinary sensory nerves, therefore, stimulation of any part of the nerve is referred to the *peripheral* extremity. Now, the optic nerve differs only in the fact that the impression is referred *beyond* the peripheral extremity and *out into space*.

This seems a great difference, but remember the gradations already spoken of (page 96). In touch and taste the reference is only to the peripheral extremity, because the necessary condition of sensation is direct contact. In smell we have indeed a sensation in the nose, but we already refer it to a distant body, because the condition of sensation is air-borne particles. Finally, in hearing, and especially in sight, we lose entirely the sense of contact or local impression, and refer it wholly into space.

Illustrations of the Law.—We shall now try to make the law clear by many illustrative experiments:

EXPERIMENT 1.—If we could bare the retina and touch its surface we would not feel it, but would see a *flash of light*—Where? In space and in a direction exactly opposite, or at right angles to, the touched surface. If the optic nerve be laid bare and pinched we would feel nothing, but would see a flash of light in space opposite that part of the retina where the pinched fibers are distributed. Of course we can not deliberately make this experiment, but the flash of light is observed in passing electricity through the nerve, and also in cases of extirpation of the eye at the moment of rupture of the optic nerve.

EXPERIMENT 2. *Phosphenes.*—Close the eyes, and then press the finger into a corner of one of them. A brilliant-colored circle is seen in the field of darkness opposite the point pressed. These are called phosphenes. In my own case they are brilliant golden rings, with steel-blue centers. They are caused by the indentation of the sclerotic and, through it, the retina. But any change whatever in the retina shows itself as an appearance in space.

EXPERIMENT 3. *Muscæ Volitantes.*—Look at a white wall, or better, a bright sky. Nearly all observers will see specks or clouds or tangled threads in the bright field, slowly gravitating downward. They are called "muscæ volitantes," or flying gnats. What are they? They are slight imperfections in the vitreous body. These less transparent spots cast their shadows on the retinal bottom. But any variation of the retinal surface shows itself as an appearance in the field of view directly opposite.

EXPERIMENT 4. *Purkinje's Figures.*—Darken the room; close one eye, say the left; hold a lighted candle very near the open eye, three or four inches, and to the right side, so that the retina is strongly illuminated. Gaze on the opposite wall until the field of view becomes darkened by excess of light. Now move the candle about, back and forth, up and down. Presently we see a shadowy specter covering the whole wall, like a great bodiless spider with branching legs, or a spectral tree with leafless branches. What is it? It is an exact but greatly enlarged image of the blood vessels of the retina (Fig. 86). These, ramifying in the granular layer, and therefore in front of the bacillary or receptive layer, cast their shadows on the latter. But any change or variation of this layer is seen as an appearance in space.

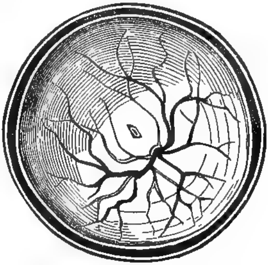

FIG. 86.—Internal view of the retina, showing the retinal vessels ramifying over the surface, but avoiding the central spot. (After Cleland.)

EXPERIMENT 5. *Ocular Spectra—After-Images.*—Gaze steadily at the setting sun a moment, and then turn away and look at the wall, the sky, or at a distant building. A colored image follows the eye and is cast on what it looks at. Why so? The sun's image makes so strong an impression on the retina that it is retained for a considerable time; it makes a *brand* on the retina. But every change or variation in the retina, whether shadow or image or brand, shows itself as an appearance in the field of view.

We have taken the extreme case of the sun, but any bright object, such as a candle flame in a dark room or a stained-glass window, will produce a similar effect. In the case of bright colors, as in stained-glass windows, the after-image is of a complementary color. Red is seen as green and *vice versa*; blue as orange-yellow and *vice versa*. But to discuss these color phenomena would carry us too far.

Generalization of these Facts.—We have seen that all changes or variations of whatever kind in the retina, whether images of objects, or shadows, or brands, show themselves as appearances in space. *Therefore space itself as perceived by the eye is an externalization or outward reference of retinal states.* With the eyes open, the field of *view* crowded with objects is the externalization of the stimulated retina crowded with images; with the eyes shut, the field of *darkness* is still the externalization of the unstimulated retina. The sense of space before the eyes is ineradicable. We can not rid ourselves of it. In the dark or with the eyes shut it is still there, as the field of darkness. It is in front, not behind the head. It is a positive appearance, which may be roughly outlined and may be described. It is not black, but rather dark-gray or brown, with confused markings and cloudings and sometimes colored spaces scattered throughout. Thus we have an abiding sense of space as the external representative of the retina, even though we see no object in it, precisely as we have an abiding sense of a hand, even though we feel nothing with it.

The Second Law of Vision; the Law of Direction.—The previous law asserts the perception of space as the externalization of retinal states, and therefore the reference of all retinal images to that space. This law gives the *direction* of the external reference. In several of the preceding experiments we have alluded to their general direction. We come now to define it exactly.

The law may be given thus: Any impression on a rod or cone of the bacillary layer is referred by the rod or cone back into space *end on*—i. e., at right angles to the retinal surface. Or it may be otherwise expressed thus: The impression produced by light from any radiant point in space is referred *back along the ray line* to the place whence it came. Either of these formulæ is sufficient for general statement, but the former is probably the more exact. The latter, however, we will use for illustration. Thus we have two concaves, the spatial and the retinal; two worlds, a macrocosm and a microcosm; and these correspond with one another point for point, and exchange with one another by impression and by external reference along the lines connecting them. This is represented in Fig. 87. In this figure, of all the rays proceeding from a radiant point and gathered by the lens to a focal point on the retina, we take only the *central ray*, for this represents the resultant impression. These central rays cross one another at the nodal point *n*. If now *a*, *b*, *e*, be three stars, then the light from *a* impresses the retina at *a′*, and is referred straight back along the

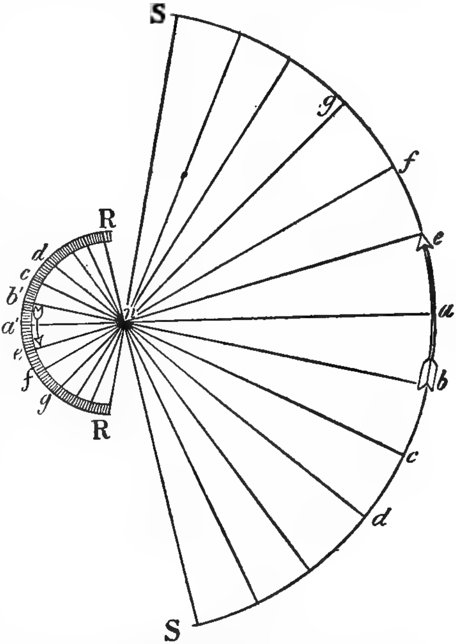

FIG. 87.—Diagram representing corresponding points, retinal and spatial.

ray line to its proper place. Light from *b* passes through the nodal point *n* and strikes a rod or cone in the upper part of the retina, *b′*, and is referred back along the ray line to *b*. Similarly light from *e* passes a little downward through *n* and impresses the lower part of the retina, and is referred back to its proper place below. Thus the three stars will be seen in proper relative positions. Thus the lower part of the retina corresponds to the upper part of the field of view, and the upper part of the retina to the lower part of the field; the right side of the retina to the left side of the field, and the left side of the retina to the right side of the field; and in each case with the utmost exactness, point for point. Every rod and cone, as it were, knows its own point in space, and refers its impressions there.

Comparison with Other Senses.—Now, this is no unique law peculiar to sight alone, but a general law of sense-reference, though refined to the last degree in this sense. In the case of any impression on a sensitive surface the cause is referred in a general way along the line of impression. Suppose we are captive, bound and blindfolded, and surrounded on all sides by Apache Indians and a target for their arrows, could we not tell roughly the direction of each shooting Apache by the direction of the punch of his arrow? Now, every radiant is shooting rays into the eye. Is it not natural that every impinging ray should be referred back along the line of its flight to the point whence it came? Now, the retina is specially and wonderfully organized to do this with mathematical exactness.

These two laws, the law of spatial reference and the law of direction, are fundamental. The one explains why impressions made in ourselves are referred outward into space. The retina, or the brain through the retina, *creates visible space.* The other gives the direction of such reference, the exact place of all objects and radiants in space. Together they explain all the phenomena of monocular vision except the perception of color. With this exception, the whole science of monocular vision is but an explication of these two laws. All that we have further to do, therefore, is to take up several important subjects and show how completely they are explained by these laws.

1. ERECT VISION.

Statement of the Problem.—We have seen that the retinal images are inverted. We have also seen that these images are referred, as it were projected, outward into space, and are seen there as external images, the signs and facsimiles of the objects which produced them. How is it, then, that objects are seen in their natural positions—i. e., *erect?* This problem has puzzled thinkers ever since the inverted retinal image became known.

True Solution.—But there is no mystery at all about it, if we clearly understand the law of direction. Most reasoners on the subject do not seem to perceive that the problem of erectness of objects does not differ at all from that of *seeing objects in their right places.* The latter concerns the true position of *objects*, the former the true position of *radiants.* Objects are composed wholly of radiant and retinal images of corresponding focal points. Now, if images are referred each back along its ray line to its proper place in space, then also the focal points of these images are similarly referred each to its proper place. Now, as ray lines from radiants cross one another at the nodal point and thus invert the image, so the reference lines recross at the same point, and thus *reinvert the image in the very act of external reference.* This is shown in Fig. 86, except that now an object replaces the *stars.* It is evident that the two ends of the arrow must be seen, each in its proper place, and therefore *erect*. Suppose we stand at night in the open air beneath the star-lit sky. Is it any mystery that the stars are seen each in its proper place? Now, every object consists of an infinite number of starlike radiants, and each radiant is referred back along its ray line to its proper place.

2. THE FOVEA AND ITS SPATIAL REPRESENTATION.

The fovea, or central spot, is directly in the axis of the eye—the south pole of the globe. It differs from other parts of the retina in several respects: 1. The fibrous layer and the larger part of the nuclear layer is wanting, so that the bacillary layer is more directly exposed than elsewhere to the direct action of light. 2. This part of the bacillary layer consists of cones only. 3. The cones here are much smaller than elsewhere. From the absence of the other layers this point is depressed, hence the name fovea, a pit. It is evidently the most highly organized part of the retina.

Its spatial representative is the spot we look at—the point of sight, or rather the *line* of sight, and a small area about it. When we look at anything the axis of the eye is turned directly upon it, and the image of the thing falls on the fovea. The point we look at and a small area about it are seen distinctly. If we look steadily at the point and at the same time observe our perception of objects in other parts of the field of view, we find that while their presence is plain enough, their exact form and surface-detail are more and more imperfectly perceived as we go from the point of sight. This is not the result of imperfect image, but of imperfect perception of the image; not the result of an imperfect instrument, but imperfect retinal response. We can not have a better illustration of this than the act of reading.

We see perfectly the word we look at, but words right and left are increasingly illegible, and therefore we are compelled to run the eye along the line, so that the image of every word falls successively on the fovea. The eye is the most restless of organs. In looking at a scene we sweep the point of sight about and gather up the results in memory, and thus seem to see the whole scene distinctly. But really we see distinctly only a very small area. The explanation of this is doubtless found in retinal structure. As already seen (page 120) the cones of the fovea are connected each with its own fiber, whereas one fiber is connected with *several* rods.

Is this limitation of distinct vision a defect? I think not. Suppose we saw all parts of the field of view with equal distinctness: it would be impossible to fix *thoughtful attention* on the thing looked at. But the development of the higher faculties of the mind is conditioned on the ability to *fix the attention.* Thus there are three kinds or grades of vision: 1. *Simple seeing*, which may be unconscious and involuntary. 2. *Looking*, or the voluntary act of sight. 3. *Observing*, or the thoughtful act of sight. This last is characteristic of man alone.

Minimum Visibile.—What is the limit of sight as to smallness? We answer, There is nothing so small that it can not be seen if there be light enough. A star is the nearest to a mathematical point that we can well conceive. We may magnify it three thousand diameters, and still it is a point. And yet a star may be seen plainly enough. The only sense in which there is a *minimum visibile* at all is the smallest thing that can be seen *as a magnitude*—the smallest distance between two stars that they can be seen as *two*, the smallest distance between two dots or two lines that they can still be seen as *two.* This undoubtedly depends on the size of the cones of the fovea. If the images fall on one cone, the two dots are seen as one; but if far enough apart to fall on two cones, they are seen as two. Taking the foveal cones as one seventy-five-hundredth of an inch (one three-hundredth millimetre) in diameter, and the nodal point as six tenths of an inch (fifteen millimetres) from the fovea, and the point of sight as *ten* inches, the *minimum visibile* ought to be about one four-hundred-and-fiftieth of an inch (one eighteenth millimetre). This is about the fact for good eyes. If the point of sight be *six* inches, as it may be in young normal eyes, the minimum will be one seven-hundred-and-fiftieth of an inch (one thirtieth millimetre).

Comparison with Touch.—The only sense with which we can make comparison in this regard is touch, because these two are the only senses that take cognizance of dimension. There is also a *minimum tactile*—i. e., the smallest distance between two tactile impressions in which they can be felt as *two*. This varies greatly in different parts of the body.

EXPERIMENT.—Take a pair of dividers, arm the points with small shot or bits of cork, so as not to prick the patient. Now try, on a blindfolded person, the distance of separation between the points when these are felt as two. It will be found that on the middle of the back the separation must be two to three inches; on the outside of the forearm or back of the hand, about one half or three quarters of an inch; on the finger tips, about one twelfth of an inch; and on the tip of the tongue, about one twenty-fifth of an inch, or one millimetre. In the retina it is one seventy-five-hundredth of an inch.

3. BLIND SPOT.

We have already seen (page 118) that there is another spot where all the layers of the retina are not present—viz., just where the optic nerve enters the eye. As the optic nerve consists of fibers and as it spreads these as an innermost layer, all other layers must be absent here. Now as the bacillary layer is the sensitive layer, it follows that the spot must be blind.

Experimental Proof of a Blind Spot.—EXPERIMENT I.—Make the spots on a sheet of paper, a few inches apart, thus:

Shut the left eye and look with the right steadily at the left figure, *a*, while the paper or page is slowly brought nearer the face. At a certain distance—about nine inches for the above figures—the right-hand figure, *b*, will disappear, but on continuing the approach it again reappears. The image of *b* has traveled across the blind spot and come out on the other side.

EXPERIMENT 2.—Standing up, put a small coin on the table and a finger of the left hand beside it. Now, shutting the left eye and looking at the finger with the right eye, move the finger slowly to the left and follow it with the eye. At a certain point the coin disappears from view, but reappears on continuing the movement of the finger.

EXPERIMENT 3.—Look at a bright star with one eye, say the right. Now move the point of sight slowly and steadily to the left, horizontally. At a certain point the star will disappear, only, however, to reappear on continuing the movement of the point of sight in the same direction. In this manner almost any object, if not too large, may be made to disappear from view. A man sitting at a distance of, say, one hundred feet may be made to disappear.

Diagrammatic Illustration.—The condition under which the disappearance occurs is represented in the diagram (Fig. 88). The eyes, *R* and *L*, are supposed to come nearer to the two objects, *A* and *B*, *L* being shut and *R* looking across at *A*. The image of *A* falls all the time on the fovea, *a*. The image of *B* falls on the inner or nasal side of the fovea at *b*, but not far enough to reach the entrance of the optic nerve, *o* (R_1) (1). But as the face comes nearer the eye *R* turns more and more, the image of *B* falls first *near* the place (2), then on the place (3) of the entrance of the optic nerve. As *R* approaches still nearer (4), the image of *B* has crossed and appeared on the other or nasal side of the optic entrance and reappears.

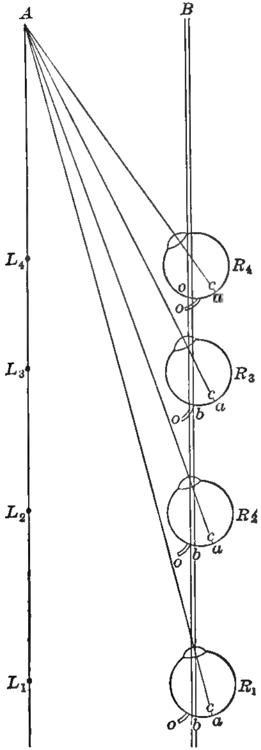

FIG. 88.

Spatial Representative of the Blind Spot.—Every part of the retina has its representative in the field of view. Therefore the blind spot has also. Why, then, do we not see it? When both eyes are open, of course we do not see it, because we see with the one eye the spot which represents the blind spot of the other eye. There is no place that represents the blind spot of both eyes. But even with one eye shut we see nothing. In fact, the expectation of seeing such a representative shows a misconception. The only true representative of a blind spot must be an invisible spot. It can not be differentiated from the rest of the field.

Nevertheless the *place* of the representative of the blind spot *can be perceived in the field of darkness.* At night in the dark—when the retina by long rest is very sensitive—if the visual plane be lowered toward the feet, and then the eyes be turned quickly and strongly to one side or the other, two brilliant stars with dark centers are seen to flash out for a moment in the dark field (Fig. 89). The phenomenon is produced by a pull on the optic nerves. The dark center is the spatial representative of the blind spot, and the brilliant radiating circle is produced by irritation of the surrounding bacillary layer.

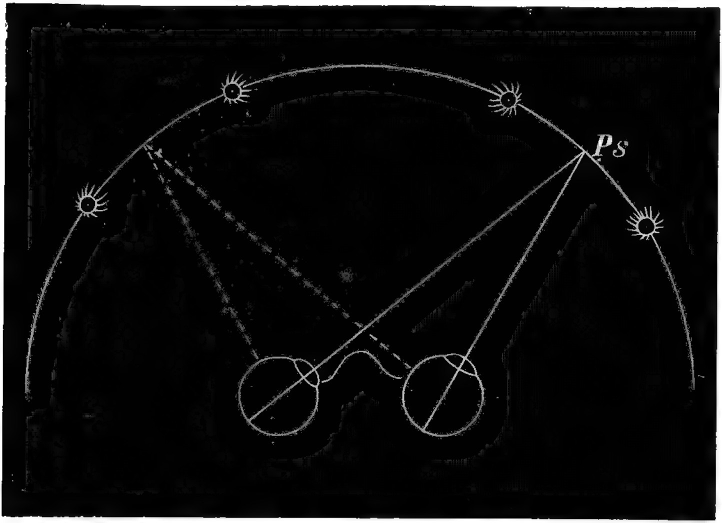

FIG. 89.—Diagram showing place of the invisible spots in the field of vision. The full lines show the eyes turned to the right; the dotted lines the same turned to the left. *Ps* = point of sight.

COLOR PERCEPTION AND COLOR-BLINDNESS.

We have thus far treated of perception of light only as intensity and direction. But another primary perception is that of color.

Intensity versus Color.—As there are two kinds of perception of sound—viz., sound as simple sound or *noise*, loud or faint, and sound as *tone* or *pitch*, high or low, acute or grave—so there are two kinds of perception of light, viz., light as simple light, bright or faint, and light as *color*. In both sound and light the one is a question of *quantity*, the other of *quality*. In both cases the one is a question of *strength* of vibration or wave-height, the other of *rate* of vibration or wave length. In both, too, there is a limit to the *range* of perception. In the case of sound the range is great—viz., from the lowest, sixteen per second, to the highest, some thirty to forty thousand per second, or more than eleven octaves. In the case of light it is very restricted, four hundred million-million to nearly eight hundred million-million, or about one octave.

Primary versus Mixed Colors.—Primary or pure colors are such as are *simple* sensations. Mixed or secondary colors are such as may be made by mixtures of the primaries in various proportions. The former are few, the latter almost infinite in number. Both primary and secondary colors may be again mixed with black or white, and give rise to an infinite number of *shades* of each.

Primary Colors.—There is much difference of view as to which and how many colors should be called primary. Brewster (and Newton before him) made three—viz., red, yellow, and blue, rejecting green because it can be made by mixing blue and yellow pigments. Young, and after him Helmholtz and nearly all physicists, make also three, but they are red, green, and violet or blue approaching violet, rejecting yellow because a mixture of spectral red and spectral green makes a kind of yellow. From the purely physical point of view undoubtly Helmholtz and the physicists are right, and

Brewster wrong, for pigments are never pure colors. A mixture of blue and yellow pigments makes green, because both of the components contain some green; and when they are mixed, the yellow and blue kill one another, and the green of both comes out.

Hering differs from both the preceding. He makes six primary colors—viz., white, black, red, yellow, green, and blue. Furthermore, according to him, these constitute three pairs of complementaries—viz., white and black, red and green, yellow and blue. There is but one objection that can be made to Hering's view—viz., his inclusion of white and black. These should be put into a different category—viz., that of *shade* instead of *color*, of intensity or *quantity* instead of *quality*. Leaving out these, Hering's four colors, or two pairs of complementaries, are red and green, yellow and blue. Undoubtedly from the point of view of sensation, unplagued by any physical considerations, Hering is right. As color-sensations these are perfectly simple and wholly distinct, and this is true of no other colors. Scarlet and orange are plainly and visibly a mixture of red and yellow, purple a mixture of blue and red, and even violet is a blue with a glow of red. White and black are also indeed pure simple sensations as Hering maintains, but *color* is not the proper word to express these sensations.

Theory of Color Perception; General Theory.—1. Color is a simple sensation and incapable of analysis into any simpler elements. It must be, therefore, the result of retinal structure. 2. It is an endowment of the cones and not of the rods. This is shown by the fact that the distribution of color perception over the surface of the retina is identical with the distribution in number and fineness of the cones. In the fovea there is nothing but cones, and these are very small, and the color perception is therefore keenest at the point of sight and a small area about it. As we go outward from the fovea in all directions, we find the cones are fewer and larger, until there are none at all on the margins of the retina. So, correspondingly, the perception of color is more and more imperfect as we go from the point of sight to the margins of the field of view, where it is finally lost entirely. 3. There must be some response of the retina characteristic of each color. We may imagine that *different* cones are adapted to vibrate responsively—co-vibrate—with different colors. Or we may imagine different substances in all the cones which are photochemically affected each by a particular color. This latter seems the more probable view. We shall call such substances *color-substances.* Thus we have, say, a red color-substance, meaning not that the substance is red, but that it is photochemically affected by a certain rate of vibration and produces the sensation of red.

Special Theories.—Applying this to the different views as to primary colors, according to Helmholtz, there are in the retinal cones three kinds of color-substance which are responsive to three rates of vibration—viz., red, green, and violet rays, respectively, and these give rise to the corresponding color sensations. If two of them are affected, they produce mixed colors. If all are affected in certain proportions, we have *white.* Or, to put it another way: pure colors affect only one, mixed colors two or more, white light *all* in certain proportions. According to Hering there are only *two* color-substances (three, if we include white and black); the one by *opposite affections* produces the complementaries red and green, the other by opposite affections the complementaries yellow and blue; and the essential nature of complementariness, especially their mutual destructiveness, is the necessary result of these opposite affections of the same substance.

Mrs. Franklin has recently brought forward a view which deserves and has received much attention. She thinks that color perception, like all other faculties, has been gradually evolved. The steps were as follows: First of all, in the early stages of evolution there was but one color-substance in both the rods and the cones This she calls gray color-substance, because it is photochemically affected by, and gives rise to, the perception of white and black and all shades between—i. e., grays. At that time only white and shades, but not colors, were perceived. Next, some of this substance in the cones, but not in the rods, was differentiated into two color-substances—viz., *yellow* and *blue*—which, separately affected, give rise to these two colors respectively, but simultaneously affected, to white and shades. Lastly, one of these two—viz., yellow—was again differentiated into red and green; but these by simultaneous affection give rise still to yellow.

COLOR-BLINDNESS.

Many people seem to discriminate colors imperfectly, but only because they do not observe carefully. They see colors perfectly well, but have not learned to name them. This is *not* color-blindness.

What is Color-Blindness?—The color-blind do not see certain colors at all as colors, but *only as shades.* To take one example: The commonest form of color-blindness is that for the colors red and green. For such a person the red berries and green leaves of a cherry orchard, or the red carnations and the green lawn on which they grow, look much alike, and neither of them red or green, but *gray.* In a word, they look much as a stereogram of the scene would look to an ordinary person looking through the stereoscope; for the iodized plate is also blind for these colors.

Cause of Color-Blindness.—Color-blindness is a defect of retinal structure. In the case of the color-blind one or more of the color substances are wanting. In the red-green blind, for example, the red color-substance and the green color-substance of Helmholtz are both wanting. Or, according to Hering's better view, the one substance which, by opposite affections, produces these complementaries, is wanting, and that is the reason why these two are usually associated. Such persons see yellow and blue perfectly well. According to Mrs. Franklin, color-blindness is an example of atavism—i. e., a reversion to a primitive condition. Total color-blindness, which, though rare, sometimes occurs, is a relapse to the earliest condition. There is only gray substance in the retina. Red-green blindness is a relapse to the second stage, in which some of the gray substance has been differentiated into yellow and blue, but the yellow has not been further differentiated; while normal vision is the third or perfect stage, in which the yellow has been further differentiated into red and green.

What the Color-Blind really See.—By the color-blind *pure* colors are either seen correctly or not seen at all as colors, but only as shades. The mixed colors they always see incorrectly. Taking the commonest form of color-blindness, the red-green blindness, the following schedule shows what they see and why:

Pure colors.

I.

See correctly.

a. *White* and *black* and all shades of the same—i. e., grays.
b. *Yellow* and all shades of the same—i. e., browns.
c. *Blue* and all shades of the same—i. e., slate blues.

II.

Do not see at all as Colors.

a. Reds are seen as shades or grays.
b. Greens are seen as shades or grays.

III.

See incorrectly.

Mixed colors.

a. Scarlet = red and yellow—i. e., gray and yellow = dark brown.
b. Orange = red and yellow—i. e., gray and yellow = lighter brown.
c. Bluish green = blue and green—i. e., blue and gray = slate-blue.
d. Yellowish green = yellow and green—i. e., yellow and gray = brown.
e. Purple = red and blue—i. e., gray and blue = slate-blue.

Tests.—It might seem that so striking a phenomenon needs no test. Every one must know it. But this is far from the fact. On the contrary, a man may be color-blind unknown to himself and to his friends. He may have observed some instances of curious confusion of colors, but these are attributed to imperfect knowledge of color names. In the case of persons in responsible positions, such as locomotive-engine drivers, ship steersmen, etc., where color signals are used, it is very important that ability to see colors correctly should be tested. The simplest test and one of the best is a box full of skeins of yarn of all colors and shades, and several of each. Such a box is placed before the person to be tested, and he is directed to sort them and match the colors. All normal-sighted people would match them alike and correctly, but the color-blind make the most extraordinary mistakes. Certain shades of red and green and gray are put together as the same; similarly certain shades of scarlet and brown or purple and slate-blue.

By these tests the remarkable fact is brought out that this defect is much more common in men than in women. About one in every twenty-five men are more or less color-blind, while among women hardly one in a thousand is thus affected.

SECTION V.

Binocular Vision.

All the phenomena thus far treated are essential to vision. They would still be found if, like the cyclops Polyphemus, we had but one eye in the middle of the forehead. But, in addition to these, there are certain other phenomena which are wholly the result of the use of *two* eyes as *one instrument.* These belong to *binocular vision.* Observe, it is not the mere having of two eyes which gives rise to these phenomena. We might have a hundred eyes and have no binocular phenomena, for each eye may act independently, as is the case in many lower animals. *The two eyes must act as one instrument.*

The phenomena now about to be described are far more illusory, more psychical, more difficult to be observed. Although we are forming judgments based on them every day of our lives, yet they usually drop out of consciousness, and by many persons are recalled to consciousness with difficulty. For this reason we shall be compelled to treat them much more cursorily than their importance deserves.*

SINGLE AND DOUBLE VISION.

Double Vision.—We have two eyes, two retinæ, and two fields of view—their spatial representatives—though they indeed partly overlap and form a common field. We have also two retinal images of each object, and two external images, the spatial representatives of the two retinal images. Why, then, do we not see everything double? So indeed we often do, but without observing it. It is necessary first of all to prove this. I do so by some simple experiments.

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* This subject is fully treated in my book Sight.

Experiment 1.—Hold up the finger against the opposite wall or against the sky, and look not at the finger but at the wall or sky. *Two fingers are seen*, shadowy, transparent, because they hide nothing; the place covered by each is seen by the other eye. While still looking at the sky or wall, shut the *right* eye; the *left* image disappears. Shut the *left* eye; the *right* image disappears. Evidently the right image belongs to the left eye and the left image to the right eye. Such are called heteronymously double images.

Experiment 2.—Hold the two forefingers, one before the other, directly in front—i. e., in the middle plane of the head, and twelve to fifteen inches apart. Look at the farther finger; the nearer one is double. Look at the nearer finger; the farther one is double. By shutting alternately first one eye and then the other it will be found that in the former case the images each belong to the eye on the *opposite* side—i. e., are heteronymous, while in the latter case they belong each respectively to the eye on the *same side*. Such are called *homonymous*.

We might multiply experiments indefinitely, but these are sufficient to show that we often see objects double. They show more, viz., that when we look at an object we see it single, but all objects beyond or this side of the point of sight are doubled, but in opposite ways—in the former case homonymously, in the latter heteronymously. This doubling of objects is evidently the necessary result of the two retinal images. But the questions occur: Why should we see objects single at all? What are the positions of the two retinal images when objects are seen single?

Single Vision.—Since there are two retinal images of every object and two external images, their spatial representatives, it is evident that single vision can only take place when the two *external* images are *superposed* and *coincide perfectly;* and this takes place when the retinal images fall on *corresponding* points of the two retinæ. It is necessary to define these exactly.

Corresponding Points.—Corresponding points are points exactly similarly situated in the two retinæ. The foveæ are, of course, *par excellence* corresponding points, and all other corresponding points are symmetrically arranged about these. If R and L (Fig. 90) represent projections of the two retinæ, and *c c* the centers of the foveæ, and vertical and horizontal lines be drawn through the central spots, then points similarly situated in reference to these—viz., *e e'*, *d d'*—are corresponding points. Or, suppose the two retinæ be placed one on the other in geometric coincidence, then the points—the rods and cones—which coincide are corresponding rods or cones. It follows that the two right or shaded halves are corresponding halves, and similarly the two left or unshaded halves—i. e., points similarly situated in the two right halves or left halves—are corresponding. But the two inner or nasal halves have no corresponding points, nor have the two external or temporal halves any correspondents.

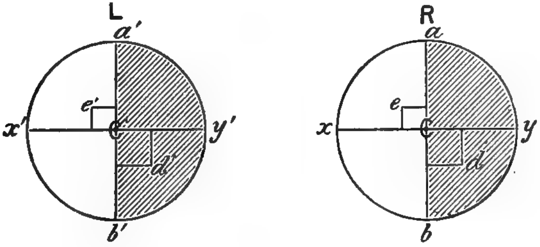

FIG. 90.—Diagram showing corresponding halves of the retinæ.

The Third Law of Vision; the Law of Corresponding Points.—We restate now the conditions of single vision as a law. *When the two retinal images of* *any object fall on corresponding points, then the external images are thrown to the same place and are superposed and seen single, but when the two retinal images of an object fall on non-corresponding points then the external*

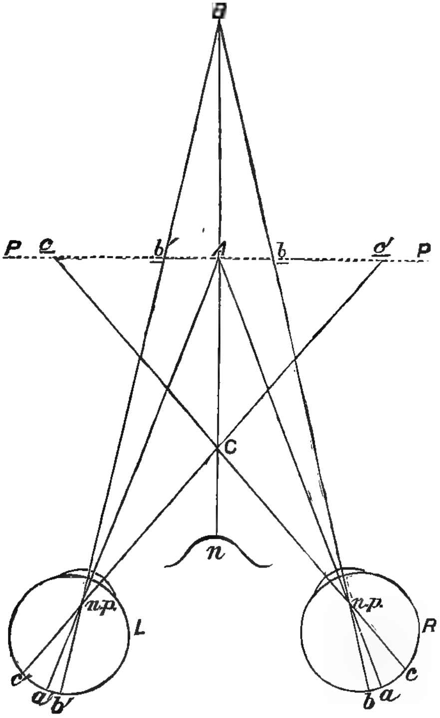

FIG. 91.

images are thrown to different places and are seen double. Now it is at once seen why we see single what we look at; for then the axes of the two eyeballs are converged on the object and the images fall on the central spots or foveæ, and these are *par excellence* corresponding points. Why we see double all objects nearer and farther off than the point of sight, and differently double in the two cases, is shown in the diagram (Fig. 91). Let *A*, *B*, and *C* be three objects in the median plane, and the eyes *R* and *L* be fixed on *A*. The images of *A* will fall on the central spots and be seen single; but the images of *B* will fall on the two nasal halves, *b b'*, but all points in these are non-correspondent and therefore *B* will be seen double. Similarly *C* will be seen double because its images fall on the two temporal halves. The kind of doubling in each case may be shown by referring all the external images to the plane of sight, *P P* It is then seen that the images *b b'* of *B* are homonymous, while the images *c c'* of *C* are heteronymous. That is, as we before found, objects nearer than the point of sight are doubled heteronymously while objects farther than the point of sight are doubled homonymously.

Horopteric Circle.—As already shown, objects beyond or on *this side* of the point of sight are seen double. But how is it with points about the same distance, but right or left, or above or below that point? Take first right and left. Let *R* and *L* (Fig. 92) be the two eyes and *A* the point of sight. Draw a circle through *A* and through the nodal points *n n'*. This is the horopteric circle, or circle of single vision, of Müller. For if the eyes be fixed on *A*, any object at that point will be seen single because its images are on the central spots *a a'*, but at the same time *B* or any other point in the circle will also be seen single because its images will fall on *b b'*, which are obviously corresponding points. But this is not true of any point *B'* in the plane *P P*.

Horopter.—We have taken points right and left. If there be also points above and below seen single at the same time, then there would be a *surface* of single vision. Such a supposed *surface of single vision with the point of sight fixed* is called *the horopter*. Whether there be such a surface at all, and if there be, what is its form, are very complex and difficult questions which can not be discussed here.*

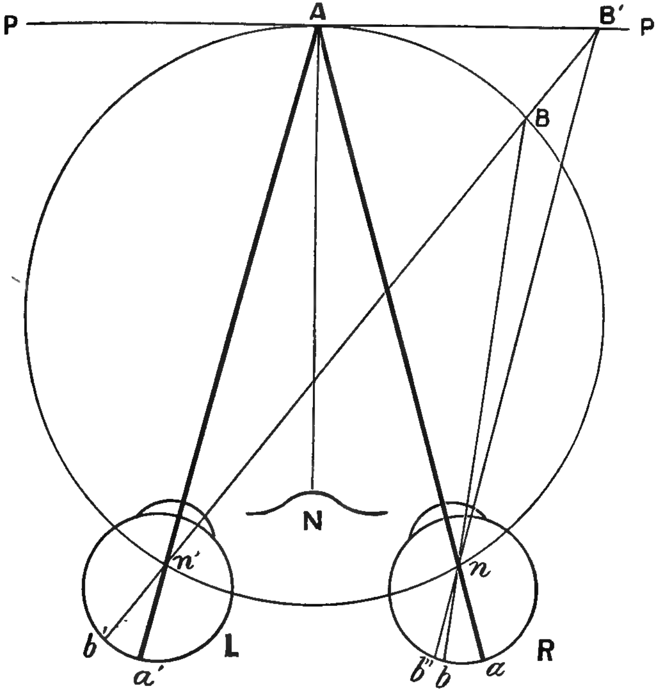

FIG. 92.—The horopteric circle of Müller: *R* and *L*, two eyes; *n n'*, point of crossing of ray lines—nodal point; *A*, point of sight; *B*, some other point in the horopteric circle *A n n'*; *a a'*, central spots; *a a'*, *b b'*, retinal images of *A* and *B*.

The Relation of the Chiasm to Corresponding Points.—The union of the optic nerves to form a

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* They are fully discussed in author's book Sight.

chiasm (Fig. 81, page 116) is undoubtedly related in some way with the use of the two eyes as one instrument, and therefore with the existence of corresponding points. The fibers of the optic roots partly cross and partly do not cross, as shown in the diagram (Fig. 93).

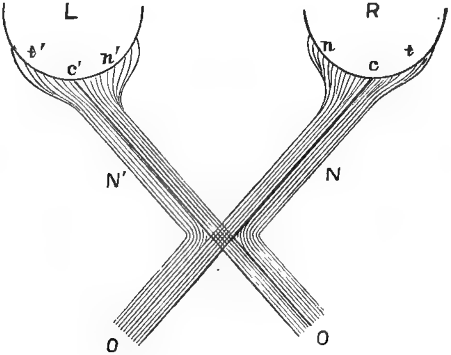

FIG. 93.—*O O'*, optic roots; *N N'*, optic nerves; *R* and *L*, sections of the two eyes; *c c'*, central spots; *n n'*, the nasal halves, and *t t'*, the temporal halves, of the retinæ.

Thus *each* root supplies *both* eyes, and conversely each *eye* is controlled by *both sides of the brain.* The existence of a true chiasm with fibers crossed in this peculiar way may therefore be taken as evidence of the existence of corresponding points and the possession of binocular vision.

The Two Adjustments of the Eyes.—There are two fundamental adjustments of the eyes in every act of looking, viz., the *focal* adjustment, or accommodation, and the *axial* adjustment, or turning the axes so as to converge on the object looked at. The one is necessary for *distinct* vision, the other for *single* vision. Associated with these, but far less important, is a third, viz., pupillary contraction.

Two Kinds of Corresponding Points.—We have already (page 127) spoken of corresponding points, retinal and spatial. We have just explained the corresponding points of the two retinæ. Now we assert that the *corresponding points in the two retinæ have the same spatial correspondent.* So that there is a kind of triangular correspondence between the two eyes and space.

The Two Fundamental Laws of Vision.—There are also, as we have seen, two fundamental laws of vision—the *law of direction* and the *law of corresponding points.* The one explains the apparent anomaly of *erect* vision with *inverted* retinal image, the other the apparent anomaly of *single* vision with *two* retinal images. The one is the fundamental law of monocular, the other of binocular vision. We have seen how all the phenomena of monocular vision flow logically from the one. Now we proceed to show how all the phenomena of binocular vision follow necessarily from the other. There is, however, a third law underlying both and more fundamental than either—viz., the law of outward or spatial reference of all retinal states.

BINOCULAR PERSPECTIVE.

The law of external reference gives space. The law of direction gives two dimensions of space—i. e., up and down and from side to side. Now, the law of corresponding points gives the third dimension of space—i. e., depth or distance from the observer. The perception of this third dimension, so far as it is dependent on the use of the two eyes as one instrument, is our next subject. We begin again with experiments:

EXPERIMENT 1.—We repeat that given on page 143, but for another purpose. Place the two forefingers, one before the other, in the median plane, and separated, say, a foot from one another. We have already shown that when we look at the nearer finger we see it single, but the farther finger is doubled homonymously. When we look at the farther finger we see that one single; but now the nearer one is doubled heteronymously. Now observe, further, that we are clearly conscious that it requires more convergence, and therefore more effort, to look at the nearer finger and see it single, and less convergence and less effort of the ocular muscles to look at the farther finger and see that single. In other words, we run the point of sight back and forth from one finger to the other by greater and less convergence, and thus acquire a distinct perception of distance between the two. It is literally a process of rapid triangulation, with the interocular distance as the *base line*. The same is true of all objects in space at different distances if the distance of the nearer one be not too great.

Experiment 2.—But single objects also occupy depth of space. Take, therefore, next a rod, say a foot long; hold in the median plane, a little below the horizontal line, with the nearer end six to eight inches from the face. Looked at with one eye, say the right, the rod is seen projected thus / ; looked at with the left eye, \. Now, it is evident that these two images can not combine. When we open both eyes and look at the farther end, the nearer end is doubled heteronymously, and we see the rod as an inverted V, with the open end toward us, thus Λ ; when we look at the nearer end, the farther end is doubled homonymously, and we see a V with the point toward us, thus V ; when we look at the middle, we see the two images cross in the middle to make an X, thus X. Thus we run the point of sight back and forth from one end to the other, by greater and less convergence uniting each point looked at, and acquire thus a distinct perception of the distance between the two ends. The same is true of all objects occupying depth of space.

Thus, then, we may safely generalize: In viewing a single object occupying considerable depth of space, or a scene with objects one beyond the other, it is evident that the retinal images of the object or of the scene in the two eyes, and therefore the external images—their spatial representatives—or the way the object or scene looks to the two eyes, respectively, are different, because taken from *different points of view.* Therefore they can not be united as a whole, but only in parts at a time. When we look at the foreground, objects in the background are double; when we look at the background objects in the foreground are double. Thus we run the the point of sight back and forth, uniting successively different parts of the scene, and acquire thus a clear perception of depth of space between.

Limitation of Clear Vision.—See, then, the extreme limitation of distinct vision and of single vision. As distinct vision is confined to a small area about the point of sight, and we must therefore sweep about this point and gather up the result in memory, even so single vision is limited to the distance of the point of sight, and we must run the point of sight back and forth, uniting successively different parts of the scene, thus *probing* space and gauging its depth, and gather up the results in memory.

Different Forms of Perspective.—Of course, there are other ways of judging of relative distance—other forms of perspective. It may be well, therefore, to give these, and very briefly compare them:

1. *Aërial Perspective.*—We judge of distance by the color of the air through which we look. The atmosphere is not absolutely transparent, but bluish. Distant objects, like mountains, are dimmer and bluer in pro-

portion to their distance, and we judge of distance in this way.

2. *Mathematical Perspective.*—The angular diameter of objects, and therefore the size of the retinal image, is mathematically proportioned to the distance. Therefore objects seem small in proportion to their distance. Parallel lines, like railway tracks, converge, and houses on the two sides of a street converge and grow smaller with distance. We judge of distance quite accurately in this way.

3. *Binocular Perspective.*—This, as already explained, is a judgment of distance by running the point of sight back and forth, successively uniting double images by greater and less convergence, and thus gauging space.

4. *Focal Perspective.*—When with one eye we look at a very near object, farther ones are dim, and *vice versa.* We are aware of voluntary effort of accommodation for distinct vision of near objects, and judge of relative distance in this way also.

Distance at which these Operate.—Now, of these four kinds, the focal operates for only about twenty feet. Beyond this the accommodation is a vanishing quantity. The binocular perspective operates for about one quarter to one half mile. Beyond this it, too, becomes a vanishing quantity. The other two operate without limit.

The painter can imitate the first and second, and much of his art consists in skillfully introducing an appearance of distance by dimming and bluing and making smaller the objects in the background of his picture. The other two he can not imitate. The lack of focal perspective is, however, of little importance, because landscape pictures are usually viewed at a considerable distance. But the lack of binocular perspective seriously interferes with the illusion which he seeks to produce. Hence the perspective is far clearer when the picture is looked at with one eye only.

JUDGMENTS OF SIZE AND DISTANCE.

The eye perceives *at once* direction up and down and right and left, and therefore *outline* form and surface contents, for this is a combination of directions. Thus *two* dimensions of space—viz., *angular* diameter in all directions—are given *immediately*. But this does not give *size*, unless distance, or the *third* dimension, is also known. Now, this third dimension is not given in sense, but is a *judgment*. The direct gifts of sight are light, its *intensity*, its *color*, and its *direction*, and therefore also outline form. But size, distance, and solid form are judgments based on these gifts. Moreover, size and distance are closely correlated, so that a mistake in one will cause a corresponding mistake in the other.

Distance.—We judge of distance by the various forms of perspective already explained. Being a judgment, we are liable to error. We often say "our senses deceive us." Not so. We make false judgments on true reports of the senses.

Size.—The size of an object is judged by its *angular* diameter, or size of its retinal image, multiplied by its estimated distance. For example, in Fig. 94 the retinal image *a* may be made by *A* or *A′* or *A″*, and the apparent size of the spatial correspondent will vary ac-

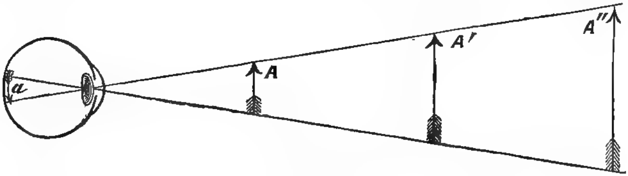

FIG. 94.

cordingly. If we imagine it at *A*, it will look the size of *A*, but if we imagine it at the distance *A''*, it will seem to be four times as large. If its real size and place is *A''*, and we imagine it to be at *A*, it will seem many times too small. If, on the other hand, its real size and distance is represented as *A* and we imagine it at *A''*, it will look many times too large. For example, if we hold up a finger before one eye (the other being shut), very near to the eye, say an inch, its image completely covers a large building one hundred yards distant. Now, if we imagined the finger one hundred yards distant, it would look as large as the building.

The fact of dependence of apparent size on estimated distance is well shown in the case of the sun and the moon. We are accustomed to estimate the distance of terrestrial objects, but have no means of judging of the distance of celestial objects. Therefore different persons will differ in the most extraordinary way about the apparent size of the sun or the moon. Some will say that they look about the size of a saucer, others the size of a dinner plate, and others the size of the head of a barrel. There are some extreme cases of persons who say they look about the size of an orange, and others as big as a cart wheel.

The mathematical relation between apparent size and estimated distance is well shown by spectral images. Look at the setting sun steadily for a moment. The image of the sun is branded on the retina so strongly that the brand remains for some time. Now, every change in the retina, whether it be image or shadow or brand, is seen as something in the field of view. With the sun brand still on the retina, look where we will—on the wall, on the floor, on the sky—we see a spectral image of the sun. Now as to the size. Look on a sheet of paper two feet off; the image cast on the sheet is about a quarter of an inch in diameter. Look at the wall twenty feet off; the image is a little more than two inches in diameter. Look at a building one hundred feet off; the image is about ten inches in diameter.

Illustrations meet us on every side. In a fog objects look large, because, being dim, they are supposed farther off than they really are. In the exceptionally clear atmosphere of Colorado or Nevada objects at first seem smaller because they seem nearer than they are, and they seem nearer because they are seen so plainly.

Form.—*Outline* form is a combination of directions of radiants, and is therefore seen immediately. We are not deceived. But *solid* form is always a judgment. We judge sometimes by binocular perspective, sometimes by shading produced by light. We may be deceived by skillful shading of a picture, as in scene painting.

Gradations of Judgments.—There are all degrees of complexity of judgments from simple gifts of sight on the one hand to the most complex intellectual judgments on the other. 1. Light, its intensity, color, and direction. These are direct gifts, are ultimate facts, and therefore incapable of analysis. 2. Then come *outline* form and surface contents. These are given immediately, and therefore are not liable to deception, but are capable of analysis into simpler elements—viz., a *combination of directions*. 3. Next comes *solid* form, which is a judgment, based partly on binocular perspective and partly on the shading of light. Here, for the first time, we are liable to deception. 4. Then come the complex judgments of relative distance and size of objects in an extensive landscape. All of these judgments are so rapid that they are usually not recognized as judgments at all. I therefore call them *visual* judgments. 5. These pass by insensible gradations to the simpler intellectual judgments, and these, in their turn, into the most complex process of thought-work.

SECTION VI.

Comparative Physiology and Morphology of the Eye.

VERTEBRATES.

Mammals.—The structure of the eye and the physiology of vision in all mammals and, indeed, in all vertebrates is substantially the same as that already given for man, yet there are some points of difference worthy of note.

Color.—The iris is, we have seen, a continuation of the choroid coat. Normally and most usually, therefore, it has the dark, chocolate-brown color characteristic of the pigment of that coat. Doubtless this is the original and normal color of the human eye. The blue and gray are the result of peculiar structure, together with a deficiency in pigment. Nearly all mammals have the normal brown color. In the cat tribe, however, as is well known, it is brilliant yellow.

Pupil.—The form of the pupil is usually round, as in man, but in the two most highly specialized and differentiated orders—the cat tribe on the one hand, and the grazing animals on the other—the pupil is greatly elongated, vertically in the former and horizontally in the latter. The vertical elongation is probably connected with the habit of springing on its prey; the horizontal elongation, certainly with wide horizontal view, necessary in grazing. This shape of the pupil, combined with the prominence of the eyes and their position on the margin of a broad front, makes the view of these animals sweep the whole horizon without turning the head or even the eyes.

Tapetum.—In many mammals, especially those of nocturnal habits, such as the cat tribe and ruminants, there is found at the bottom of the retinal concave a large patch, which has a bright, iridescent metallic luster. It is called the tapetum. It is a modification of the *choroid* coat for the purpose of reflection of light. The use of it is not well understood, but it is believed to double the impression of feeble light by making it pass *twice* through the retina. It is this that causes the shining of the eyes in the dark, if a bright light is present.

Fovea.—There is in all mammals a *central area*, which is a little more sensitive; but a true fovea, with its three characteristics (explained on page 121), is not found in any mammal below man, except the anthropoid apes.

Birds.—The iris in birds is very various in color, most commonly the normal brown, but sometimes yellow, as in birds of prey, sometimes *scarlet-red* (summer duck), and sometimes *porcelain-white* (white-eyed vireo).

Sclerotic Bones.—In all birds and many reptiles we find a series of bony plates in the front part of the sclerotic and radiating from the margin of the iris. These are beveled on the margins, and fit together in such wise as to slide a little over one another. By appropriate muscles these may be made to squeeze the ball so as to adapt it to clear vision of very near objects (Figs. 95 and 96).

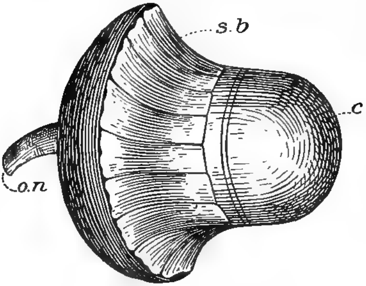

FIG. 95.—Eye of an owl: *on*, optic nerve; *c*, cornea; *sb*, sclerotic bones.

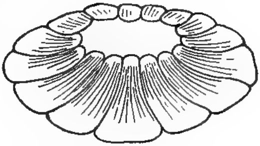

FIG. 96.—Sclerotic bones separated and viewed in perspective.

Nictitating Membrane.—Birds have in the inner corner of the eye a fold of the conjunctiva which may be drawn upward over the eye, wiping it and protecting it from injury without entirely excluding the light, for it is semitransparent (Fig. 97). A remnant of this membrane, in useless condition, is found even in man.

Fovea.—Birds not only have a fovea, but in some there are *two* in each eye. The most distinct of these is in the axis of the eye, and therefore at the bottom of the retinal concave. Now since the optic axes are not parallel, as in man, but are widely divergent (Fig. 100, page 162), the side of the head must be turned toward an object in order that its image shall fall on this fovea. We will speak of this again under binocular vision in vertebrates.

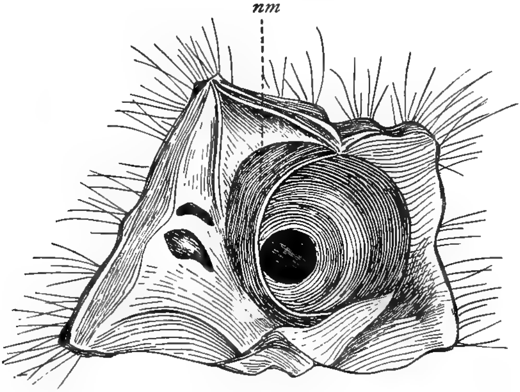

FIG. 97.—Eye of a bird showing (*nm*) the nictitating membrane.

Reptiles.—These are in many ways similar to birds. The sclerotic bones are found in lizards and turtles (Fig. 98), though not in crocodiles and snakes. In some reptiles—e. g., in snakes—the lids are absent. The dry, horny epidermis passes directly over the cornea of the eye, and in skin-shedding comes off with the rest of the epiderm. Also some lizards—e. g., chameleon and phrynosoma—have a distinct fovea.

Fishes.—In these the lids are wanting, the eyes being kept moist by the water. The *lens* of fishes is very peculiar. It is perfectly spherical and much denser than in land animals. Both of these qualities give greater refractive power. This is necessary on account of the medium in which they live, for the refractive power of the eye is the difference between that of the medium and of the lenses. This is well illustrated in the case of the diver. Even in the most transparent water vision is very imperfect if the eye is immersed. If the diver wishes to see distinctly under water he must supplement the refractive power of the eyes by strong double convex lenses, or else by double *concave air spectacles.* Such spectacles may be easily extemporized by putting two watch glasses back to back and cementing impermeable paper about the margins. It is evident that these would act precisely like two convex water-lenses in air.

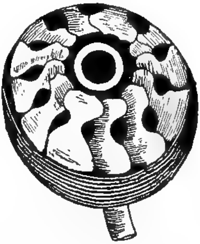

FIG. 98.—Lizard's eye showing the sclerotic bones. (After Wiedersheim.)

The *ciliary muscles* are wanting in fishes. They first appear in amphibians—i. e., in the lowest land vertebrates. Fishes, therefore, can not accommodate the eyes for various distances by changing the form of the lens, for it is already spherical. Their eyes are passively adjusted for *near* objects. They probably accommodate for distant objects by drawing the lens back nearer to the retina.

Binocular Vision in Vertebrates.—There are three points of structure which throw light on this subject—viz., (1) the *optic chiasm*, (2) the position of the optic axis, and (3) the *fovea.*

Chiasm.—There is great diversity in the mode of crossing of the optic nerves. In fishes they cross bodily (Fig. 99, *a*), or else one pierces the other (*b*). In reptiles they form a kind of basket-work (*c* and *d*). Thus far there is a complete crossing of fibers in a more or less complex way. Each side of the brain controls the opposite eye. But in birds, and especially in mammals, half of the fibers cross and half do not (*e*), as shown more fully in Fig. 93, page 148. By this arrangement each side of the brain supplies both eyes, and each eye is controlled by both sides of the brain; and therefore the two eyes co-operate as one instrument. This arrangement is necessary to binocular vision. This, therefore, is the only *true chiasm*. It is probable, therefore, that no animals below birds have binocular vision. This is confirmed by the position of the eyes, which is our next point.

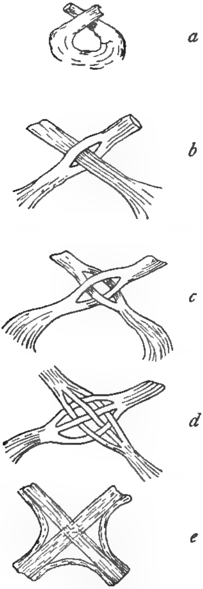

FIG. 99.—Different modes of crossing of the optic nerves: *a* and *b*, fishes; *c* and *d*, reptiles; *e*, mammals.

Position of the Eyes.—The *position of the axes of the eyes* has an evident relation to binocular vision. In *man* the two eyes are directly in front, with the axes parallel in a *passive state*. From this state of parallelism they may be easily converged on a near object. They are therefore in the best possible position for binocular vision. The same is true, and perhaps in equal degree, in *apes*. But below this the eyes are wider and wider apart, and set more and more on the side of the head.

The difficulty of converging on a near point becomes greater; the common field of view is more restricted, until in fishes the eyes are completely on the side of the head; the optic axes diverge one hundred and eighty degrees; convergence on a point is impossible; each eye has its own field of view, which do not overlap to make a common field, and therefore they can not have binocular vision.

All mammals (except perhaps whales) probably enjoy binocular vision in various degrees of perfection. Birds also probably are similarly endowed (although their eyes are so widely divergent), but this is by virtue of a peculiar structure, to be spoken of under the next head.

Fovea.—This is not only the most sensitive spot of the retina, but it is the center about which the corresponding points of the two retinæ are symmetrically arranged. It is undoubtedly necessary for binocular vision in *its highest perfection.* Now, this pitlike spot is found among mammals only in man and the anthropoid apes. Mammals generally have indeed a central area (which may become a tapetum), about the center of which corresponding points are symmetrically arranged, but no true fovea. It is probable that in them the advantages of accurate observation of a single thing is sacrificed to the much greater advantages of somewhat distinct vision over a wide field.

In birds the fovea again appears, and yet their optic axes are so widely divergent as to make it impossible to converge these axes on a point (see Fig. 100). Nevertheless, birds seem to have binocular vision, but this is by virtue of *another fovea.* In other words, among all animals birds are peculiar in having *two foveæ in each eye*, one monocular and the other binocular. The monocular ones, *a a′*, are axial and are the more distinct; the binocular ones, *b b'*, are far removed from the axis on the temporal side, and so situated that lines drawn through them and through the pupils are parallel. These axes can be converged on a given point, and doubtless corresponding points are symmetrically arranged about them and not about the other. The central or monocular fovea is the most distinct, and therefore the monocular vision is better than the binocular. This is the reason why birds—for example, the domestic fowl—in looking attentively turn the head and look with one eye.

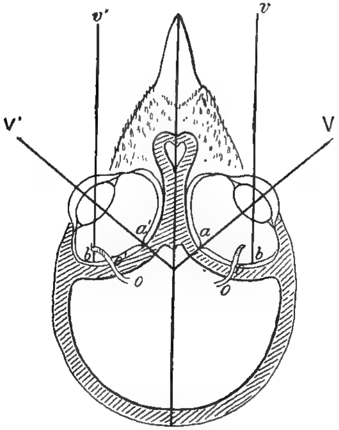

FIG. 100.—Section of bird's head (after Slonaker): *V V'*, monocular visual lines; *v v'*, binocular visual lines; *a a'*, *b b'*, central and temporal foveæ respectively.

Below birds, except in some lizards, nothing like a distinct fovea is found.

It seems certain, therefore, that binocular vision in its *most perfect form* is found only in man and the higher apes, and thence becomes gradually less and less perfect until it disappears entirely in the lowest vertebrates. It is almost needless to add that it is not found at all in invertebrates.

INVERTEBRATES.

In all that follows we are compelled to be very brief, touching only most salient points. Some of these points will come up again under *Evolution of the Eye*.

We pass over the arthropods, because in most of them the structure of the eye is so different from what we have described in vertebrates that no comparison can be instituted. In them we find a different *kind* of instrument and not a mere modification and simplification of that already studied. We shall come back to these after completing the comparison in the case of other invertebrates.

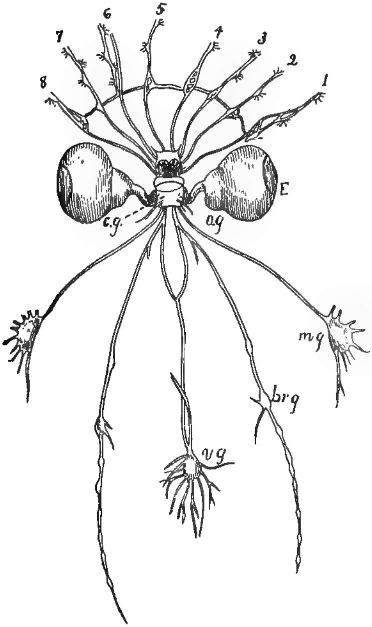

FIG. 101.—Nervous system of an argonaut, showing the eyes : *cg*, cephalic ganglion ; *og*, the optic ganglion ; *mg*, *brg*, *vg*, the ganglia of the mantle, the branchiæ, and the viscera, respectively ; *E*, eye. (After Cuvier.)

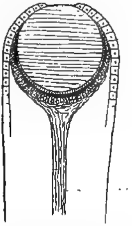

FIG. 102.—The eye of a snail on the end of the tentacle, magnified.

Mollusca : Cephalopods.—The higher cephalopods, such as the squid and cuttlefish, have large eyes and by far the most perfect below vertebrates (Fig. 101). Their instrumental structure is substantially like that of vertebrates and is fully as perfect as that of a fish. There are, indeed, some very significant differences, especially in the retina, but these will come in our discussion of the evolution of the eye.

In the *gastropods* the *lens* is wanting, the vitreous humor being the only refractive medium. The eyes of these are, of course, situated about the head, and often, as in snails, on the ends or at the base of the tentacles or so-called horns (Fig. 102).

The *acephala*, or bivalves, as the name indicates, are without distinct head, and the eyes or eye-spots are strung along on the margins of the mantle, as in pecten. But in many lower acephala and in echinodermata and cœlenterata the lens or any kind of refracting image-making instrument disappears, and the eye is reduced to a *deposit* of pigment to absorb the light and a *specialized* nerve to respond to light. These are called *eye-spots.* They differ from true eyes in not forming an image. They perceive *light*, but not *objects.* They have the specialized nerve, but not the image-making instrument.

Arthropods.—We passed over these because out of the direct line of evolution. We now return.

Many arthropods—for example, the spider—have eyes on the same plan as other invertebrates, but usually very small. But the most characteristic eye of arthropods is the compound eye of insects and crustaceans. It is necessary, however, before describing these, to say something of the *simple* eye of arthropods.

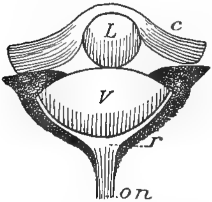

FIG. 103.—Eye of a spider: *L*, lens; *V*, vitreous humor; *r*, retina; *c*, cornea; *on*, optic nerve.

Simple Eye.—If a spider be examined with a hand lens, a number of brilliant, gemlike spots are seen on the front part of the cephalothorax. They are usually in groups of four, six, and eight on each side. These are the eyes. Though small, they are somewhat perfect for invertebrate eyes, for we find a cornea, *c* (Fig. 103), a lens, *L*, a vitreous humor, *V*, a retina, *r*, and an optic nerve, *on.*

Compound Eye.—The compound eye of insects and crustaceans is very different. If we examine the head of any insect, such as a fly, a dragon fly, a butterfly, or a beetle, we find that it consists largely of two great hemispherical masses, often of brilliant metallic luster, green, or purple, or yellow. These are the two compound eyes (Fig. 104). If their surface be examined with a hand lens, or, better, if the outer transparent corneal portion be removed and placed under a microscope, we see that it consists of thousands (twenty-eight thousand in the dragon fly) of transparent hexagonal plates nicely fitted together (Fig. 105). Each plate covers a hexagonal prism, which runs back to abut against the convex surface of the optic ganglion, which acts as the retina and connects in its turn through the optic nerve with the cephalic ganglion. Each tube is lined with pigment, which may be likened to a choroid, and filled with a transparent substance, which may be likened to the vitreous humor. The whole is covered with a hexagonal corneal plate, which is thickened into a kind of lens over each prism. One prismatic element is called an *ommatidium* (Fig. 106).

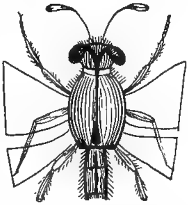

FIG. 104.—Anterior part of a dragon fly, showing the compound eyes.

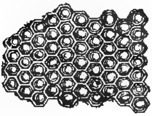

FIG. 105.—A portion of corneal surface of the compound eye magnified.

Now see in a general way (for it is not well understood) how vision is accomplished by this instrument. Remember, the condition of distinct image is that each radiant should impress its own focal point on the retina. Rays from several points must not mix (page 104). Now if an object, *A B* (Fig. 106), be placed before such an eye, the central ray from each point, *A B C*, passes down the corresponding tube and impresses its own point on the retina, and thus forms the image. Rays passing into other tubes strike the pigmented sides and are quenched, and thus mixing is prevented, but with great loss of light.

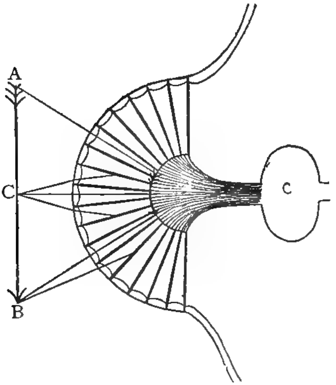

FIG. 106. — Diagram section through compound eye: *C*, cephalic ganglion.

Comparison with Simple Eyes. — Comparing now with normal eyes of invertebrates, we see great differences in several respects. 1. In ordinary eyes distinctness is reached by bringing all the rays from each radiant to a single focal point on the retina. In this method, on the contrary, the same result is secured, but with great loss of light, by allowing only the central rays from each radiant to reach and impress the retina. 2. In all other eyes, vertebrate or invertebrate, the image is *inverted*; in this, on the contrary, it is *erect* (Fig. 106). Nevertheless, in this case also, by the law of direction, the object is seen erect. The reason is that in all other eyes the recipient surface is *concave*, and therefore reinverts the image in the act of external reference, while in this it is convex, and does not reinvert the image. 3. In vertebrate eyes a wide field is got by free motion of the eye in its socket; but in compound eyes it is got by the sphericity of the large surface. In crustacea, where the sphericity is less great, the eye is placed on the end of a movable stalk. It is probable that the sight of the compound eye is very imperfect except at short distance.

Origin of the Compound Eye.—The spider has many very small simple eyes in two groups, one on each side of the head. Now imagine the number greatly increased, the size correspondingly diminished, and then the whole group crowded together until by mutual pressure they are squeezed and elongated into prismatic tubes, and we have a general idea of the probable process of change.

EVOLUTION OF THE EYE.

The exquisite beauty of the mechanism of the eye makes its evolution extremely interesting; but heretofore it has seemed an insoluble mystery. Recently, however, much light has been thrown on the subject.

1. Invertebrate Eye.—General sensibility to light is coextensive with life itself. But it is a law in biology that any useful function will be gradually separated from other functions, localized in an organ, and then improved indefinitely. How did a light-perceiving organ begin? It probably began to be formed under the stimulus of light itself, as follows:

(1) On the exposed epithelial surface certain spots became *pigmented*, and thus more absorbent of light; the nerves to these spots became specialized to respond to the light; the epithelial cells of these spots became slightly modified by elongation into rodlike form; and already we have an *eye-spot*, the simplest beginnings of an eye. Why this effect should occur only *in spots* we know not, any more than we know why freckles should come in spots. Such eye-spots may occur anywhere in exposed surfaces, but more commonly on the most sensitive part, viz., the head, when there is a head. This first step is found in very many lowest animals, especially in lowest mollusks (Fig. 107, *a*).

(2) The next step is a slight saucerlike depression of the pigmented spot with an increased pigmentation and elongation of the cells. This step is found in the sword shell (*Solen*), in which the eye spots are strung all along the edge of the mantle as the only exposed part, for these animals are headless (Fig. 107, *b*).

(3) In the next step the depression becomes deep, cuplike. Evidently here there is a stronger impression of light by reverberation in the hollow and consequently a greater specialization of cells for response. This step is found in the limpet or *Patella*, and the organ is situated in the head, for this is a gastropod. Already we begin to see in the pigmentary layer a choroid and in the elongated rodlike cells a bacillary layer of a retina (Fig. 107, *c*).

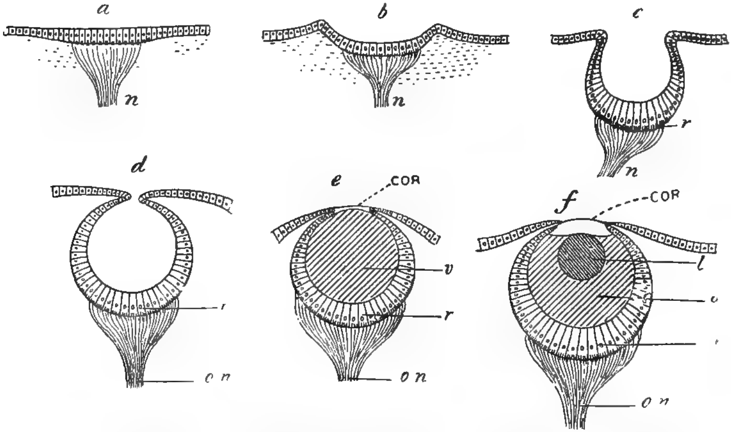

FIG. 107.—Diagram representing the different stages in the evolution of the invertebrate eye: *a b c*, eye-spots, no image; *d*, pin-hole image; *e*, simple lens image; *f*, compound lens image; *r*, retina; *on*, optic nerve; *v*, vitreous humor; *l*, lens; *cor*, cornea.

Thus far we have only eye-spots, not an eye proper; only a specialized layer of nerve terminals, not an image-making instrument; an organ perceiving *light*, but not yet seeing *objects*.

(4) In the next step, which is found in the nautilus, the cup-shaped depression is closed in above until it becomes a hollow vesicle with only a pin-hole opening atop. Now for the first time we have an image, an inverted image, on what is now plainly a retina (Fig. 107, *d*). Now for the first time there is a perception not only of light, but also *objects*. In a word, we have a true eye. But the sight of objects is still imperfect, for it is only a pin-hole image.

(5) In the next step the pin-hole opening closes, but the point of closure remains transparent as a cornea, and the cavity or vesicle thus formed (optic vesicle) is filled by secretion with a transparent refractive substance which may be regarded as a vitreous humor. We have now for the first time a lens image, but yet only a *simple* lens image (Fig. 107, *e*). This is the case in the snail and many other gastropods.

(6) Finally in the squid the last stage in this strange, eventful history is found. In these there is a cuticular ingrowth from the corneal surface which finally separates as a crystalline lens (Fig. 107, *f*), and thus we have a compound lens image.

That these are really the steps of evolution of the eye is proved by the fact that in embryonic development the squid's eye passes through all these stages. It is first seen as a dark spot, then as a saucerlike depression, then as a cup-shaped depression, then as a hollow cavity with a pin-hole aperture; then the aperture closes and the vesicle fills, and, lastly, the crystalline lens is formed by cuticular ingrowth from the cornea. This is the most perfect eye found among invertebrates.

In the invertebrate eye there is yet no chiasm (Fig.

101, page 163), nor is there any fovea. There are certainly no corresponding points of the two retinæ, and therefore no binocular vision; also, as we shall see presently, no blind spot.

2. The Vertebrate Eye.—There are two essential differences between the invertebrate and the vertebrate eye. (1) In the former the nerve fibers terminate forward in the posterior ends of the rods in the most natural way, as in the case of nerve terminals, in all other sense-organs. The bacillary layer is the innermost layer of the retina, and exposed directly to the action of light. In the vertebrate eye, on the contrary, the bacillary layer is the *outermost* layer of the retina, and therefore the fibers have to go forward beyond and turn back and terminate in the *anterior* ends of the rods. This is wholly exceptional not only among eyes, but among special sense-organs. It is this course of the fibers which makes a blind spot, and therefore the invertebrate eye can not have a blind spot.

(2) In invertebrates the whole eye, both the retina and the lenses, is made by *infolding* of an external epithelial surface. In vertebrates, on the contrary, the instrumental part, especially the crystalline lens, is made in this way, but the retinal part is made, as embryonic development shows, from the brain, by an *outfolding* of the cerebral vesicle.

The steps of the development of the vertebrate eye are briefly as follows: (1) The brain is developed as three vesicles. The anterior one is the thalamus (Fig. 22, page 37), which is the basal part of the cerebrum, and we shall call this the *cerebral vesicle.* (2) From the cerebral vesicle by *outfolding* is formed on each side the *optic vesicles* (*O V*, Fig. 108, A), which become more and more constricted off until they are connected only by a narrow neck, which becomes the optic nerve (Fig. 108, B).

(3) Meanwhile the infolding from the epidermal surface has formed the lens. (4) Then the optic vesicle becomes folded back upon itself like a double nightcap, so as to leave a large space between it and the lens. The anterior or back-folded layer of the double nightcap becomes the retina, and the posterior layer the choroid (Fig. 108, C). (5) The two folds come in contact and the vesicle is obliterated. The space between the concave retina and the lens is filled and forms the vitreous humor, the whole becomes encysted by the sclerotic, and the eye is finished. Now observe that the cerebral vesicle and the optic vesicle are lined with epithelium. When this is folded back the pos-

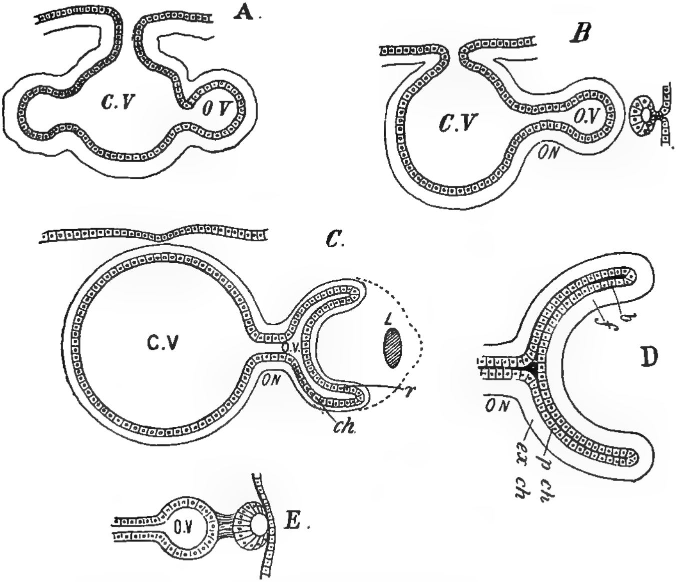

FIG. 108.—Diagram representing different stages in the development of the vertebrate eye: *C V*, cerebral vesicle; *O V*, optic vesicle; *r*, retina; *ch*, choroid; *b*, bacillary layer; *f*, fibrous layer; *l*, lens.

terior or epithelial layer of the back-folded nightcap becomes the bacillary layer of the retina, while the anterior layer of the same is the fibrous layer of the retina.

The difference between the vertebrate and invertebrate retina is great, but not so great as at first seems. In both cases the bacillary layer is formed of epithelial cells—in the one of *exterior* epithelium of skin, in the other of *interior* epithelium of the brain. But the lining epithelium of the brain is itself an infolded portion of the epiderm (Fig. 108, A and B).

Transition from Invertebrate to Vertebrate Eye.—If vertebrates came from some form of invertebrates, as undoubtedly they did, how was the vertebrate eye evolved out of the invertebrate eye? This is a very difficult question. 1. Of course, the vertebrate type of eye must have branched off very low down and before the invertebrate type was fully declared. 2. Much of the difficulty has come of identifying the crystalline lens of the vertebrate eye with the same of the invertebrate eye. On the contrary, it corresponds to the whole eye of the invertebrates. It is formed in the same way, viz., by infolding of the epidermal surface, while the lens of invertebrates is formed by cuticular ingrowth from the corneal surface. The retina of the vertebrate eye is something superadded to the whole eye of invertebrates, the retinal part of the latter having been aborted and modified to form the back part of the vertebrate lens.

Thus much seems certain, but how the change came about is obscure. We may imagine (*a*) some low form of invertebrate with very imperfect invertebrate eye, the infolded epiderm functioning as usual as retina, but this very close to cephalic ganglion. The light stimulating the cephalic ganglion might well provoke the formation of another and better retina. This functions as retina, while the whole invertebrate eye is transformed into a lens. Or (*b*) some low form may have had a pigmented spot on each side of the anterior part of the head. In the formation of the brain and spinal cord by infolding of epiderm these spots might well be carried into the cerebral vesicle and thence into the optic vesicle and become a retina. Meanwhile the lens was formed by infolding, as already explained.

Further Evolution of the Vertebrate Eye.—However this may be, once the vertebrate plan is established the process of improvement goes on again steadily. In fishes the position of eyes on the side of the head and the absence of true chiasm show that there are as yet no corresponding points, and therefore no binocular vision. The ciliary muscle is also wanting, and the eye can not be accommodated to accurate vision for various distances in the same way as in land vertebrates. The eye is no better than that of the squid.

But in land animals the lens becomes flattened to double convex shape, and may now be accommodated to different distances by action of the ciliary muscle. A true chiasm is not formed, and therefore binocular vision is not evolved until we reach birds. Meanwhile the eyes are moved more and more to position in front, with increasing capability to converge on a given point; corresponding points are established in the retinæ; binocular vision and judgments appertaining thereto become possible and more and more perfect. Finally, there is added a fovea, and with it the ability to fix undivided attention on the objects looked at, and this, in its turn, is at least one necessary condition of the evolution of the higher faculties of the mind.

SECTION VII.

Sense of Hearing and its Organ, the Ear.

Sight and hearing are the two higher senses. In these alone the impression of the sensible body is not on the specialized nerve *directly*, but indirectly through the vibrations of a medium. In these alone, therefore, in addition to the specialized *nerve* and in front of it, there is a mechanical instrument for making the impression stronger and more definite.

The eye is undoubtedly the most refined mechanism in the animal body, and yet its structure is more easily explained than that of the ear. The structure of the ear is not only very complex, but it is lodged in intricately winding passages in the interior of the hardest bone in the body. In these passages the branches of the eighth pair of nerves are distributed and specialized to respond to vibrations of the air.

Structure of the Human Ear.—The ear consists of three general parts—the *exterior*, the *middle*, and the *interior* ear. The first two are air-filled, the third is entirely cut off from the air and is water-filled. The first two are instrumental; the third alone contains the specialized nerve (Fig. 109).

The exterior ear includes all that is visible from the outside—i. e., as far as the membrane of the drum. It consists of the conch and the meatus. The conch collects the aërial vibrations, and the meatus carries them to the membrane of the drum. The meatus secretes a kind of wax—ear wax—which by accumulation may cause partial deafness, but is easily removed.

The mid-ear is a cavity just beyond the membrane of the drum. It is about one third of an inch in diameter in direction at right angles to the drumhead, and three quarters of an inch in a direction up and down. It is connected with the throat by a slender tube—the *Eustachian tube*—and is therefore air-filled. The closure of this tube by inflammation of the throat is a frequent cause of partial deafness. By holding the nose and blowing hard, air may be forced through the Eustachian tube into the drum, and cause sensible pressure on the membrane of the drum.

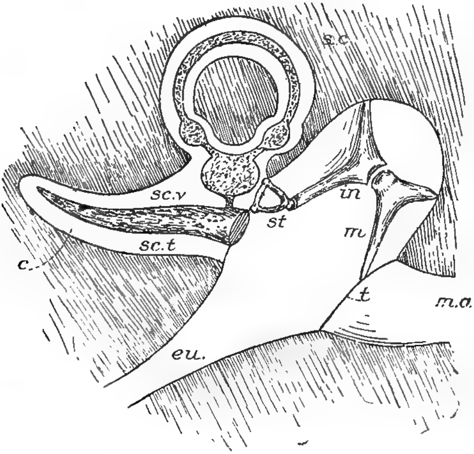

FIG. 109.—Simplified diagram representing a section through the ear; the cochlea is supposed to be unrolled: *ma*, meatus auditorius; *t*, tympanic membrane; *m*, *in*, *st*, the ossicles; *sc*, semicircular canals; *c*, cochlea; *scv*, *sct*, scala vestibuli and scala tympani; *eu*, eustachian tube. The shaded part represents bone. (From Huxley.)

This cavity is separated from the outer ear by the membrana tympani, and from the inner ear by a bony wall, in which are two openings closed with membrane, viz., the *foramen rotundum* and *foramen ovale*. These membranes act as counter-drumheads to the membrane of the drum.

Ossicles.—Running across from the membrane of the drum to the foramen ovale is a chain of three little bones, called the *malleus* (hammer), the *incus* (anvil), and the *stapes* (stirrup). These are articulated together and to the walls of the cavity in a somewhat intricate way, but evidently contrived to carry vibrations of the drumhead to the interior ear, for the malleus is attached to the drumhead, the stapes to the membrane of the foramen ovale, and the incus is intermediate. Sound vibrations of the air cause corresponding vibrations of the drumhead (*t*), and these are carried along the chain of bones and shake the membrane of the oval opening, and therefore the water filling the inner ear, where its further effects will be given after the inner ear is described. The actual shapes of these bones are shown in Fig. 110.

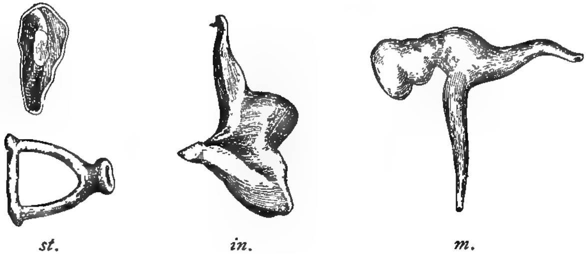

FIG. 110.—Ossicles, enlarged: *st*, stapes; *in*, incus; *m*, malleus.

Interior Ear, or Labyrinth.—The real receptive part of the ear is here. All other parts are purely instrumental. It is called the labyrinth because of the complex winding passages in which the branches of the auditory nerve are distributed. The labyrinth may be best described under two heads, viz., the *bony* labyrinth and the *membranous* labyrinth. The bony labyrinth consists of winding cavities in the solid bone; the membranous labyrinth is a membranous apparatus lodged in these cavities. Each of these two parts consists of three parts, viz., the *vestibule*, the *semicircular canals*, and the *cochlea*. There is therefore a bony vestibule, semicircular canals, and cochlea, and a membranous vestibule (vestibular sac), semicircular canals, and cochlea. All these parts in the membranous apparatus have forms similar to the bony cavity in which they are lodged, but are much smaller, so that there is considerable space between the true receptive membranous part and the cavity in which it is lodged. This space is filled with a watery liquid called *perilymph*. The membranous apparatus is also filled with a liquid called *endolymph*. In the diagram (Fig. 109) the dotted parts represent the membranous labyrinth.

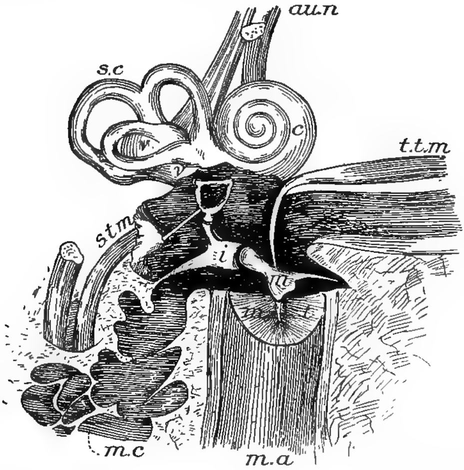

FIG. 111.—Outer and middle ear seen in section, and the inner as a cast of the bony labyrinth: *ma*, meatus auditorius; *mc*, mastoid cells; *t*, tympanic membrane; *m*, malleus; *i*, the incus; *v*, vestibule; *c*, cochlea; *sc*, semicircular canals; *aun*, auditory nerve. (After Cleland.)

Bony Labyrinth.—The *vestibule* is a hollow space about the size of a wheat grain. It is called the vestibule because it is the general hall into which open all the winding passages. It is separated from the tympanic cavity by a wall in which is the membrane-closed oval opening. Out of this hall go out and return again three slender tubes—the semicircular canals. Two of these unite at one end and enter by a common opening, so that there are five openings into the vestibule instead of six. At *one* end of each canal there is a flasklike enlargement.

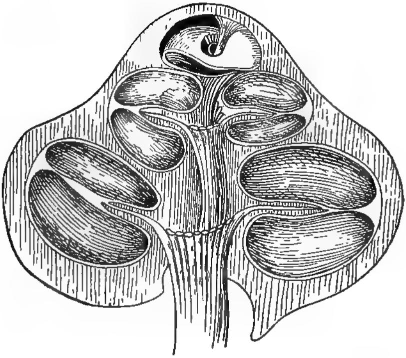

FIG. 112.—Section of the cochlea showing the winding cavity.

The bony *cochlea* is a spiral cavity like a spiral stairway, winding about a central pillar two and a half times and growing smaller to the end (Fig. 112). The name is taken from its resemblance to the shell of a snail.

Membranous Labyrinth.—In the bony labyrinthine cavity just described is lodged the membranous parts of the same names. The membranous vestibule, or *vestibular sac*, within the cavity of the bony vestibule is a small sac from which go and return the three membranous semicircular canals, each with its flask-shaped enlargement at one end, called the *ampullæ.* The auditory nerves are distributed on the vestibular sac and on the ampullæ, the fibers terminating directly on the interior surface (Fig. 113). In the vestibular sac and attached to hairlike nerve terminals there are several little sandlike grains of carbonate of lime (otoliths). By motion of the endolymph these are shaken and affect the hairlike nerve terminals, which thus become delicate perceivers of the slightest movements caused by vibration. Again, in the ampullæ the nerve fibers terminate in little stiffish hairs projecting from the walls toward the center like the hairs in a mule's ears (Fig. 114). Vibratory shakings of the endolymph, passing up from the vestibular sac through the ampullæ into the semicircular canals and back to the vestibular sac, set these hairs trembling, and hence they also become delicate perceivers of slight vibration.

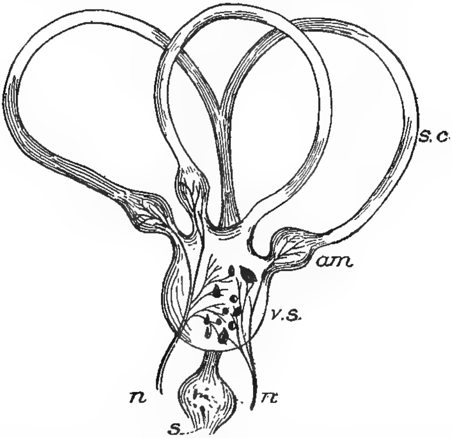

FIG. 113.—*vs*, vestibule sac; *sc*, membranous semicircular canals; *am*, ampulla; *n*, nerve; *s*, sacculus.

Membranous Cochlea.—We have compared the bony cochlea to a hollow stairway winding about a central pillar; now the membranous cochlea may be compared to the *stair* in this *stairway*, running across from a bony ledge on the pillar to the outer wall of the stairway, and dividing it into two semicylindrical spiral hollows, one above and one below, but not quite reaching the extreme end; so that vibration might run spirally around in the upper way, over at the top, and down spirally by the lower way. These two ways are called the one *scala vestibuli*, because it opens into the cavity of the *bony* vestibule, and the other the *scala tympani*, because it abuts against the tympanum, being separated from it only by the membrane of the foramen rotundum. The whole bony cavity of the cochlea is of course filled with perilymph.

We have spoken as if there were but *one* membrane separating the scala vestibuli from the scala tympani, but really there are *two*, and these are separated by a little space which is filled with endolymph. This space is called the *scala media* and connects through the sacculus with the vestibular sac. Now in the scala media are found a great number of stiffish rods running from the central pillar to the outer wall, like stair rods, and of diminishing length to the very end. These are the *rods of Corti*. There are several thousands of them. A branch of the auditory nerve runs up the central pillar and sends its fibers into the scala media, and the rods of Corti are supposed to be the percipient terminals of these fibers, as are the rods and cones of the retina terminals of the fibers of the optic nerve. Here again, therefore, we have a most delicate arrangement for perceiving the slightest vibratory movement

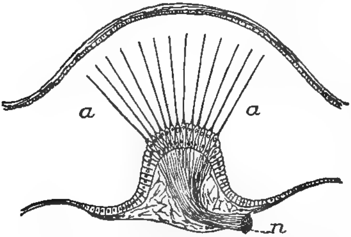

FIG. 114.—Section through an ampulla, showing a branch of the auditory nerve, *n*, and the sensitive hairs, *a a*.

of the lymph. All this membranous apparatus is connected throughout (Fig. 115).

Mode of Action of the Whole.—Sound vibrations of the air are gathered by the conch, carried by the meatus to the drumhead, and through the chain of bones to the *stapes*; the shaking of the stapes communicates a vibratory motion to the perilymph, and this to the endolymph of the vestibular sac. The shaking of this causes the otoliths to agitate the nerve terminals exposed on the interior of the sac. The vibratory movement now divides in several branches. Three of these go up through the semicircular canals, shaking the hairs of the ampullæ in which nerve fibers terminate. Still another branch runs spirally up the scala vestibuli over at the extreme end and down spirally by the scala tympani. These vibrations are communicated to the endolymph of the scala media and impress the rods of Corti.

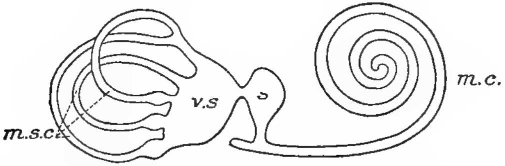

FIG. 115.—The whole membranous labyrinth: *vs*, vestibular sac; *s*, the sacculus; *msc*, membranous semicircular canals; *mc*, the membranous cochlea. (After Cleland.)

The Distinctive Functions of these Parts.—It is believed that there is a distinctive function of each of these several parts. The vestibular sac with its otoliths seems especially adapted to perceive the slightest sound as *sound* or noise, while the cochlea with its rods of *graduated* lengths seems specially adapted to the perception of sound as *tone* or *pitch*, and therefore for the perception of music. These rods might well be supposed to respond each to a special rate of vibration, somewhat as a note on a violin falling on *all* the strings of a piano only *one* will respond, viz., that one which vibrates in unison—co-vibrates—with the given note.

The semicircular canals with their ampullæ and terminal hairs may concur with the vestibular sac and otoliths in perceiving sound as noise, but they are also supposed to have another function.

We have not yet drawn attention to the remarkable fact that these three canals are set in three rectangular plains, one vertical fore and aft, one vertical from side to side, and the third horizontal (Fig. 116, page 183). The least movement of the head back and forth, as in *nodding*, would move the water in the vertical fore-and-aft canal and would be perceived by the hairs of its ampulla. Similarly movements of the head from side to side, as in *wagging*, would be perceived by the ampulla of the canal set in the vertical transverse plain; while rotation of the head on the spinal column, as in the *sign of negation*, would be perceived by the ampulla of the horizontal canal. In other words, these canals with their ampullæ are a most delicate indicator of the position and movement of the head, and therefore necessary for maintaining the *equilibrium* of the body. Surely this is a fundamental and most important function. Many experiments seem to substantiate this view.*

The perception of *direction*, which is so mathematically exact in the case of the eye, is extremely *inexact* in the case of the ear. It is this inexactness which is utilized by the ventriloquist in producing his deceptions.

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* Some would go further and say this is the sole function, and others still further and say the only organ of hearing is the cochlea. This, however, seems improbable.

COMPARATIVE MORPHOLOGY AND PHYSIOLOGY OF THE EAR.

In no other organ do we find so regular a simplification in descending the scale of animals.

In *mammals* the structure and function of the ear are almost exactly what we described in man. The only important differences are the greater size and efficiency of the external ear as gatherers of sound waves, and the movableness of the ear by the use of appropriate muscles by which animals perceive direction better than we. These muscles exist even in man, but in a rudimentary and therefore useless condition. The hearing of most mammals is keener than that of man, as they rely much on this sense for their safety.

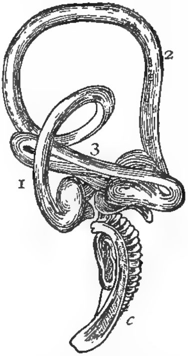

FIG. 116.—Interior ear of a bird, showing cochlea (*c*) uncoiled. The semicircular canals in three rectangular planes are also shown. (From Parker.)

Birds.—The first important simplification is found in birds. In the *exterior ear* the conch is entirely wanting and the meatus is very shallow, so that the membrane of the drum is very near the surface of the head. In the *mid-ear* the chain of bones is reduced substantially to one, the *columella* (which represents the stapes and probably the malleus), and the tympanic cavity is broadly connected with the throat instead of by a slender Eustachian tube. In the *interior ear* we find the cochlea much *shorter* and *uncoiled* (Fig. 116).

Reptiles.—In reptiles the exterior ear is gone; the membrane of the drum is at the surface, covered with skin and often with muscle. The *mid-ear* is very similar to that of birds, but the interior ear has lost, or nearly lost, the cochlea.

In amphibians the whole of the mid-ear as well as the exterior ear is lost; only the interior ear remains, and this is reduced to vestibule and semicircular canals, the cochlea being wanting.

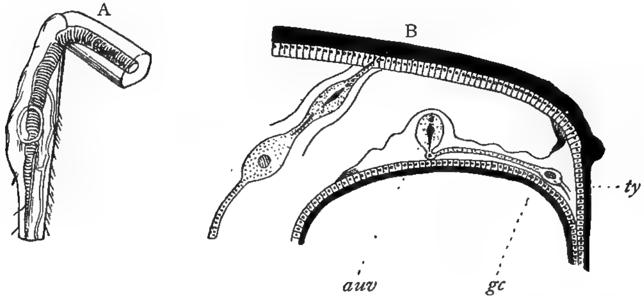

FIG. 117.—A, tibia of a grasshopper (*Meconemia*), with auditory organ. B, section of the same enlarged: *ty*, tympanic membrane; *auv*, auditory vesicle; *gc*, ganglionic cell. (From Packard.)

In *fishes* we have still the vestibular sac and membranous semicircular canals, but the bone has not grown *completely* about these so as to make bony cavities of similar shape; nor are the cavities of the ear cut off from the brain cavity.

Finally in *invertebrates* the ear is reduced to a *vestibular sac and otoliths.* These, therefore, are the most fundamental and necessary parts of an organ of hearing.

The hearing organs of invertebrates, however, are much diversified in form and position. In insects they are found sometimes in the first joint of the abdomen, as in some grasshoppers; sometimes in the lower joint (tibia) of the leg, as in other grasshoppers; and probably sometimes in the antennæ. Insects certainly hear, for they produce sounds which are intended to be heard. In all the cases above mentioned there is a hollow reverberatory cavity, with a tense membrane, *ty* (which may be compared to a membrana tympani, or, better, with the membrane of the foramen ovale), a vestibular sac, *auv*, containing otoliths (Fig. 117). In *crustaceans* is found a similar organ, sometimes on the anterior lower surface of the cephalothorax, as in crabs, and sometimes on the basal joint of the antennæ, as in lobsters.

Mollusca.—*In cephalopod mollusks* the hearing organ is in the head just below the brain, as a cavity in the cartilage filled with endolymph and containing otoliths (Fig. 118). In *gastropods* it is a capsule of condensed connective tissue lined with epithelium, filled with liquid and containing otoliths, situated just below the œsophageal ganglion.* In *acephala* a similar capsule has been found at the base of the gills which is supposed to have a similar function.

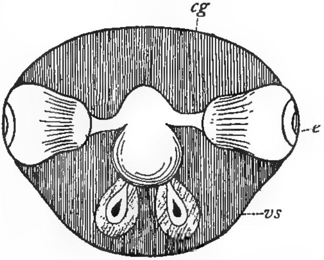

FIG. 118.—Section through the head of a squid, showing the auditory organ: *vs*, vestibular sac and otoliths; *cg*, cephalic ganglion; *e*, the eye.

Below this a hearing organ has not been found. Whether there be a nerve specialized for hearing is not known, as we can judge only by the existence of some apparatus like a capsule and otoliths.

Thus far the most essential part of the ear is the vestibular sac with its otoliths. But in spiders and certain insects there is found another type of hearing organs which may be compared not to the vestibular sac, but to the hairs of the ampullæ. In spiders, on the feelers are found cup-shaped hollows, from the bottom

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* Nat., iv, 518; Arch. des Sci., xliv, 261, 1872.

of which arise a fine tapering hair, into which runs a nerve fiber. The vibrations of the air reverberated in the hollow determines corresponding vibrations of the hair and affect the nerve.

This style of hearing organ reaches its highest perfection in the mosquito, especially in the male mosquito.*

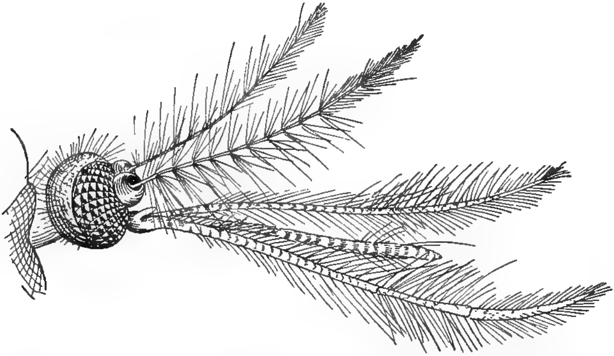

FIG. 119.—Head of a mosquito. The two lower and longer antennæ are feelers, the two upper ones with radiating hairs are auditory. (After Mayer.)

Fig. 119 represents the head of the male mosquito with its compound eyes and auditory organs. There are two kinds of antennæ: the one (the lower in the figure) are feelers or organs of touch, the other (the upper) are organs of hearing. As in the spider, these come from the bottom of hollow cups, which probably act as resonators, increasing the air vibrations; and the long hair-like, many-branching antennæ respond by co-vibrations. A nerve runs up each antenna and sends a fiber to every branch. Surely this is an admirable arrangement for responding to aërial vibrations.

But, according to the investigations of Mayer and

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* Mayer, Am. Jour., viii, 81, 1874; Arch. des Sci., li, 263, 1874.

Johnston, it is also admirably adapted to appreciate both musical tone and direction. If a mosquito be fixed under the microscope and a sound be made on a violin, among the many hairs of all lengths only a few are observed to vibrate in response, viz., those which by length are adapted to co-vibrate. Again, it was observed that in making the sound in different parts of the room, of the hairs pointing in all directions only those vibrated strongly which were at right angles to the direction of the sound. They probably perceive direction much better than we do.*

Leaving out, however, these last contrivances as out of the direct line of evolution, and regarding the vestibular sac and otoliths as the simplest form of hearing organ, the simplification as we go down the scale is very regular and may in a general way be expressed by the following diagram, which, with the legend, will be readily understood and requires no further explanation:

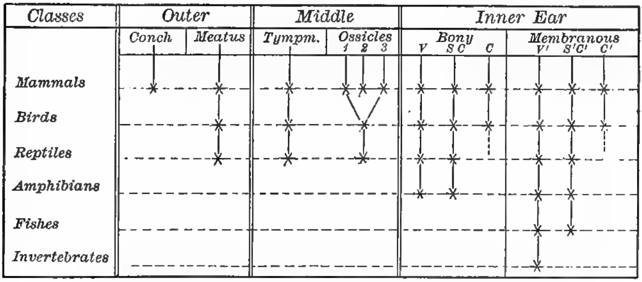

FIG. 120.—Diagram showing the gradual simplification of the hearing organ as we go down the scale. The stars represent the presence of the parts named above. Middle ear, 1, 2, 3, ossicles; inner ear, *V*, *SC*, *C*, bony vestibule, semicircular canals, and cochlea; *V'*, *S'C'*, *C'*, membranous same parts. The dotted continuations of the cochlea line mean that rudiments of cochlea are found in some reptiles.

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* Observe here that the greatest effect is produced when the sound-waves strike the sensitive hairs broadside, and becomes nothing when it strikes *end on*. In the case of sight the very re-

Therefore in the evolution of the organic kingdom the most necessary and first evolved part of a hearing organ was the vestibular sac and otoliths. These are found in the higher invertebrates. Then in fishes there were added the semicircular canals. Next the bone grew about these parts, so as to shut them off from the brain cavity, and at the same time inclosed them in such wise as to form cavities of shape similar to the organs themselves. This is found in the amphibians. Then the mid-ear was added, with its tympanic membrane and at least one ossicle. This is the case in reptiles. Then in birds a cochlea was added and a shallow meatus. Finally, in mammals the cochlea was greatly elongated, and therefore coiled, more links were added to the chain of ossicles, the whole apparatus was sunk deeper into the head and with a longer meatus, and the conch was added.

SECTION VIII.

Lower Senses.

The three lower senses will be more rapidly dispatched, because the impression in these is directly on the specialized nerve without the intermediation of an instrument. We have therefore only the specialized nerve and terminals to deal with, and the affections of these are so inscrutable that we can have little to say.

SENSE OF SMELL AND ITS ORGAN, THE NOSTRIL.

The nostril in man is a quadrangular cavity, passing directly backward from the face to the throat (Fig. 121). It is covered in front by the overhanging nose, but in

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verse is true—i. e., the effect is greatest when the rods are struck *end on*. The reason of the difference is that sound waves are waves of longitudinal vibration, while light waves are waves of transverse vibration.

the skeleton it is largely, though not entirely, exposed. It is bounded on each side by parts of the maxillary bone, and the orbital plates of the ethmoid, *opl*; above, it is separated from the brain cavity by a thin plate perforated with many holes—the cribriform or colander plate of the ethmoid, *cpl*—and below, from the mouth cavity, by the palatal plates, which form the roof of the mouth and floor of the nasal cavity, *rm*. It is divided into two symmetric halves (right and left nostril) by a bony septum, the vomer, which is continued into the cartilaginous septum of the nose. Each nostril is again divided by the turbinated or scroll bones into an upper and lower part, which differ in structure and function. The lower part is comparatively simple, the upper part complex; the one is lined with the ordinary epithelium of the alimentary passages, the other by a peculiar smooth epithelium.

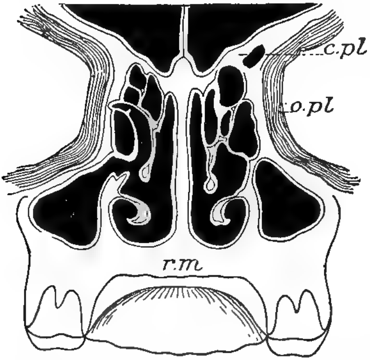

FIG. 121.—Vertical section through the cavity of the nostril: *rm*, roof of mouth; *opl*, orbital plate; *cpl*, cribriform plate.

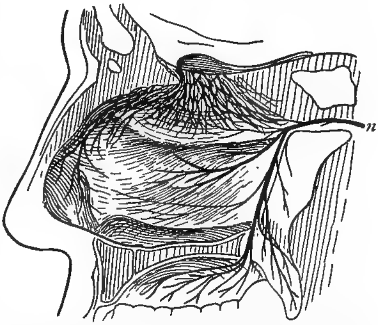

FIG. 122.—Vertical fore-and-aft section through one nostril, showing the olfactory nerve coming down from the olfactory lobe and the nerve of feeling coming from behind.

The former is supplied by a branch of the fifth pair of nerves (Fig. 122, *n*), which are the nerves of common sensation for the face; the latter is supplied by the first pair, or olfactory nerve. The former lies along the floor of the cavity and passes directly to the throat; the latter lies above the general passage to the throat and lungs. The function of the former is *breathing*, of the latter is *smelling*. Each of these have connections with the other cavities, the former with cavities in the cheek bones, the latter with cavities in the frontal bones over the brows. Inflammation sometimes extends from the nostrils into these cavities.

Smelling.—The olfactory lobes rest directly on the cribriform plate of the ethmoid, which here forms a part of the floor of the cranium. It sends out a large number of nerves through the holes of the colander directly down and into the nostrils, and these ramify over its upper chambers and their terminal bulbs are exposed on the surface (Fig. 122). Particles of odoriferous substances are carried by the air current, and, coming in contact with the olfactory terminals, produce the sensation we call *smell*. The peculiar form of the terminals sensitive to odors is shown in Fig. 123.

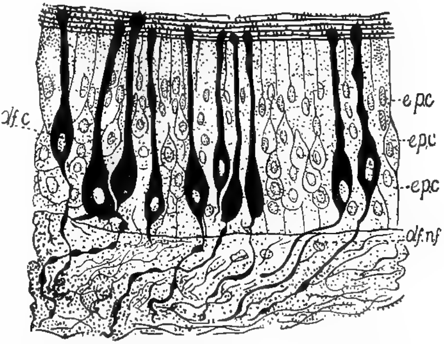

FIG. 123.—Nerve terminals of the olfactory nerves: *olfc*, olfactory cells; *olfnf*, olfactory nerve fibers; *epc*, epithelial cells.

Any sensation may be involuntary or voluntary. Thus *seeing* may be involuntary, but *looking* is voluntary.

Hearing may be involuntary, but *listening* is voluntary. So smelling may be involuntary, but *sniffing* is a voluntary act of smelling. In sniffing we draw in the air suddenly and then stop it. The air is thus forced more thoroughly into the upper chambers.

Odoriferous particles being air-borne, it is evident that a substance can not be smelled unless it is volatile. The amount of matter in the air which may be detected by this sense is so infinitesimally small that it can not be estimated. No chemical test can compare with it in delicacy.

COMPARATIVE PHYSIOLOGY OF SMELL.

We judge of the delicacy of this sense in other animals in three ways—viz., by the size of the olfactory lobes, by the complexity of the olfactory surfaces, and by the habits of the animal. Judging by either or all of these, there can be no doubt of the enormous superiority of *mammals* over man. This is especially true of carnivores, which hunt by smell, and of herbivores, which detect danger by the same sense. Referring to Fig. 41 (page 76), we see at once the great size of the olfactory lobes in mammals. Making a transverse section through the nostrils of a dog, a horse, or a cow, we observe at once the great complexity of its chambers. The same superiority is brought out still more strongly by observation of habits. Think of the keenness of the smell of a dog, who follows his master's tracks an hour after he has passed; or of a hound tracking a deer; or, again, of a deer sniffing the air and detecting the hunter a mile away. It is probable that among mammals and lower vertebrates generally smell, not sight, is the most important and most *objective* sense. In passing through a strange country *we* take *ocular* notes, and may return the same way by the use of these. A dog under similar circumstances takes *olfactory* notes for the same purpose.

Judging in the same way, *birds* are doubtless superior to man, though greatly inferior to mammals. It is commonly supposed that vultures are especially distinguished for keenness of scent; but experiments of Audubon and Bachman show that they are inferior in this respect to dogs. A stuffed deer attracted vultures from the clouds, but dogs paid no attention to it. But a real carcass concealed from view was quickly discovered by dogs, while circling vultures did not detect it.

In all the lower land vertebrates, such as reptiles and amphibians, the olfactory lobes form an important lobe of the brain, and their smell is *probably* correspondingly developed, but no observations have been made to test it. We therefore pass on.

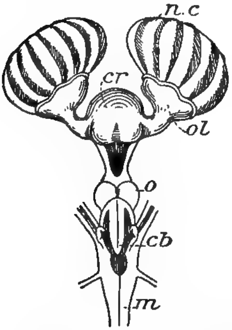

FIG. 124.—Brain of a shark: *m*, medulla; *cb*, cerebellum; *o*, optic lobes; *cr*, cerebrum; *ol*, olfactory lobes; *nc*, capsule of the olfactory nerve. (From Gegenbaur.)

Thus far vertebrates are air-breathing, the odoriferous particles are air-borne, and the smelling organs are therefore connected with the *breathing passages.* But fishes breathe water, not air, by gills, not nostrils. Smells with them are therefore water-borne, not air-borne. The organs in fishes are two deep pits near the end of the snout, in the usual position of nostrils, but do not yet open into the throat. The interior of these pits are plicated in a complex manner (Fig. 250, page 369), so as to increase the surface of contact with odorous particles, and large nerves from the olfactory lobes are distributed in them. In sharks, those bloodhounds of the sea, the olfactory pits are particularly complex, and the olfactory lobes are of enormous size, often as large or even larger than the cerebrum (Fig. 124).

Invertebrates.—That many invertebrates, especially insects, have a keen sense of smell is clearly evidenced by the fact of their being attracted by odors, as blow-flies by putrid flesh or butterflies by the fragrance of flowers. But where the organs of this sense are situated is not certainly known. The reason why it is so difficult to determine is that there is no instrument connected with the sense by which we can know it. It is probable, however, that in the case of insects it is situated in the antennæ. Insects are air-breathing. The breathing tubes, as we shall see hereafter, penetrate every part of the body, but especially pass into and to the end of all branches in the antennæ. In spiders, too, the organ of smell, as well as of hearing, is supposed to have been found in the feelers.*

In still lower invertebrates the organs of smell have not been certainly detected.

SENSE OF TASTE AND ITS ORGAN, THE TONGUE.

What we usually call taste is a complex sensation, a mixture of several sensations. It is impossible to discuss the subject scientifically without analysis. There is usually a mixture of three sensations belonging to as many different kinds of nerves—viz., common sensation, smell, and taste proper.

Examples of mixture of gustation with common sensation are numerous. The same batch of dough may be so mixed and baked that it shall be heavy and stick to the teeth in chewing, or may be light and spongy. The one we call disagreeable, the other agreeable, to the

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* Dahl, An. and Mag. Nat. Hist., xiv, 329, 1884.

taste. The true taste is exactly the same in both; the real difference is in the *feel* of the alimentary bolus as it is chewed and moved about in the mouth. The same parcel of rice may be cooked thoroughly and yet in such wise that each grain shall stand in separate and self-reliant individuality, or in such wise that all individuality is lost in a common socialistic mush. We all know the entire difference in what we call the *taste*. But really it is a difference in the *feel* only. There is very little taste of any kind in rice, but what there is is exactly the same in the two cases.

It is far more difficult to separate taste and smell, and yet even popular language has taken note of the difference. It is embodied in the two words *savor* and *flavor*. Savors are tastes, flavors are smells. We have heard of "salt that had lost its savor,"* but never its flavor, for it has none to lose. It is necessary to remember, then, that what we call *flavors* are not *tastes* at all, but *smells*. They are affections of the olfactory nerves, not the gustatory. They are all, therefore, volatile substances, essential oils, compound ethers, etc. They can all be smelled without eating.

Examples.—Coffee or tea, so far as taste in the ordinary sense is concerned, has two principles: a bitter astringent principle, which is a taste, and a *flavor*, which is a smell. This last is due to a volatile substance, which may be all driven off by long boiling. In a broiled steak the slight saltiness is nearly all that affects the gustatory nerve. Its pleasant flavor is an affection of the olfactory nerve entirely. It can be enjoyed without tasting at all. The same is true of all fruits. In a

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* The salt used by the poor of Palestine is said to have been very impure—in fact, a sort of *salty earth*, from which the salt was easily washed out.

strawberry we have, first, the pleasant combination of acid and sweet. This is taste proper. Then there is also the peculiar flavor characteristic of that fruit, which, of course, is a smell. In wine—e. g., champagne—we have first the pungency of the CO_2. This is common sensation. Then the pleasant combination of acid and sweet. This is taste proper. And last, the characteristic flavor, aroma, or bouquet. This is a smell.

Examples of Tastes.—As thus limited and defined, the tastes are few in number, while the flavors are almost infinite. They are: (1) *Sweet.* Pure white sugar has no flavor, and therefore no smell. Brown sugar has, because it has a smell. (2) *Sour.* Pure lime juice, or citric or tartaric acid, has no flavor, but a very intense taste, but vinegar has a flavor, because it has also a smell; it is volatile. (3) *Bitter.* Quinine, or morphine, or strychnine has a most intense taste but no smell, and therefore no flavor. (4) *Salty.* In the other three there is scarcely any variety at all in each, but in saltiness there is much variety, although the taste of chloride of sodium is the type. There can hardly be said to be any other pure tastes besides these four.

The proof of the essential difference between tastes and flavors is found in the fact that a bad cold, if it affects the upper chambers of the nostrils, is said to destroy the taste. It does not destroy the taste of sugar, or lemon juice, or quinine, or salt. It destroys the sense of smell, and therefore the appreciation of flavors. If we hold the nose, flavors are almost destroyed; not entirely, however, because some will come in by the back door—i. e., by the throat into the nose.

If it be asked, If this be so, why are we not satisfied with smelling? the answer is plain. Not only is the flavor stronger when taken as food, because it then is taken in both ways, front door and back door, but mainly because there is in that case a combination of pleasant sensations. For example, what we call the taste of a ripe peach is first the delicious softness and juiciness. This is a *feeling*. Then the agreeable combination of acid and sweet. This is taste proper. And last, the whole is glorified and crowned by the exquisite flavor, which, as already shown, is a *smell.*

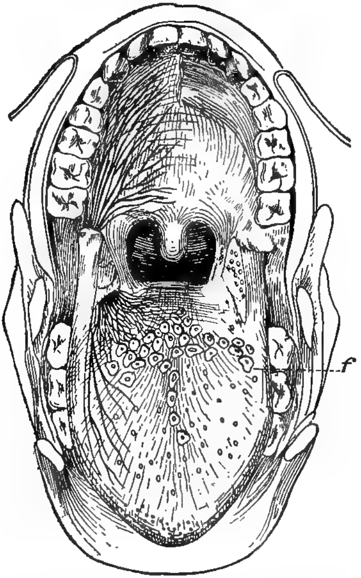

FIG. 125.—Interior of mouth, showing the papillæ of the tongue and the distribution of the nerves of taste : *f*, fungiform papilla. (After Huxley.)

Organ of Taste.—As thus limited, the organ of taste is the tongue, especially the *back part* of the tongue and the adjacent parts of the throat, and still more especially certain large papillæ in that part of the tongue (Fig. 125). There are two kinds of papillæ on the tongue—one kind large and flat, mushroom-like,* the other small and conical. Those of the one kind are found only on the back part of the tongue and are taste papillæ; those of the other are found in every part, but mainly near the tip, and are tactile papillæ. There are three kinds of nerves distributed to this nimble little organ : (1) A branch of the fifth pair (Fig. 33, *5*, page 51). This gives common sensation. It is distributed to all

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* These are again subdivided into fungiform and circumvallate.

parts of the tongue, but more and more toward the tip. (2) The glosso-pharyngeal (Fig. 33, *9*). This also is distributed to all parts, but mainly to the back part and adjacent parts of the throat. This is supposed to be the special nerve of taste. (3) The hypoglossal (Fig. 33, *12*). This is a motor nerve, and presides over the movements of the tongue. Through these three it becomes a tactile organ, a tasting organ, and a talking organ. The manner in which the nerves terminate in the taste papillæ is shown in Fig. 125. The flat fungoid papillæ are eminently adapted by shape to retain liquids in contact with the *taste bulbs.*

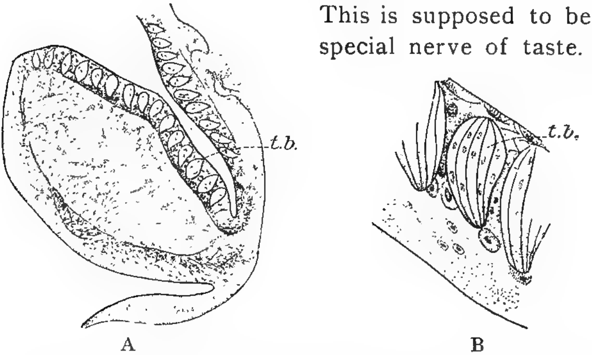

FIG. 126.—A fungiform papilla, showing the taste bulbs (*tb*) of a rabbit: A, magnified; B, highly magnified. (After Tuckerman.)

COMPARATIVE PHYSIOLOGY OF TASTE.

There are only two ways in which we can judge of the keenness of taste in lower animals, viz., by the organization of the tongue—i. e., its softness, and especially the development of its papillæ, and by observation of the habits of the animal. Judging in these ways, there is probably little difference in this regard between man and *mammals.* The main difference is that man much more than mammals takes food for the enjoyment of its taste. The urgency of appetite in mammals forbids the leisurely enjoyment of taste as such.

Birds have no teeth. They do not masticate, but bolt their food. In many cases, too, their food, as, for example, seeds and the like, is hard and tasteless. It is probable, therefore, that their sense of taste is more imperfect than that of mammals.

Reptiles, *amphibians*, and *fishes* all swallow their food without mastication. They have teeth; but they are prehensile, not masticatory. We know little of their sense of taste, but it is probably feeble.

Of taste among *invertebrates* we know nothing, except in the case of insects. These are doubtless attracted to food mainly by smell; but sweets—sugar, honey, nectar of flowers—are sought and enjoyed by bees, ants, butterflies, and flies.

THE SENSE OF TOUCH AND ITS ORGANS.

Here, again, and even more than in the case of taste, scientific discussion is impossible without analysis. The word *feeling* includes very many distinct sensations. For example: lay the hand on the table, palm upward. (1) Lay a card across the finger tips; we have a sense or feeling of *contact*. (2) Instead of a card let it be a ten-pound weight; we now have in addition a feeling of *pressure*. (3) Let the weight be fifty pounds; we have now in addition a feeling of *pain*. (4) Let the weight be hot or cold; we have now a corresponding feeling of *heat* or *cold*. (5) Now lift the hand from the table; in addition to all the preceding, we have a feeling of weight or *resistance to our muscular effort*—we feel the heft. Thus, then, there are many kinds of sensations included in the word *feeling*. These are so different that they are probably perceived by different specialized nerves. It is almost certain, according to recent observations,* that different nerve fibers take cognizance of contact, pain, heat, cold, and muscular resistance (Fig. 68, page 95). In physics *cold* is a negative term, a mere absence of heat; but in physiology, as we all know, it is a very *positive* sensation.

Now, it is impossible to take up all the sensations in detail. We take only that which is the most universal and fundamental, viz., *contact* (pressure being only a stronger contact). This, together with the muscular sense of resistance, gives us *externality*, or the *existence* of the external world.

Again, it is necessary to distinguish between general sensibility and special sense of touch. The former, together with the so-called muscular sense, gives the *existence* of the external world; the latter may be regarded as the same, specially organized to give definite knowledge of some of its properties, such as shape, hardness, roughness, etc. These two kinds of sense of contact are by no means developed in the same degree. The conjunctiva of the eye is exquisitely sensitive to contact, but it does not appreciate the properties of the touching body as does the finger tips or the tongue tip. The same difference, it will be remembered, we found in the retina. Mere sensitiveness to light is keenest a little way from the central spot, but this spot alone is specially organized to give us accurate knowledge of shape, color, etc.

General Organ of Touch.—The general organ for perception of contact is the skin and portions of the mucous membranes near the outlets of the passages, especially the mouth. This is for *all* contact. Besides, there are certain portions of the skin specially organized as organs of touch, such as the hands and the parts about the mouth.

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* Sci., vii, 151, 1886, and 459, 1886.

General Structure of the Skin.—The skin consists of two parts—dermis and epidermis. The dermis consists of fibers crossing one another in all directions, and, as it were, felted together. It is very strong and very highly organized, full of blood vessels and nerves. The epidermis contains no blood vessels or nerves, and is not organized at all. It consists wholly of epithelial cells; living nucleated cells in contact with the dermis, but becoming more lifeless and flatter as we go from the dermis to the surface, where they continually pass off as scales or scarf. The nerve fibers come to the epidermis, but do not penetrate it. They terminate near some of the cells of the lowest layer (Fig. 127).

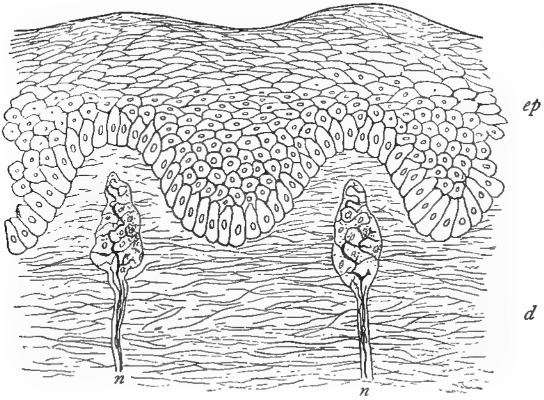

FIG. 127.—Section through the epidermis (*ep*) and the dermis (*d*): *n*, nerves of touch terminating in tactile corpuscles.

Special Organ of Touch.—Wherever the skin is specially organized for touch it is thrown into ridges, as on the finger tips, or else rises into papillæ, as on the tongue (Fig. 128). In the case of ridges there is a *row* of tactile corpuscles or bulbs in each ridge; in the case of papillæ each one contains a tactile bulb. A sensory fiber enters and terminates in each bulb. These are therefore end organs or terminals. The epidermis proper is not sensitive; it only protects the sensitive dermis from too rude contact.

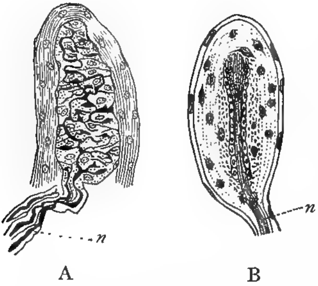

FIG. 128.—Tactile corpuscles: A, from the finger of a man; B, from the skin of a bird; *n*, nerves. (After Wiedersheim.)

Minimum Tactile.—We have already alluded to this subject in comparing sight with touch (page 132). We repeat it here in its proper connection. If a pair of dividers be opened widely and the skin be touched with the points (blunted a little so that they do not prick) we feel two distinct impressions. If we now bring the points nearer and nearer together, repeating the experiment until we feel but one impression, the nearest distance apart that we can still feel two impressions is called the *minimum tactile.* It is a measure of capacity to give definite knowledge by touch. It differs greatly in different parts of the skin. On the middle of the back it is about three inches, on the arm or back of the hand about one half to three quarters of an inch, on the finger tips about one twelfth of an inch, on the tip of the tongue about one twenty-fourth of an inch, or one millimetre.

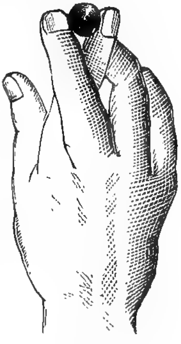

FIG. 129.

Double Tactile Images.—There is here also a kind of double images comparable to the double images of sight. If the middle finger be crossed over the forefinger, and a small object, like a bullet or a pea, be rolled beneath the crossed tips, *two* objects are distinctly felt (Fig. 129). It is because the impressions are on unaccustomed or non-corresponding points of the fingers.

COMPARATIVE PHYSIOLOGY OF TOUCH.

In our rapid survey in passing down the scale, it is necessary to keep in mind the distinction between general sensibility and special sense. They are indeed almost in inverse proportions.

Mammals.—Man differs from *mammals* chiefly in the use of the hand as an organ of touch. Indeed the fore limbs are liberated from the function of support and progression expressly for this purpose. In other mammals, with the exception of apes, the special tact organ is localized elsewhere, generally in the prehensile organ wherever that may be, most usually about the mouth, as the lips, the snout, the tongue. In such cases we may often find a strong development of papillæ, as on the nose of the dog or on the sole of the foot of all unhoofed animals.

In birds the *beak* is an exquisitely sensitive organ of touch. Sensory nerves are abundantly distributed at its base and beneath the horny sheath, exactly as in the case of our finger nails, which are also delicate organs of touch. The strong papillæ on the feet of birds show that they are good organs of touch. The general sensibility of birds is probably inferior to that of mammals on account of the thick covering of feathers.

Reptiles are all of them more or less covered with dry horny or bony scales which must diminish their general sensibility, nor have they any well-marked organ specially organized for touch. They are probably poorly endowed both in general and special sensibility.

In *amphibians*, so far as concerns general sensibility, we have the extreme opposite condition—i. e., a moist, active, sensitive skin—but there are no special organs of touch.

Fishes are probably similar to amphibians in regard to general sensibility. They also have a moist, sensitive, mucous surface, and therefore general sensibility well developed. In addition, many of them have special organs of touch (feelers) about the mouth.

In *arthropods* we have again the other extreme. They all have a hard skeletal coat of mail on the outside, which almost entirely cuts off general sensibility; but to compensate they are endowed with very delicate special organs of touch, as, for example, the long antennæ of insects and crustaceans.

In *mollusca* we pass again to the other extreme. A universal characteristic of mollusca is that they are everywhere, except when inclosed in shell, covered with a soft, active, mucous surface, which is endowed with great sensibility. Many also, in addition, have good tactile organs, such as the grasping arms of cephalopods and the so-called horns or feelers of snails and other gastropods.

In *echinoderms* the body is again usually incased in immovable shell, as in echinus; but again we find compensation in their long, delicate tentacles, which are feelers as well as locomotive organs.

Again the pendulum swings back in *cœlenterates* (medusæ and polyps), where we find again the soft, active mucous surface sensitively responsive to contact. Their long tentacles also doubtless act as touch organs, though perhaps imperfectly.

Finally, in *protozoa* we find only general sensibility of the lowest grade, to what extent conscious we can not tell. From this lowest form of response to external stimulus have been differentiated by evolution not only the different forms of feeling, such as heat and cold, pain, and touch proper, but also all the higher and more special forms of sense.

SECTION IX.

The Voice and its Organ, the Larynx.

The voice is not one of the senses, nor is the larynx a sense organ, but its close relation with the sense of hearing makes this the proper place to take it up.

There are *three kinds of voice*—viz., the *call* or cry, the *song*, and *speech*. The first is the *simple* voice, the second the *harmonically modulated* voice, the third the *intelligently articulated* voice. The first is common to all or nearly all air-breathing vertebrates; the second is peculiar to man and perhaps birds; the third is characteristic of man alone, although an imitated speech may be taught by man to some birds. We take first

I. SIMPLE VOICE.

The Larynx.—*Its Position and Relation.*—The organ of the voice is the larynx. There are two pipes leading from the throat into the cavity of the trunk—the gullet or *œsophagus*, and the windpipe or *trachea*. The one leads into the stomach, the other into the lungs; the one is the passage for *food*, the other for *air* in breathing. The trachea is in front, and may be felt with the hand, for it is hard, being kept open by a series of bony or cartilaginous rings, so that the air passes through without resistance. The gullet is a soft, extensible pipe, collapsed when not occupied by food. Crowning the trachea and opening into the throat, just behind the root of the tongue, is the *larynx*. Now, it will be seen (Fig.

130), that the passage of the food from the mouth to the stomach and of the air from the nostrils to the lungs cross one another in the throat. Therefore there must be a valve which shall close the larynx when the food is passing, otherwise the food, especially liquids, would fall into the larynx in swallowing. This would produce great irritation and pain. This valve is the *epiglottis.* When we swallow, the larynx is drawn up by certain muscles with great force toward the roof of the throat. In this position the food in passing presses down the epiglottis and closes perfectly the opening of the larynx. The relation of the epiglottis to the larynx is seen in Fig. 131. At the junction of the epiglottis with the larynx there are a kind of cords (false vocal cords), which are supposed to have some function in modifying the voice.

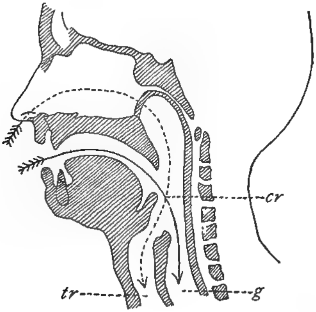

FIG. 130.—Section of head, showing the relations of the air passage and the food passage: *g*, gullet; *tr*, trachea; *cr*, the point of crossing.

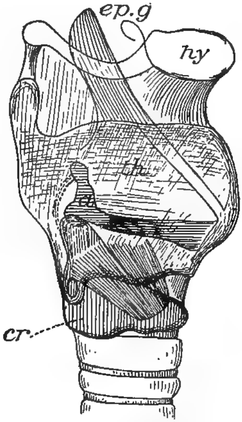

FIG. 131.—Side view of larynx: *hy*, hyoid; *epg*, epiglottis; *th*, thyroid; *cr*, cricoid; *a*, arytenoid. The different parts are seen in transparency.

EXPERIMENT.—Put your finger on the Adam's apple (larynx), and try to hold it down while you swallow. You will find it impossible. It rises in spite of your effort.

*Structure.**—Aside from the epiglottis, the larynx proper consists of four cartilages, the *cricoid*, the *thyroid*, and the two *arytenoids*. The cricoid is a cartilaginous ring, which sits directly on the top of the trachea. It is narrow in front and very wide behind (Fig. 132, A). The thyroid is the largest cartilage. Its singular irregular form, which can hardly be described in words, is seen in Fig. 132, B. It is bent on itself in the form of a V, opening backward, and the point of the V forms the point of the Adam's apple in front. The arytenoids are two triangular cartilages in the form seen in Fig. 132, C. These four pieces are put together in such wise that the lower posterior horns of the thyroid are articulated, i. e., movably attached to the sides of the cricoid low down (*a*), so that the wide gap between the two arms of the thyroid V, is *partly* filled up by the cricoid. Now the two arytenoids sit directly on the top of the cricoid (Figs. 131 and 134) between the legs of the thyroid, and thus fill up the wide space more fully. This is the skeleton or framework. The rest of the larynx is made up of muscles, except the most important part of all, which we now proceed to describe.

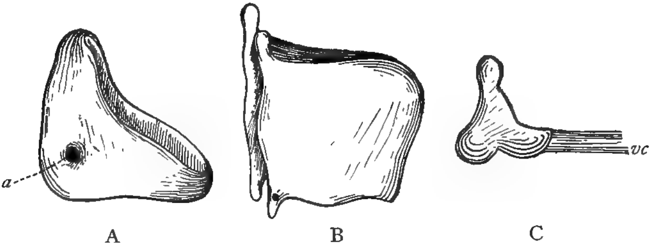

FIG. 132.—Cartilages of the larynx: A, cricoid; B, thyroid; C, arytenoid, with the vocal cord (*vc*) attached; *a*, crico-thyroid articulation.

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* There should be a large model for demonstration of these parts.

The Glottis and its Vocal Cords.—The cavity of the larynx is divided into an upper and lower chamber by a transverse partition—the glottis. In the glottis there is a fore-and-aft opening—the *rima glottidis* or *chink of the glottis.* This chink is bounded on each side by a firm tendinous cord—the *vocal cords.* These cords are attached in front to the V point of the thyroid, and behind to the two arytenoids (Fig. 133, also Fig. 131). The tension of these cords and the size of the chink or opening between them varies very much under different conditions. This is determined by observations with the laryngoscope. (1) In quiet breathing the chink is wide open, the cords lax, and the breath comes and goes noiselessly (Fig. 135, A). (2) In aspiration (sighing) the opening remains much the same, but the breath is driven through with a rushing sound. The position of the cords is somewhat as seen in Fig. 133. (3) In making a vocal sound three changes are observed, viz., the vocal cords are brought *nearer together*, they be-

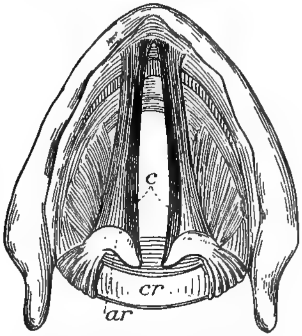

FIG. 133.—View of the larynx from above: *ar*, the arytenoids; *cr*, the cricoid; *c*, vocal cords with the rima or opening between.

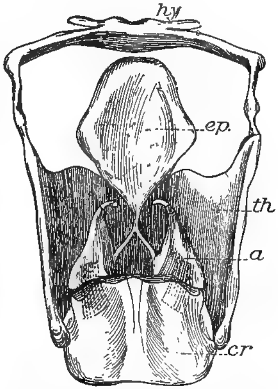

FIG. 134.—View from behind: *cr*, cricoid; *th*, thyroid; *a*, arytenoid; *ep*, epiglottis; *hy*, hyoid bones.

come tense, and the edges are observed to *vibrate.* (4) If the vocal sound is high-pitched, the chink becomes very narrow, the cords very tense, and the vibration caused by air driven through very rapid (Fig. 135, B). (5) In the highest soprano head notes the cords are still tenser, more pressed together, so that the air is driven through only a small opening in the middle, and the vibration is, of course, still more rapid (Fig. 135, C). (6) Finally, in violent straining or strong muscular effort the glottis closes absolutely air-tight (Fig. 135, D). We first fill the lungs, then close the glottis, so as to fix

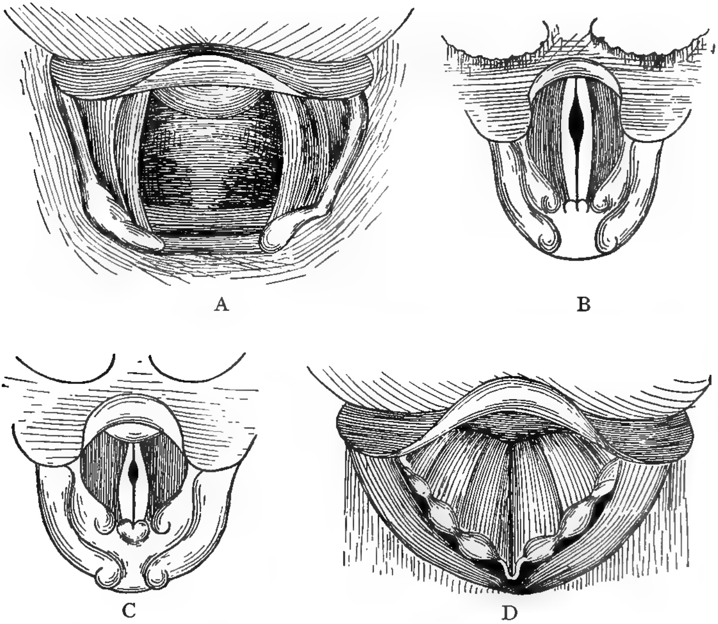

FIG. 135.—Glottis as seen with the laryngoscope: A, in simple breathing; B and C, in singing; D, in straining.

the chest as a fulcrum for the action of the great muscles of the trunk and limbs.

MUSCLES OF THE LARYNX.

The muscles by which these changes are accomplished are numerous, some tightening, some loosening the cords, some closing the chink. The following are the main ones:

Crico-thyroids................	Tensors.
Crico-arytenoids, posterior.....	
Thyro-arytenoids.............	Relaxers.
Inter-arytenoids...............	Closers.
Crico-arytenoids, lateral.......	

Of the tensors, the crico-thyroid, as seen in Fig. 130 arising from the cricoid, takes hold of the thyroid and pulls it downward, and its upper part *forward.* The crico-arytenoids, arising from the cricoid behind, take hold of the arytenoids and pull them *backward.* These may be seen in Fig. 134, being indicated by the dotted spaces. These two, the one pulling the angle of the thyroid *forward* and the other pulling the arytenoids *backward*, stretch the vocal cords. These, therefore, are the stretchers or *tensors* of the cords.

The *relaxers* must pull the thyroid and the arytenoids toward one another. This is done by the thyro-arytenoids, which run fore and aft within the larynx from the thyroid to the arytenoids just outside of the vocal cords. They are seen in Fig. 133.

The *closers* are of two kinds—one, the inter-arytenoid, runs from arytenoid to arytenoid and brings these together; the other, the lateral crico-arytenoids, rotate the arytenoids in such wise as to bring together the forward projecting points to which the cords are attached. These can not be well shown except on a model.

APPLICATION.—In quiet breathing all the muscles are relaxed; the opening is wide, and the breath comes and goes quietly. In *aspiration* the condition of the laryngeal muscles is much the same, but the breath is driven more strongly by the respiratory muscles so as to make a rushing noise, but *not* a *vocal* sound. In making a vocal sound the tensors and the closers are brought into action, the cords are made more and more tense and pressed closer and closer together, and the breath is driven through with greater and greater velocity, producing more and more rapid vibration in proportion as the pitch of the voice is higher. The cavities of the mouth and nose above and of the trachea and bronchi below act as resonators to increase the volume and modify the character of the sound.

2. SONG.

We have spoken thus far only of the simple voice. Singing is only the skillful modulation of the voice according to the laws of harmony. This is done by skillful use of the vocal muscle in producing a pure sound, and a skillful changing of the play of these muscles so as to modulate the pitch, guided by the ear, and, lastly, a skillful modification of the resonant cavities of the throat, mouth, and nose. We all know the wonderful result.

The Larynx as a Musical Instrument.—But what kind of instrument is the larynx? To what shall we compare it? Some have compared it to a wind instrument, especially a tongued instrument, like an organ pipe, or a clarinet, some to a bird-call. But the favorite comparison is with the stringed instrument, as is shown by the term vocal *cords.* But the least reflection is sufficient to show that the comparison is not true. The vocal cords are only about three quarters of an inch long in the male and half an inch in the female. Now, since strings must be tense in order to vibrate elastically at all, and since, further, other things being equal, they make higher pitch in proportion as they are shorter, it is evident that strings of any such length as this, if tense enough to vibrate at all, could only produce an inconceivably high note. But see the range of the voice! To what, then, shall we compare it?

It is strange that no one has thought to compare it to an ordinary *horn*—a stage horn, for example, or, better, a French horn. In this instrument the sound is modulated exactly as in the larynx—viz., by the *tension* and the pressing together of the *lips of the performer*. The edges of the rima glottidis ought to be called the *vocal lips*, as indeed they are, and not the vocal *cords*, which they are not in any sense. The analogy between the two instruments is perfect. The performer on the horn presses his lips together tighter, and makes them tenser and the opening between them smaller in proportion as he desires a higher note. He then drives the air between the tense lips so as to set their edges in vibration; this vibration, by alternate partial closing and opening of the aperture, gives rise to successive jets or pulses of the out-driven breath, and this in its turn gives corresponding pulses to the air in the sounding cavity of the horn. Precisely the same, as we have seen, takes place in the larynx. The only wonder is that so small an instrument as the larynx and the mouth cavity should be capable of such marvelous effects.

3. SPEECH.

Of course the subject of speech concerns other sciences besides physiology. But the mechanism of the production of the various sounds used in speech belongs to physiology alone. We need no apology, therefore, for taking it up briefly.

There are two kinds of speech—viz., *vocal* and *whispered.* The one is the articulation of the *voice*, the other of the *aspiration.*

Speech may be defined as a succession of vowel sounds interrupted and separated by consonants. Vowels are modifications of the voice. Consonants are the *modes* of interruption. There are two kinds of modifications of the voice—viz., modification of *pitch*, high or low, and modification of the *timbre* or *quality* of the voice. The former is done in the larynx, as already explained; the latter is done by changes in the mouth cavity. The vowels are modifications in timbre, not in pitch. The larynx has nothing to do with it. We have a good illustration of what we mean by timbre in the sounds of different musical instruments. The same musical note may be made on the flute, the clarionet, the violin, or the bugle, but how different is the *quality* of the sound in each case!

Vowels.—We give a series of seven vowels in such order as to show and easily describe the changes in the mouth cavity, thus: *ē, ā, ah, au, ō, oo, ü.* (1) Bring the teeth near together, retract the lips a little, bring the tongue forward until it nearly touches the teeth, and then make a sound with the larynx; the sound is the long *ee*, and can not be anything else. (2) Other things remaining the same, separate the teeth a little more and draw back the tongue a little, and make a sound of the same pitch; the sound now appears as *a* in *fate*, and can not be anything else. (3) Open the mouth much wider, draw back the tongue still more, and again make a sound of the same pitch; it comes out now as *a* in *far*, and it can not be anything else. (4) Separate the jaws as much as possible, draw back the tongue as far as possible, but bring the lips a little nearer together in front; and the same note now becomes *au* in *awe.* (5) Now bring the jaws again a little more together and the tongue not quite so much retracted, the lips drawn more together, and a little protruded, and the same note becomes *o*, as in *lo!* (6) Bring the jaws still more together and the tongue a very little more to the front, and the lips more drawn together and more protruded, and the same note now becomes *oo* as in *tool.* (7) Finally, with all parts remaining as in the last, bring the tip of the tongue forward as in the first position, as in making *ee*, and the same note now becomes *ü*, or the French *u*, or the German *ü* with the *Umlaut.*

Consonants.—Articulation is the breaking of the voice into segments. The vowels are the segments, the consonants the modes of breaking, or interruption. The interruption may be complete, as in *b*, *p*, *d*, *t*, *k*, and *g* hard, or may be incomplete, as in *s*, *f*, *l*, *r*, etc. The interruption may be by the lips, as in *p*, *b*, *m*, or between the tongue and teeth, as in *t*, *d*, *n*, or between the tongue and roof of the mouth, as in *k* and *g* hard. Again, every one of these may be non-vocalized or vocalized, so that we may make two parallel series of consonants, the terms of which correspond each to each, only differing in the fact that one is vocal and the other not. Since whispered speech is articulation of the aspiration, it is easy to see why it is difficult to distinguish the corresponding terms of this series in whispering.

Non-vocal.	*Vocal.*
p	*b*
t	*d*
k	*g* hard
s	*z*
f	*v*
ch	*j* or *g* soft
sh	*j* French
th	*th* soft

There are other modes of classifying consonants, but our object is only to bring out principles.

COMPARATIVE PHYSIOLOGY OF THE VOICE.

Mammals.—The structure of the larynx and the mode of making a voice is precisely the same in mammals as in man. The only difference is that by constant use in modulating the voice in speech and in song the larynx of man is much more flexible.

Birds.—Next to man, birds have the greatest power of modulating the voice, for many of them sing and some may be taught an imperfect speech. But both the speech and the song of birds have an entirely different significance from that of man. This, however, belongs to psychology, not physiology.*

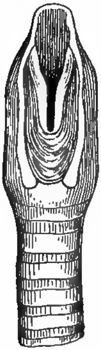

FIG. 136.—Larynx of a bird.

We should expect, then, that the larynx of birds would be highly developed. On the contrary, it is far inferior to that of mammals (Fig. 136). But the larynx is not the organ of song in birds. The larynx is used only in the simpler and harsher sounds, such as cries of pain, distress, or anger, and perhaps the simple chirp. Their singing organ is another organ—the syrinx.

Syrinx.—The bird, then, has two organs of voice, the larynx and the syrinx. The larynx is in the usual place at the top of the trachea and opening into the throat; the syrinx is at the *lower end* of the trachea. It is made up of the enlarged lower rings of the trachea and upper rings of the two bronchi. Fig. 137, A, B, C, are different views of this organ. Observe (1) that the rings of the bronchi in this part are only a little more than half rings, and the bronchi are completed on the inner side looking toward one another by a *tense* membrane, which acts as a resonator. (2) On transverse section (Fig. 138) we see transverse floors across the openings of the bronchi into the trachea and a true rima glottidis bounded by vocal

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* From Animals to Man, Monist, vi, p. 356, 1896.

cords in each. (3) Rising up from the fore-and-aft cartilage formed by the union of the two bronchi, observe a tense membrane with scythe-like edge—semilunar membrane (Fig. 137, C).

Mode of Action.—The several rings of this apparatus are movable on one another. By appropriate muscles the resonating membrane may be made more or less tense—the vocal cords may be stretched and the lips of the rima pressed together so as to vibrate with various degrees of rapidity and give rise to various notes when the air is driven through them. The cavity of the syrinx, the tense membrane of the bronchi, and the whole cavity of the trachea above act as resonators, increasing the volume of the sound. The semilunar membrane is found only in the best singers, and is supposed to produce the trilling so characteristic of some birds.

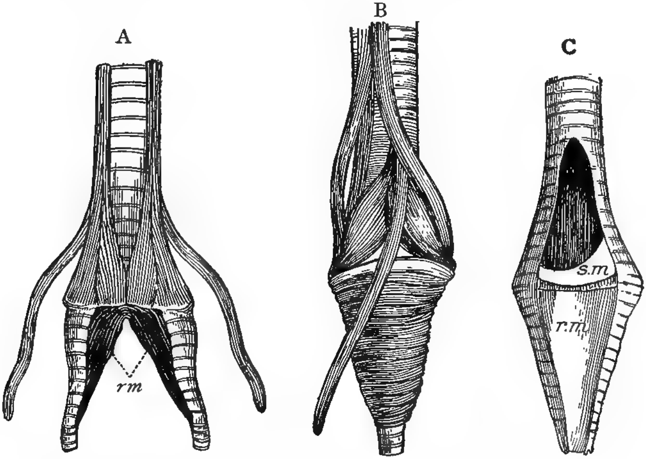

FIG. 137.—Syrinx: A, front view; B, side view; C, section through the lower part of the trachea and between the legs of the bronchi, showing the resonating membrane on the inner side of one bronchus: *rm*, resonating membrane; *sm*, semilunar membrane.

Reptiles.—As a class these are silent, although a few do make sounds intended as calls.

In *amphibians*, however, especially in frogs, we have again animals abundantly *vocal.* Their vocal organs are indeed very imperfect, but their lungs, which are hollow sacs capable of great distention, act as powerful resonant cavities, giving considerable volume to their voice.

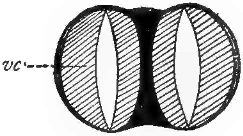

FIG. 138.—Transverse section just above the bronchi : *vc*, vocal cords.

Fishes, being gill-breathers or water-breathers, can have no voice in a proper sense. Probably some of them do make audible sounds, but not vocal.

Arthropods ; Insects.—True voice is confined to air-breathing vertebrates, and is connected with respiratory passages; but if we extend the term to any sounds intended to be heard by mates, then we may include insects also among natural musicians. If birds are the *vocalists*, then are insects the *instrumentalists* of Nature.

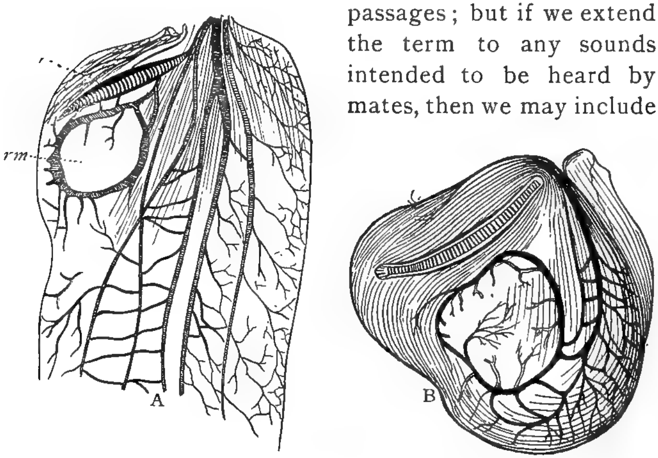

FIG. 139.—A, sonant organ of an orthopter : *rm*, resonating membrane ; *r*, rasp. B, the same, magnified.

We all know the cheerful chirp of the "*cricket* on the hearth," the insistent, contradictory, answering cry of the *katydid*, the deafening clatter of the *cicada.* The organs by which these noises are made are very various and interesting. Most of these sonant insects belong to the grasshopper order (orthopter). In these the anterior pair of wings are somewhat hard, with strong stiff ribs and tense membrane between. Sometimes the hind leg is rubbed against ridges on the stiff edges of the front wings. These wirelike ribs are especially stiff in the overlapping parts on the back. Sometimes these parts in the two wings are rubbed together with a rapid vibratory motion, the stiff membrane between them acting as resonators. Often a kind of rasp is added to produce more effect (Fig. 139).

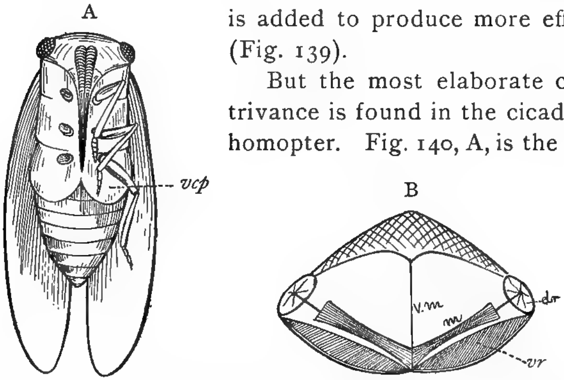

FIG. 140.—A, view of the under side of a cicada (natural size); the legs are removed on one side: *vcp*, ventral cover plate. B, section a little enlarged: *vm*, vertical membrane; *m*, muscle; *dr*, drumhead; *vr*, ventral resonator. (After Lloyd-Morgan.)

But the most elaborate contrivance is found in the cicada, a homopter. Fig. 140, A, is the under side of the insect, natural size. Lifting up the ventral cover plates, *vcp*, a tense membrane is disclosed (*vr*). This is a resonant membrane. Beyond this there is an enormous cavity, almost filling the whole body, and divided into two by a thin vertical septum (*vm*, Fig. 140, B).

This cavity is closed below by the membrane already spoken of, *vr*; but above on each side it is closed by a very tense membrane like a drumhead (Fig. 140, B, *dr*). This drumhead is stiffened by radiating ribs which are a little convex outward. A slender tendon coming from a muscle, *m*, in the cavity is attached to the center of radiation of the ribs. By the action of the muscle the stiff convex drumhead is drawn in with a clack, and again springs out with a clack when the muscle is relaxed. The muscle contracts and relaxes with a rapid vibratory motion, and this gives rise to the characteristic clattering noise of these creatures.

It is hardly necessary to say that the humming and buzzing sounds so common in insects while flying are due wholly to the rapid vibration of the wings.

Animals in other and lower departments are not known to make sounds intended to be heard.

CHAPTER III.

MUSCULAR AND SKELETAL SYSTEMS.

We have seen (page 26) that four systems are concerned with the distinctive functions of animal life, viz., the nervous system, the sense organs, the muscular system, and the skeletal system. We have finished the first two. We now take up the second two.

The object of both these is to produce motion. But motion is coextensive with life, and therefore not peculiar to animals. What is really characteristic of animals, except the very lowest, is the use of a peculiar apparatus of nerve and muscle to give greater efficiency to the motion. In the lowest animals we have only *general sensibility* and *general contractility.* As we rise in the scale nerve and muscle are introduced, but not yet skeleton. The muscle acts directly on the body to give motion and locomotion. Only in animals somewhat advanced in the scale the skeleton is introduced to give greater velocity and precision to the motion.

SECTION I.

Muscular System.

We have already explained the *tissue* called muscular. Its one property is that it contracts under stimulus of any kind. Now, a muscle, as an *organ*, is composed of an aggregation of several tissues, of which the muscular is most abundant and characteristic. But besides muscular tissue it has connective tissue to web it together, nerves to stimulate it, and blood vessels to nourish it.

Kinds.—There are two kinds of muscle—voluntary and involuntary—differing from one another in many respects. (*a*) The one is found on the *exterior*, the other in the *interior* of the body. (*b*) The one is *red*, the other is *white*. (*c*) The fibers of the one are transversely *striated*, of the other are *non-striated*. (*d*) The nerve supply of the one is largely from the conscio-voluntary system, of the other from the reflex system. (*e*) In the voluntary muscle the fibers are massed into a distinct organ, having a distinct name, and all coöperate through a tendon to produce *one* motion; while the involuntary muscle exists in sheets of parallel fibers, surrounding hollow organs (stomach, intestines, bladder, etc.), has no tendon, and the fibers do not contract *coöperatively*, but *consecutively*, by a contraction propagated from fiber to fiber. (*f*) The voluntary muscles contract quickly and powerfully, the involuntary slowly and feebly. (*g*) Lastly, the voluntary are attached to the skeleton, while the involuntary are not attached to the skeleton, but surround hollow organs.

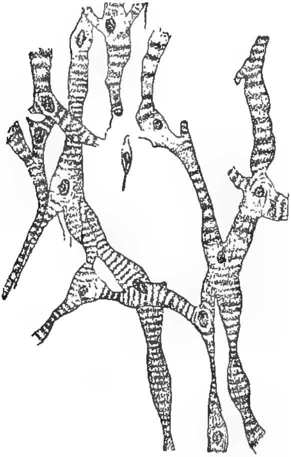

FIG. 141.—Muscular fibers of the heart of the embryo monkey. (After Kent.)

There are some muscles, however, which are intermediate. The most striking case is the heart. The muscle of the heart is red, transversely striated, and contracts powerfully, and yet it is *in*voluntary, consists of parallel fibers, and surrounds a hollow organ without skeletal attachment.

A muscular fiber is apparently evenly cylindrical, without any evidence of cellular origin. But in embryonic development it is seen to be formed by a coalescence of elongated nucleated cells. This is well seen in the fibers of the embryonic heart of the monkey (Fig. 141).

Voluntary Muscle.—*Form.*—The typical form of a voluntary muscle is seen in the muscles of the limbs—e. g., the biceps—which is shown in Fig. 146, page 228. It is attached to the skeleton at both ends. The nearer and more fixed point is called the *origin*, the farther and more movable point, the *insertion*. Between the two the largest and most contractile part is called the *belly*. The fibers all unite to form the tendon, by which it is attached to the skeleton. This is the type, but there is considerable variation. Sometimes the fibers are convergent. This is mainly in muscles connecting the limbs with the trunk, as in the deltoid, the pectoral, etc. Sometimes the fibers are nearly parallel, as in the masseters.

Structure.—A voluntary muscle is a definite mass invested by a thin fibrous membrane—*sheath*. If cut into we find it made up of bundles of fibers—*fasciculi* (Fig. 142, A). These are conspicuous in cured meat, such as corned beef. They constitute the grain of the flesh. These, too, are invested with a thin membrane of fibrous tissue. These bundles are in their turn composed of fibers lying parallel to one another in the bundle. Each fiber is also invested with a very thin sheath of fibrous tissue. The fibers themselves are supposed by some to be composed of smaller fibrillæ, but this is doubtful. Fig. 142, B, represents a single fiber, broken and twisted, showing the sheath. We may regard the whole muscle as penetrated and webbed together in all its parts with connective tissue. In a condensed form it invests each fiber; in a loose form it lies between and connects them. In a condensed form it again invests the bundles; in a loose form it lies between and connects these also. Finally, it emerges on the surface, and in a condensed form invests the whole muscle in a strong sheath, and in a loose form lies between the different muscles, connecting yet separating them. Add to this the blood vessels to nourish and nerves abundantly distributed to stimulate to contraction, and we have a good general idea of the organ we call a *muscle*.

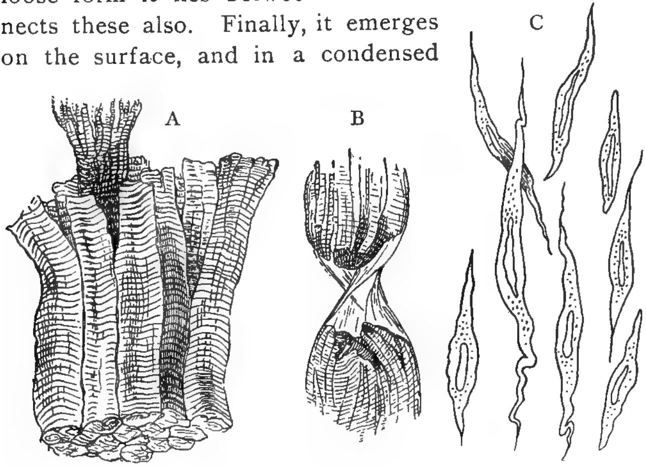

FIG. 142.—A, a fascicle of muscular fibers of voluntary muscle; B, one fiber broken to show its investing sheath; C, cells of involuntary muscle.

The tendon consists of all the sheaths of the muscle, of the bundles, and of the fibers united and continuing, and also of the transformed fibers themselves. It is therefore essentially fibrous in structure. It is the strongest—*i. e.*, has the greatest tensile strength of any organic substance known.

The only function of a muscle is to *contract*. This, indeed, is the only sign of its life. Any stimulus—mechanical, chemical, or electrical—may cause it to contract, but the normal physiological stimulus is the nerve influence, whatever that may be. When a muscle contracts it shortens, thickens, and hardens. The power with which it pulls in shortening is almost incredible.

Involuntary Muscle.—We have already sufficiently characterized this in contrasting it with the voluntary. Good examples of these are found in the muscular coats of the stomach, intestines, and bladder. Every one is familiar with this type in the white muscular substance of *tripe.*

No comparative physiology of this system is necessary, as the function, structure, and mode of action of muscle is much the same in all animals, as far as the tissue can be traced. Striation of muscular fiber is a sign of great activity, and is therefore found only in animals of considerable energy. It is conspicuous in vertebrates, and among invertebrates in arthropods, especially insects. As we go down the animal scale muscular fiber is found as low as the cœlenterates—medusæ and polyps. In protozoa it is replaced by general contractility of protoplasm.

SECTION II.

Skeletal System.

The skeleton in vertebrates is usually *bone*, because this is the most rigid of the tissues. In the lower fishes, however, and in the embryonic condition of all vertebrates cartilage takes the place of bone.

Bone is tissue hardened by deposit of lime salts, mainly phosphate. Several kinds of tissue take on this change. Thus, as to origin, we may have cartilage bone, tendon bone, and skin bone. Most of the true skeleton consists of cartilage bone, but the kneecap and several small bones in the joints are tendon bones, while the teeth and scutes are examples of skin bones. Bones are covered with a strong membrane called the periosteum.

Number of Bones in Man.—The number of bones in the human skeleton is variously estimated from a little over two hundred to about two hundred and fifty, the difference being the result of difference of view as to what ought to be included. Some include the teeth, and some do not, because these are gum structures. Some include the sesamoid or joint bones, some do not. Again many pieces are separate in the embryo, and become consolidated later. These two hundred or more pieces are articulated together into a complex structure, which is moved by the muscles.

Joints.—The articulations or joints are of two general kinds, *fixed* and *movable.* In fixed joints the pieces may be cemented together with cartilage (*symphyses*), as the hip bones with the sacrum, or they may be interdigitated or dovetailed (*suture*), as in the bones of the skull. The movable joints are also of two kinds—the *hinge joint*, when motion in one plane is required, as in the knee, elbow, etc., and the *ball-and-socket joint*, where universal motion is required, as in the shoulder and hip. Only the movable joints concern us here.

Movable Joints.—The bones in a movable joint are (*a*) enlarged at the ends where they come together, so as to make a firmer contact. (*b*) They are covered with cartilage for perfect smoothness and elasticity. (*c*) The joint is inclosed in a capsule of strong fibrous tissue to prevent displacement, and at the same time exclude the air. (*d*) The closed cavity thus formed is lined with a serous membrane, which secretes a smooth, glairy, lubricating fluid—the *synovia* or joint juice.

All of these characters, intended for easy motion and to prevent dislocation, are common to all movable joints; but to these in the case of hinge joints are added (*e*) two strong ligaments, one on each side, which hold the parts together and yet allow free motion in one plane. These are the *lateral ligaments.* They are found in all hinge joints. In addition to these (*f*), in the knee joint there are two *crossed ligaments* within the joint itself, as shown in Fig. 143.

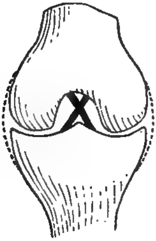

FIG. 143.—Diagrammatic view of the knee joint. The dotted lines show the position of the capsule and of the lateral ligaments; the black lines show the crossed ligaments.

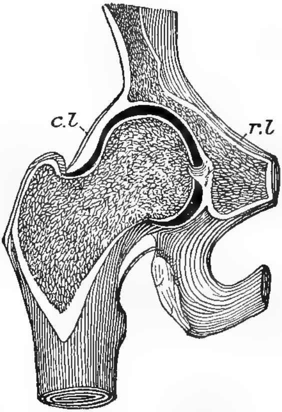

FIG. 144.—Section through the hip joint, showing the capsule (*cl*) and the round ligament (*rl*).

In ball-and-socket joints we have, of course, *a*, *b*, *c*, *d*; but in the case of the hip joint, in addition to these, there is a short, strong, round ligament running from the bottom of the deep socket to the top of the ball, as shown in the diagram (Fig. 144).

SOME EXAMPLES OF ADAPTATION.

The articulated skeleton together forms a really wonderful contrivance. Some examples of adaptation may be mentioned. I select such as lead to interesting comparisons with other vertebrates.

1. *Spinal Column.*—Observe (1) the double or S curvature. This is peculiar to man, and the result of the erect attitude. In this position it acts as a spring to prevent shocks to the brain in falling, leaping, etc. Observe (2) the intervertebral substance. This is an elastic cushion, of half an inch thickness, between all the vertebræ, and also acts to prevent concussion of the brain. It is, however, not peculiar to man.

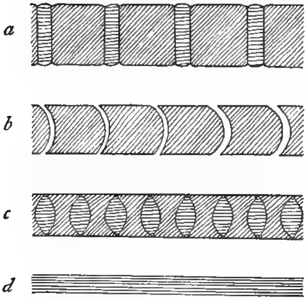

FIG. 145.—Diagram showing the characteristics of the vertebral column in mammals (*a*), reptiles (*b*), fishes (*c*), and lowest vertebrates (*d*).

Comparative Morphology of the Column.—The manner of articulation of the vertebræ is very characteristic of the different classes of vertebrates. In mammals the vertebræ are short segments of a cylinder with flat faces and intervertebral substance between (Fig. 145, *a*). In reptiles the articulation is by ball-and-socket joint. The faces of each vertebra are one of them concave and the other convex, and these fit over one another, *b*. In some reptiles the hollow face looks forward (procœlian), in others backward (opisthocœlian). In fishes the segments are double concave (amphicœlian), with double convex intervertebral substance between, *c*. Some early reptiles were like fishes in this regard. In the lowest fishes there is a continuous unsegmented cord (notochord), *d*. This is also the early condition of all vertebrates, whether in the embryonic development or in the evolution of vertebrates. This early notochord is afterward changed into a vertebral column by ossification in segments. These characteristics of the vertebral column in different classes are very important in geology.

2. *Structure of Shoulder Joint and Fore Limb.*—There is a progressive change from man to the more *specialized* mammals in the *position* of the shoulder joint, its *movableness*, the presence and movableness of the *two bones of the forearm*, and the *free use of the hand.* All these are strictly correlated, and all reach their highest point in man, because all are in him connected with the erect attitude and the consequent liberation of the fore limbs from the function of support and locomotion for higher uses. In man the shoulder joint and the arms are on the side of the body, being kept wide apart by the clavicle, and the motion of the arm is the extreme of freedom. For this freedom firmness of the joint is sacrificed. The two bones of the forearm roll the one on the other, carrying the hand with it, and the hand has the most perfect capacity for grasping. Now, as we go down the scale of mammals, the collar bone disappears, the fore limbs are brought together in front for support, the two bones of the forearm become less and less movable on one another, and the paw loses its power of grasping, until, finally, in the hoofed animals the extreme is reached; the limbs are brought closer together in front and used only for support, and therefore restricted in motion; the two bones of the forearm are consolidated into one, and therefore lose entirely all rotary motion; the paw is no longer a paw, much less a hand, but a hoof, wholly incapable of grasping.

Motion and Locomotion.—We have explained the function of muscle and of skeleton. We must now show how they co-operate to produce motion and locomotion.

1. *Limb Motion.*—Remember, then, that a muscle has two skeletal attachments—viz., the origin and insertion.

Between these there is always a joint. When the muscle contracts, its two attachments are brought nearer together, and the joint bends. Remember, again, that a muscle can only *pull*, not *push*, and therefore motion in two directions can only be effected by two opposing muscles. Again, it must be borne in mind that in animal mechanism power is nearly always *sacrificed* to *velocity*, because swiftness is more valuable in the struggle for life than slow dead strength. Therefore, of the different orders of levers, the second is rarely, almost never used, and in the first order the fulcrum is so placed that power is sacrificed to velocity.

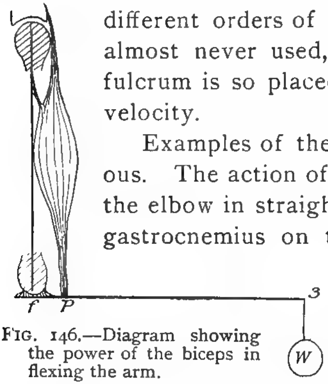

FIG. 146.—Diagram showing the power of the biceps in flexing the arm.

Examples of the first order are very numerous. The action of the triceps on the point of the elbow in straightening the arm and of the gastrocnemius on the heel bone in bringing down the toes (Fig. 148) are excellent examples. Examples of the third order are equally numerous. We again take two: 1. Action of biceps, pulling on its insertion, and flexing the elbow (Fig. 146). 2. The action of the deltoid on its insertion, in raising the arm (Fig. 147).

The prodigious force of muscular contraction may be easily calculated from these examples. Take the case of the biceps in bending the arm at the elbow. I suppose any one with average muscular vigor can hold fifty pounds in the hand with the elbow joint at right angles, as in Fig. 146. In such case, taking the distance of the insertion of the tendon, P, from the fulcrum, f, as one inch, and from the fulcrum to the weight, W, one foot, the pull of the muscle on the insertion at P necessary to hold up the weight would be $50 \times 12 = 600$ pounds.

Or take the case of the deltoid holding a weight at arm's length (Fig. 147). I suppose a man of good muscular vigor will hold at arm's length a weight of thirty pounds. Now, in order to do so, the deltoid taking hold at four inches from the fulcrum, *f*, and the weight held at two feet from the same, if it pulled directly upward it would have to pull with a force of 30 × 6 = 180 pounds. But it pulls at a small angle, and we must multiply this again by at least four—i. e., 180 × 4 = 720 pounds.

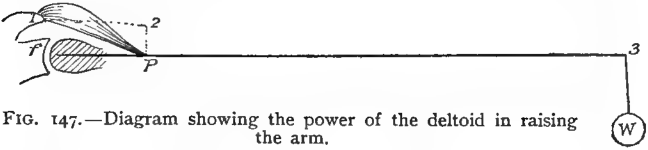

FIG. 147.—Diagram showing the power of the deltoid in raising the arm.

Or take one more—viz., the case of the gastrocnemius and soleus muscles (the calf of the leg) lifting the heel. I suppose any person of ordinary weight and vigor can take another person of average weight, say one hundred and fifty pounds, on his back, making altogether, say, three hundred pounds, and, standing on one foot, rise to tiptoe. Let us see what the strain on the tendo-Achillis is in doing so. Taking the distance from the fulcrum (*2*, Fig. 148) to the insertion of the tendon, *1*, as one inch, and the distance from the same to the ball of the toes, *3*, as six inches, then we have the proportion *1*, *2* = one inch : *2*, *3* = 6 inches :: 300 pounds : x, and x = 1,800 pounds. Or if some one objects (as has been often

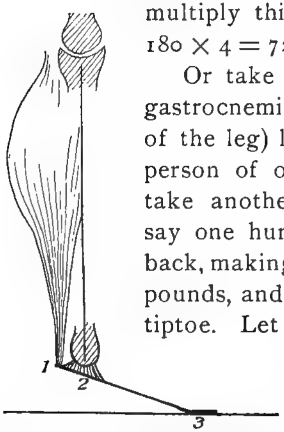

FIG. 148.—Diagram showing the power of the gastrocnemius and soleus muscles in tiptoeing.

objected) that 3 must be taken as the fixed point or fulcrum, and therefore we must treat the question as falling under the second order of levers—i. e., the power pulling upon the lever $1, 3 = 7$ inches, and the weight pushing down on the lever $2, 3 = 6$ inches, then we must remember that the muscle pulls the body downward, adding to the weight exactly as much as it pulls the heel upward. Therefore, under this conception, we must put the proportion thus—$7 : 6 :: 300 + x : x$. $7x = 6x + 1{,}800$—or $x = 1{,}800$.

It has been determined by experiment that one square inch of muscle will contract with a power equal to about one hundred to one hundred and twenty pounds. Why, then, does not the muscle break? For dead muscle can stand no such tensile strain as this. The answer is: It *would* break if it were passive, and the force was external to itself, but it is the *attraction* between the molecules of the muscle itself that develops the pull; *attraction* can not produce *separation.* Muscles do break sometimes, but always from *irregular* contraction—i. e., one part contracts while another part does not, and is therefore subject to tensile strain, just as the tendon is.

2. *Locomotion.*—In limb motion the origin or body end of the muscle is fixed, and the insertion or limb end moves; but these are interchangeable. If we fix the limb, then the body moves. Thus, for example, if we hold up the hands above the head and bring into action the great muscles about the armpit, and also the biceps, the elbow is brought down to the side and the fist to the chin; but if we fix the hands by taking hold of a bar and bring into action the *same muscles*, the body rises until the chin goes over the bar. Now locomotion is nothing more than limb motion reacting against the ground in walking, running, leaping, against the water

in swimming, and against the air in flying. For instance, let a steam engine be lifted from the rails and steam be put on; we have only *wheel motion.* But while thus working set the engine on the track, and wheel motion is changed into locomotion. Or lift a cyclist above the ground and let him work his pedals; we have now limb motion and wheel motion. But set him on the ground, and away he shoots, scorching the ground as he passes; wheel motion is converted into locomotion. Or, again, take the sprinter, hang him up in the air, and let him set his running muscles into action. We have, of course, only extravagant limb motion. But while this is going on, if we set him down on the earth, instantly limb motion is converted into rapid locomotion. There is therefore no new principle involved, and no further discussion required.

But there is still one point which must be mentioned—viz., the exquisite *co-ordination* of action of many muscles required in nearly all our motions. For example, in the simple act of *standing* there are probably at least one hundred muscles in perfect co-ordinate action to maintain the equilibrium. It is so easy and so instinctive that we are unconscious of the constant play of many muscles. If so in standing, how much more in walking, running, leaping, swimming, flying! So wonderful, indeed, is this co-ordination that it could not be learned in a lifetime if it were not largely *inherited.* A calf newly born will stand on its feet and walk. It has not learned to do so, but has inherited the capacity. A chick newly hatched will walk and use its eyes correctly and peck its food. A wild bird's egg may be taken from the nest, hatched in an incubator, and reared in a cage until the young bird is well feathered, until nerves and muscles are sufficiently developed. If then it be carried out and thrown in the air it will at once fly away with ease. Even a child, when the proper time comes—i. e., when the nervous and muscular systems are sufficiently developed—will learn to walk in a week. Even in the child a large portion of this capacity of co-ordination is inherited, though far less than in animals. The whole sum of capacity in all animals is partly inherited and partly individually acquired. In animals, and almost in proportion as they are lower in the scale, the inherited part is large in proportion to the acquired part. In man the reverse is true.

SECTION III.

Comparative Morphology and Physiology of Muscle and Skeleton.

VERTEBRATES.

So far as vertebrates are concerned, the function of muscle and skeleton is almost identical with that already explained in man, although there is great variation in the structure by means of which function is carried out. But this will be brought out in a separate chapter on the laws of animal structure in relation to the origin of organic forms by evolution. We pass, therefore, directly on to the invertebrates.

INVERTEBRATES.

The function of motion in invertebrates is so infinitely various that all that is possible in this work is to give some characteristic examples of widely different modes. The most interesting of these is that of arthropods.

ARTHROPODS.

We all know the intense muscular activity of arthropods, especially insects—the arrowy swiftness of the flight of many flies; the prodigious leaps of fleas, three hundred times their own length; the enormous masses, twenty times their own weight, dragged by ants, etc.; and yet the relation of muscle to skeleton, and therefore the mechanism of motion and locomotion, is wholly different from that of vertebrates. In vertebrates we have an *internal* skeleton and the muscles acting on it from *the outside*; in the case of arthropods we have an *external* skeleton and the muscles acting on it from *the inside*. The whole animal is inclosed in a skeletal coat of mail. The body is a hollow, jointed barrel inclosing the viscera, and the limbs are hollow pipes filled with muscle. The manner in which this arrangement is used for limb motion is shown in the following figures: Fig. 149, A and B, represents the joints of a stovepipe beveled a little on the two opposite sides so that when fitted, the one in the other, there is a small vacant space between. Now if the interfitted parts, *a a*, be riveted together, and strings, *m m'*, within the pipe be attached to the beveled margins, we have a perfect hinge joint, and pulling on one string or the other produces motion in two directions in *one plane*. Now the mechanism for limb motion in all arthropods is like this, except that we have ligaments instead of rivets, and muscle and tendon instead of strings pulled by hand. Fig. 150 shows four joints of the limb of a crab or lobster and the manner in which the muscles bend the limbs.

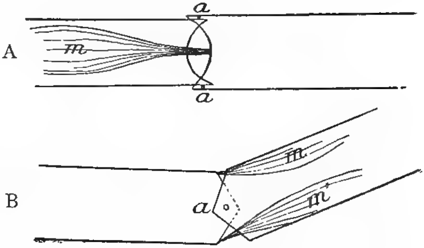

FIG. 149.—Diagram showing mode of action of muscle and skeleton in an arthropod: *a*, the joint; *m*, the muscle.

It is evident that with a hollow skeleton and muscles within, only hinge joints can be formed. A ball and socket is impossible. How, then, is universal motion effected? This is done by two hinge joints moving in planes at right angles to one another, as in the diagram, Fig. 149. If we examine the leg of any arthropod, say a lobster, we shall find that the consecutive joints are hinged alternately in planes at right angles to one another (Fig. 150).

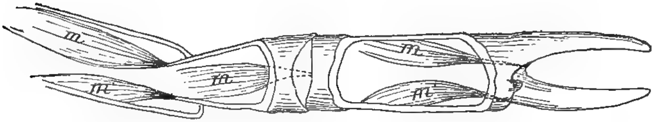

FIG. 150.—Four joints of the limb of a crustacean cut so as to show the muscles (*m m*) and their attachments.

Now of these two different modes of relation of skeleton and muscle, which is the best? We have already seen the intense locomotive activity of insects. Many writers hastily conclude that the nervous and muscular activity of insects is far greater than that of vertebrates, or else that their mechanism is superior. This is probably a mistake. The superior locomotive activity of insects is simply the result of *small size.* It is evident that, other things being equal, the contractile power of a muscle varies as its *cross section*—i. e., as the *square* of its diameter. But the weight to be moved—i. e., the weight of the body—varies as the *cube* of the diameter. Therefore, as the size of the animal increases, its weight increases faster than its muscular power. Therefore more and more of the whole energy is used up for support of weight, and less and less is left over for locomotion, until, if the animal is large enough, the whole power is used up for support, and none is left over for locomotion. There is therefore a limit to the *size of a walking animal*, and a much lower limit to the size of a *flying animal.* Contrarily, as an animal becomes smaller, the muscular energy per unit section remaining the same, the weight decreasing faster than the power, less and less proportion is necessary for support of weight, and more and more is left over for activity of all kinds. This is the true reason why small animals seem so much more vivacious than large animals.

WORMS.

In these there is no skeleton, but the muscles act directly on the body to produce motion and locomotion. We have, therefore, in these an entirely different mode of action.

Take an earthworm as a good example. In these there are two kinds of muscular fibers, viz., the *longitudinal* and the *ring* fibers. The longitudinal fibers, acting all together, *shorten* the body; acting on one side or another, bend the body to the corresponding side. The ring fibers constrict the body, and, acting all together, elongate it. But the most conspicuous peculiarity of all the fibers, both longitudinal and ring, is their *propagated* action. Watch an earthworm in locomotion. We observe a wave of constriction—i. e., contraction of ring fibers—running forward, advancing each part consecutively until it reaches the head, which then advances and takes hold; and then begins a wave of contraction of longitudinal fibers, running backward and bringing up successively the parts of the body toward the head. Usually several such waves chase each other along the body. This kind of motion is so characteristic of worms that it may be called vermicular. It is found in all animals, even the highest vertebrates, in the involuntary muscles, especially those of the stomach and intestines.

It is there wholly automatic. It is probably at least semi-automatic in the locomotion of worms.

The locomotion of all wormlike animals, as, for example, caterpillars, etc., is similar to that described.

MOLLUSCA.

Acephala.—In *oysters* there is only one *conspicuous* motion, viz., that of closing the valves. This is effected by a large muscle running transversely from valve to valve. When this is cut, as in opening an oyster, the valves fall apart. The purple spot seen on the interior of an oyster shell is the place of attachment of this muscle, and the firmer, sometimes tough, portion of the oyster is the muscle itself. When the muscle relaxes, the valves open by means of an elastic substance in the hinge of the valves; when it contracts, the valves are closed with great force.

In *clams* (Fig. 151) there are two of these transverse muscles and an additional locomotive organ, the foot, connected with the two transverse or shell muscles. This organ contains longitudinal fibers for retraction, and also oblique and transverse fibers for constriction and consequent protrusion. It is used for locomotion and also for burrowing in the mud. In locomotion it is protruded, takes hold, and then is retracted, and thus draws the body forward.

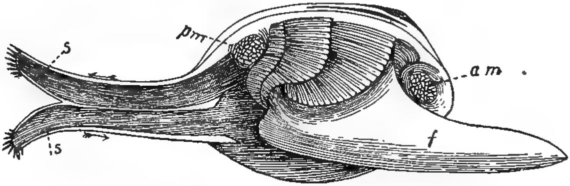

FIG. 151.—Mactra with one valve removed, showing the anterior (*am*) and the posterior (*pm*) shell muscles, and the foot (*f*). (From Gegenbaur.)

Gastropoda.—In *snails* (Fig. 152) and *slugs* the locomotive organ or *foot* is an elongated flat disk, lying along the ground, which consists of muscular fibers running in all directions, some transverse, some oblique, and some longitudinal. The longitudinal fibers shorten, the oblique and transverse constrict and lengthen. A snail or slug seems to glide slowly and continuously along without apparent mechanism. If watched carefully, however, waves of constriction and advance chase one another from one end of the foot to the other. In the case of those having a shell, as the snail, muscular fibers from the foot are attached to the interior of the shell, whereby the foot is drawn into the shell. Of course there are also small muscles, ring fibers, and longitudinal fibers for moving the tentacles.

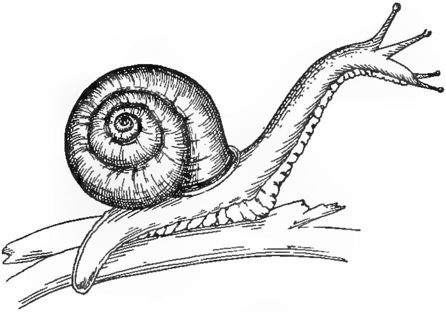

FIG. 152.—Snail walking.

Cephalopoda.—Confining ourselves to locomotion, we find here, again, a new kind. The squid and cuttlefish are invested with a thick, hollow, muscular mantle, within which are inclosed all the viscera, but with considerable space between filled with sea water. Just beneath the head protrudes a conical tube (*siphon*), valvularly connected with the hollow in such wise that when the mantle contracts the water is forced through the siphon with great force, and the animal is shot backward with great speed. Besides this rapid locomotion for escape, there is another in both the squid and cuttlefish, but different in the two cases. The squid is provided with a horizontal, arrowhead-shaped caudal fin (not shown in the diagram), which is not flapped from side to side, as in fish, nor up and down, in the manner of whales, but locomotion is effected by waves propagated backward or forward—in the one case giving rise to gentle forward, in the other to gentle backward motion. These graceful movements may be watched in an aquarium.

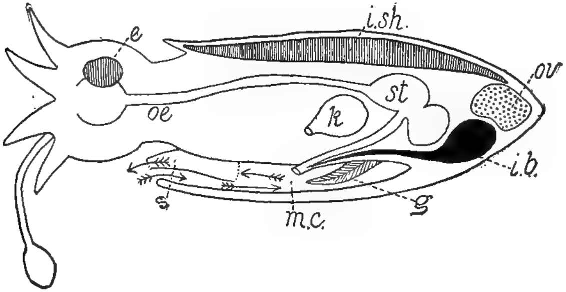

FIG. 153.—Diagram showing general structure of a squid: *mc*, the mantle cavity; *s*, the siphon; *g*, gills; *ib*, ink bag; *ish*, internal shell; *e*, eye; *oe*, œsophagus; *k*, kidney. The arrows show the direction of currents.

The short-bodied cuttlefish, on the contrary, uses its long, flexible, muscular arms for crawling on the bottom, or even for climbing up rocks.

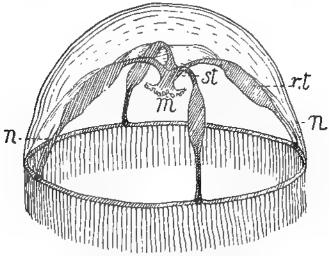

FIG. 154.—Diagram of a medusa: *n n*, nerve; *m*, mouth; *st*, stomach; *rt*, radiating tubes.

CŒLENTERATA.

Medusæ.—As we are taking only the most strikingly different modes, we pass over the echinoderms and take next the acalephs or *medusæ*. The transparent character and the saucerlike (Fig. 154) or bell-shaped form and graceful movements of these beautiful creatures are well known. Their locomotive apparatus consists of fine muscular fibers, arranged in circular and radiating manner on the interior of the saucer or bell. When these fibers contract, the saucer or bell is drawn together, the water expelled, and the animal driven in the contrary direction. When the fibers relax, the somewhat firm, gelatinous mass again expands by its own elasticity to its original form and size.

PROTOZOA.

Infusoria.—In these, again, we have a wholly different mode, viz., *ciliary motion* and *locomotion.* If the animal be fixed, as *a*, then the incessant lashing of microscopic cilia, situated mainly about the mouth, creates whirling currents, which lead down to the throat, and thus contribute to alimentation. Whatever is suitable as food goes down; what is not, is rejected and carried away by the same current. But if the body is free, *b*, the same ciliary motion, reacting against the water, produces the most vivacious *locomotion.* Under the microscope it is seen to whirl and dart about in every direction without visible means; but with the higher power, especially when the motion is slower, the incessant lashing of the cilia is visible.

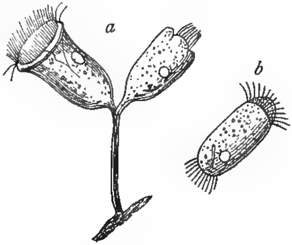

FIG. 155.—Infusoria: *a*, an attached form; *b*, a free form.

Rhizopods.—Here we have motion, as well as all other functions, reduced to simplest terms, and find its origin in *general contractility of protoplasm.* The structureless, or almost structureless, mass of living jelly contracts itself in any part and in any direction, putting out here or there a fingerlike projection or a hairlike thread, and again withdrawing and absorbing it into its substance (motion); or such a projection may take hold of some *movable* body, and then by retraction the movable body is drawn toward and absorbed as food into the animal (prehension); or, finally, if the point taken hold of is *fixed*, then the *creature* is moved and absorbed into the fingerlike projection (locomotion).

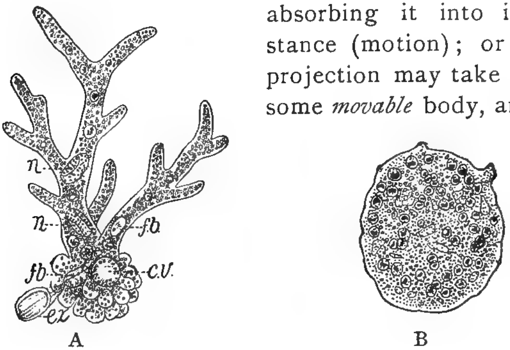

FIG. 156.—Amœba proteus (after Leidy): A, with the pseudopods extended; B, the same, with pseudopods withdrawn; *fb*, food bodies; *ex*, excrement discharged.

CHAPTER IV.

GENERAL LAWS OF ANIMAL STRUCTURE, OR GENERAL LAWS OF MORPHOLOGY, OR PHILOSOPHICAL ANATOMY.

SECTION I.

Introductory.

THIS is a subject of fascinating interest in many ways, but especially on account of its bearing on the theory of the origin of organic forms by evolution. It is for this reason mainly that we shall treat it somewhat fully.

I find it necessary, however, to make some preliminary definitions of terms.

Analogy versus Homology.—Parts or organs in different animals are said to be *analogous* when they have a similar form, and especially when they perform a similar function. Contrarily, parts or organs of different animals are said to be *homologous* when, however different their general apearance and however different their functions, they can be shown to have a *common origin*—to be, in fact, the same part, only modified in order to perform different functions. The difference between these can be best shown by examples; and the ideas involved in these terms lie at the basis of all I shall say. We will give examples from plants, as well as animals.

Examples: *Animals.*—1. The *wing* of a bird and the wing of a butterfly are *analogous* organs. They have a similar flat form, adapting to a similar function—viz., that of flying. But they are not at all homologous. They have not a common origin; the one could not have, and did not, come from the other. In a word, they are not at all the same thing. But the wing of a bird and the wing of a bat *are* homologous parts. Not only so, but both are homologous with the pectoral fin of a fish, the fore limb of a reptile or a mammal, and the arm and hand of a man; for all these, though now so different in form and function, can be shown to have a common origin by descent—to be, in fact, the same thing, only modified for various purposes.

2. The *lungs* of man and the gills of a fish are analogous parts—i. e., they perform the same function in the animal economy—viz., the *aëration of the blood.* But they are not homologous. By no possibility could one have come by modification out of the other. What, then, in the fish is the organ homologous with the lung of man? It is the *air bladder.* This is the organ which by modification became the lung of air-breathing animals. The proof of this is complete, for all the steps of the gradual change can be traced. This is shown as follows:

(*a*) In most typical fishes the air bladder is wholly isolated and used only as a float. In such cases it is colorless. But in some fishes it is connected by a slender tube with the throat, and doubtless the contained air is renewed from that source. In still other fishes it is not only connected with the throat, but air is regularly and voluntarily taken in. In such cases it is vascular and therefore reddish in color. This is the case in the gar pike (*Lepidosteus*). This fish may be observed to come at intervals to the surface and gulp down air, which is again afterward expelled in bubbles. The gill breathing is to some extent supplemented by air breathing. Finally, in a few of the most reptilian fishes (*Ceratodus* and lepidosiren) the air bladder is not only vascular, but cellular, like the lung of a frog. It is really a lung, and these animals breathe partly by gills as a fish, and partly by lungs as an amphibian reptile. It is an amphibian fish.

(*b*) Now, the condition last described is exactly that of the lowest amphibians and the early or larval condition of *all* amphibians. In fact, in the development of the individual, in the individual life history of an amphibian, we have all the stages of change of the respiratory organs from the complete gill-breathing stage to the complete lung-breathing stage. The very young tadpole breathes wholly by gills, like a fish; the frog wholly by lungs, like a reptile or a mammal. How did the change take place? By modification of the gills? No —but *by the development of another organ in the position of the air bladder of a fish.* At first, as already said, the breathing is wholly by gills, like a fish. Then by the development of an organ in the position of the air bladder of the fish and connected with the throat it begins to breathe also by a commencing lung. It now breathes equally by gills and by lungs, both water and air. This is the permanent condition of the highest fishes (lung fishes) and of the lowest amphibians (the *Perennibranchiata*), such as the siren, etc. From this time onward the gills decrease and the lungs increase, until in the adult the gills disappear and the breathing is wholly by lungs. The first argument (*a*) is strongly presumptive; the second (*b*) is demonstrative.

It is unnecessary to give further examples from animals, as all that we shall have to say in this chapter will be a continuous illustration of homology; but a few illustrations from plants will show the universality of the principle.

(1) A rhizome or rootstock—such as that of a flag, or of calamus, or of a fern—is *analogous* to a root, for

it has the underground position of a root, and probably performs some of the functions of a root. But it is homologous with a stem—it is, in fact, an underground stem, for it has the structure of a stem, it bears leaves like a stem, and in the axils of those leaves come buds, making new shoots. Moreover, in many plants, as in palms and in ferns, all gradations can be traced even in the same family from the underground, through the prostrate and inclined, to the upright position.

(2) The so-called *leaf of a cactus* is no doubt analogous to a leaf. It is flat and green, and performs the functions of a leaf—viz., the assimilation of plant food. But it is homologous with a *stem.* It is, in fact, a stem modified in shape and color to perform the function usually performed by leaves. This is proved by its structure—viz., pith, wood, and bark, with medullary rays connecting the pith and bark; and also by the gradations among cactuses between the flat, leaflike form and the cylindrical, stemlike form. Where, then, are the true homologues of the leaves? We find them in the *spines.* These are abortive leaves modified as defensive organs. They have the spiral arrangement of leaves, and in their axils come the buds which form new shoots.

3. One more example: The *acacias*—of which there are in California about twenty species, introduced from Australia—are by appearance easily divided into two groups, viz., the *feather-leaved* acacias and the *simple-leaved* acacias. These are so different in general appearance, that the mere popular observer would probably put them not only in different genera, but even in different families. But doubtless the botanists are right in putting them all in the same genus, for they are really so closely allied that the same individual may pass from one form to the other.

The fact is, the so-called leaf of the simple-leaved acacias is not homologically a leaf at all, but a leaf-stem, broadened and flattened to perform the function of a leaf. Such an organ, functionally a leaf but homologous with a leaf-stem, is called by botanists a *phyllode.* Its true nature is shown in the development of a simple-leaved acacia from a seedling. At first it bears only feather leaves, then imperfect feather leaves with flattened stems, then broadly flattened stems with a mere remnant of featherlike leaflets, and finally the leaflets are gone and only the broad leaf-stems remain. All these forms may often be seen in the same spray (Fig. 157).

FIG. 157.—A branch of young acacia, showing change from one form of leaf to the other: *a*, *b*, *c*, *d*, successive stages of change; *ls*, leaf stalk which gradually changes into the blade in *c*, *d*, and *e*.

After these illustrations, we come back to define again these terms.

Analogy is founded on *function.* Homology on *common origin* by descent. Parts of most diverse origin may be modified to perform the same function, and therefore assume a general resemblance. This is analogy. Parts of the same origin—really the *same parts* in different species—by modification for different functions may become so different that they are no longer easily recognized as the same part. This is homology. In the one case the parts *seem* like the same and behave like the same, but are really very different; in the other they are really the same part, but they seem to the superficial observer to be very different both in appearance and in behavior. In the one case there is a superficial resemblance produced by functions easily observed, and therefore determining popular names; in the other there is a deep-seated resemblance shown by *essential structure* and *structural relations*, but more or less obscured by adaptation to different functions. This deep-seated resemblance can only be found by wide comparison in the animal series and in the embryonic series, for it is in this way only that we find the steps of gradation connecting.

There are therefore two ideas underlying homology, viz., *common descent* and *adaptive modification.* Things having common origin by descent may be so modified to adapt them to different functions as to conceal their common origin. It is the duty of the morphologist to trace out the evidences of common descent in spite of the obscurations of adaptive modification.

The idea of *homology* or common origin with obscurations by adaptive modification, lies at the very basis of biology and must be universal. We have therefore an excellent example of it in essential cell structure characteristic of all living things. We have already given this illustration on page 22. All tissues have a common origin in unmodified cell structure. But in the differentiated tissues of the higher animals this common origin is so obscured by adaptive modification for function that it can not be made out except by extensive comparison in the animal scale and in the embryonic scale. Now the object of this chapter is to trace the homologies or the common origin in animal structure in spite of the obscurations produced by modification of *parts* adapting it to various *functions*, and of the *whole organism* adapting it to various places in the *economy of Nature.*

But the question occurs: How far can we trace homology? Analogy can be traced throughout the animal kingdom, because it is based on function. Doubtless, also, homology or common descent must *exist* throughout, but it is *not traceable* with certainty. The obscurations of adaptive modification completely obliterate the evidences of common origin except in animals not too far separated in character. How far, then, can we satisfactorily trace it? We answer: Only through the *primary* divisions or departments. And, conversely from the *morphological* or *evolutional point of view*, this ability to trace common origin is the true ground of primary divisions. From this point of view Agassiz's *four primary branches* from the protozoan trunk finds much justification.

Thus, then, we would say, the structure of all *vertebrates* is exactly what it would be if they all came by descent with modification from one *primal* vertebrate; and therefore we must believe they did so come. All articulates—i. e., arthropods and annulates—for like reason, came from a primal form of articulate by adaptive modification. Similarly all mollusca came by descent with modification from some primal form of mollusk; and radiates (including echinoderms and cœlenterates) from some primal form of radiate animal.

That these prime divisions also have a common origin is shown by their common cellular structure, and also by the fact that the first steps in embryonic development is the same in all. But this common origin is not shown in the completed structure.

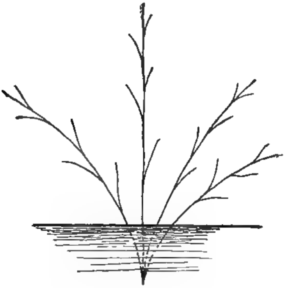

FIG. 158.—Diagram showing supposed common origin of the different phyla.

From this point of view, at least four main branches of the tree of life came from the *protozoan trunk* and grew in different directions, diverging more and more, and giving off each subordinate branches (classes, orders, families, etc.); but the point of union with the protozoan trunk and with one another is, as it were, hidden from view beneath the common ground of cellular structure. But the subordinate branches of each primary branch can be traced throughout. Diagram Fig. 158 roughly expresses what we mean.

SECTION II.

Homology of Vertebrates.

The thesis to be established is that all vertebrates have come from some primal form of vertebrate by modification. This is best shown in the skeleton, and we shall confine ourselves mainly, though not entirely, to this system. The common origin is shown, first, in the

I. GENERAL PLAN OF STRUCTURE—GENERAL HOMOLOGY.

1. All vertebrates, and *no other* animals, have an *interior skeleton*, with the muscles acting on it from the *outside* to produce motion and locomotion.

2. In all vertebrates, and in no other animals, the axis of this skeleton is a jointed backbone or vertebral column. It is this that gives name to this department. They are vertebrates or backboned animals.

3. In all vertebrates, and in no other, this axis incloses two cavities: one, the neural cavity, *n*, is above, to protect the nervous centers; and the other, the visceral cavity, *v*, below to inclose the visceral centers (Fig. 159).

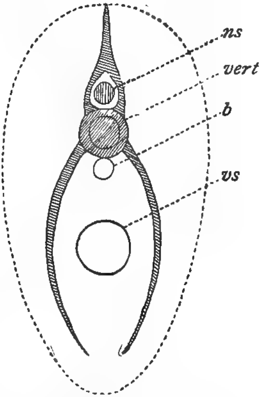

FIG. 159.—Cross section through a fish: *vs*, visceral system; *vert*, vertebra; *b*, blood system; *ns*, nervous system.

4. In all vertebrates, and in no other, the head may be regarded as a coalescence of several vertebral joints.*

5. In nearly all vertebrates, and in no other, there are two, and only two, pairs of limbs. The exceptions to this law fall under two categories—viz., those like the lowest fishes, which represent the condition before limbs were added to the skeleton, and those like snakes and like some lizards and amphibians, in which the limbs have been lost.

This general common plan of skeletal structure strongly *suggests* a common origin.

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* Some do not hold this view of the origin of the head.

II. SPECIAL HOMOLOGY.

But not only do we find a common general plan suggesting common origin, but, when examined thoughtfully, we find all vertebrate skeletons exactly corresponding, part for part, bone for bone, only modified by necessary adaptation for various functions. The modifications may be so great as to obscure the essential identity, but extensive study of comparative anatomy and embryology reveal the missing links in the continuous chain of change. The evidence here is demonstrative.

Limbs.—To show this we take the case of the limbs, partly because their structure is better known to common observation, but mainly because we have in them the two ideas of common origin and adaptive modification, both equally illustrated. The modifications here have been great, but not so great as to wholly conceal the common origin.

(*a*) **Fore Limbs.**—For fore limbs we take man's as the type or term of comparison because it is best known, and also because it is really far less modified than many others; although in this regard alone that of reptiles would be the best.

See, then, the fore limbs of various classes of vertebrates (Figs. 160, 161, 162). The same parts are similarly lettered in all, so that the legend sufficiently explains the corresponding parts. Moreover, dotted lines are drawn through the most important corresponding parts to make the comparison more easy. But it is necessary to say something more in the way of explanation concerning several of these parts.

1. *Shoulder Girdle.*—This consists of three important bones—viz., the *blade* (scapula), the *clavicle*, and the *coracoid.* The type is seen in the reptile (Fig. 162, A) which

may be regarded as the original form of the land animal. In these all the parts are large. The coracoid is as large as the blade, and is joined firmly to the sternum, making thus a firm girdle for the attachment of the fore limb. In birds also the coracoid is a large bone firmly united to the breastbone (sternum). These are types of shoulder girdle. In man the coracoid is reduced to a small

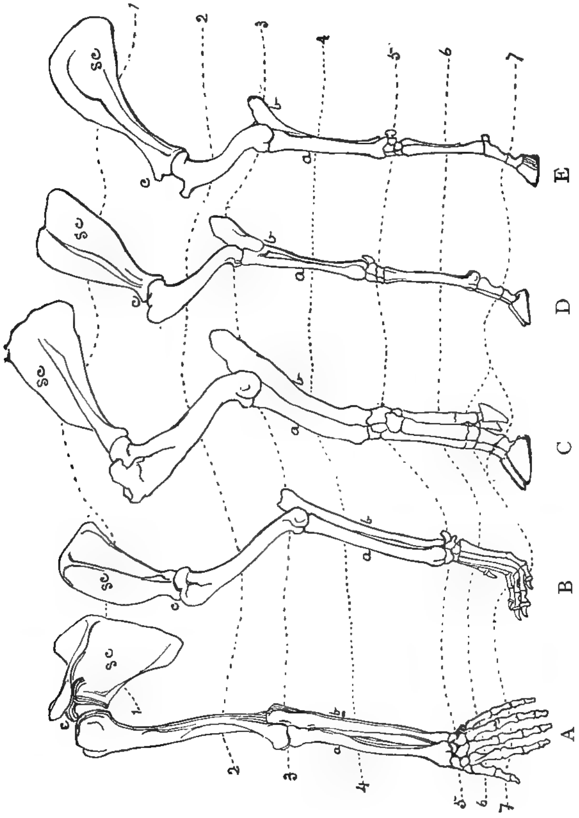

FIG. 160.—A, fore limb of man; B, dog; C, hog; D, sheep; E, horse: *sc*, scapula; *c*, coracoid; *a b*, two bones of forearm. (Taken from various sources and grouped.)

process of the blade. In most mammals the coracoid is still more reduced, and the clavicle is wanting altogether; but all the steps of its gradual obsolescence may be picked up by extensive comparison.

2. *Elbow Joint.*—In man, in monkeys, and in some other mammals, and in all reptiles, the whole limb is free of the body and the elbow joint halfway down the limb. This is undoubtedly the original and typical condition, but in all highly specialized mammals, by the shortening of the humerus, the elbow is drawn up on the side of the body so that the limb is free only from the elbow downward.

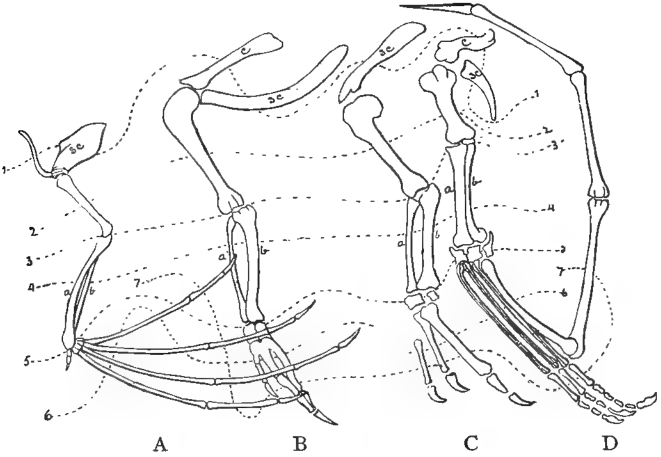

FIG. 161.—A, fore limb of bat; B, bird; C, archæopteryx; D, pterodactyl. (Lettered as in previous figure; grouped from various sources.)

3. In man, in monkeys, and many other mammals, and in all birds and reptiles, there are two bones in the forearm. But in all the more specialized mammals these are reduced to *one*, although the remnant of the other is always found forming the point of the elbow

(see figure of horse, Fig. 160, E). All the gradations are easily found.

4. *Wrist Joint.*—In man (when he comes down on all fours), in monkeys, in bears, and some other mammals, and in all *reptiles*, the wrist joint comes down to the ground—the tread is on the *whole hand*. This was the original tread of early land animals; but in all the more specialized mammals, and especially in hoofed animals, the tread is *on the toes*, and the wrist is elevated far above the ground, and in hoofed animals, as the horse and the cow, is usually, but erroneously, called the *knee*.

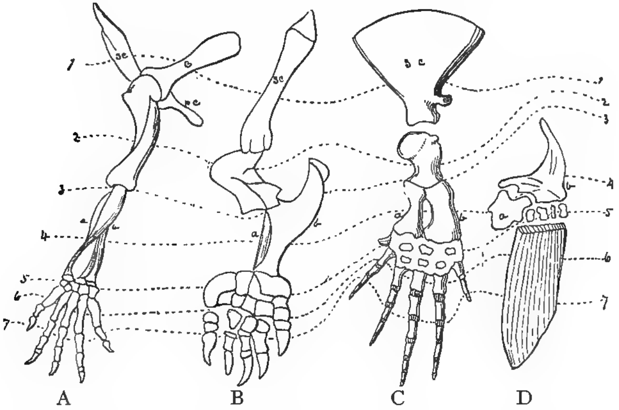

FIG. 162.—A, fore limb of turtle; B, mole; C, whale; D, fish.

5. In man, in many mammals, and in all reptiles, there are five palm bones (metacarpals) and five fingers, and this was undoubtedly the original and typical number; but in all the more specialized mammals the number of toes is reduced in some, as the carnivores, to four, in some hoofed animals to three (rhinoceros), in some to two, as in ruminants, and in the horse to one. The palm bones in ruminants are reduced to one (canon

bone) and in the horse also to one, but with two rudiments of others (splints). But in all cases we can trace all the steps of gradation. This is well shown in ruminants. In the deer, besides the two functional toes, there are two rudiments—hoofed and supplied with bones—but useless; in the cow these are further reduced to mere wartlike rudiments; in the goat and sheep they disappear entirely.

6. We need hardly call attention to the extreme modification of the hand in the bird's wing, of the whole fore limb in the whale and in the mole, and especially in this last to the elongation of the point of the elbow to increase its power of digging (Fig. 162, B) and to the still more extreme modification in the case of the pectoral fin of fishes, and the enormous elongation of one finger of the hand in the extinct flying reptile—the pterosaurs of the Mesozoic (Fig. 161, D).

It is well to observe, too, how the same part may be differently modified for the same function. This is well illustrated by the different devices used for flight in birds, in mammals (bat), and in reptiles (pterodactyls). In the bird the hand is *shortened* and consolidated, and the flat plane is formed by the addition of quill feathers. In the bat the hand is *elongated*, and a web is stretched between the greatly lengthened palm bones and fingers, leaving only one finger, the thumb, free and clawed. In the flying reptile one finger is enormously elongated and strengthened, and the web is stretched from the point of this to the hind limb, leaving the three other fingers free and clawed. It is a most significant fact, however, that these several devices are not accomplished at once, but by a gradual process through successive generations. In the earliest bird (the *Archæopteryx*) (Fig. 161, C) of the Jurassic the finger bones are not consolidated nor feathered, but are all four free and clawed.

(*b*) **Hind Limbs.**—The hind limbs are less specialized than the fore limbs. We have therefore contented ourselves with illustrations from mammals alone, as these are the most specialized of vertebrates (Fig. 163, A, B, C, D, E). We have again drawn dotted lines through

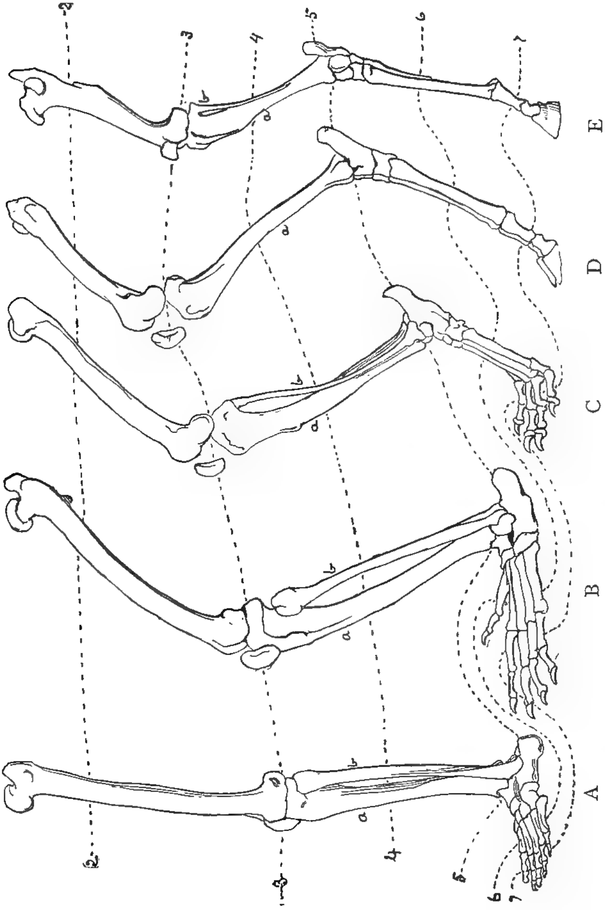

FIG. 163.—A, Hind limb of man; B, monkey; C, dog; D, sheep; E, horse.

the important corresponding parts. We draw special attention to the following points:

1. *Hip Girdle.*—This is particularly strong in all bipeds, and therefore in man, in birds, in kangaroos, and in the extinct biped reptiles (dinosaurs). The hip girdles are not represented in the figure.

2. *Position of the Knee.*—In man, in monkeys, and bears among mammals, and in all reptiles and amphibians, the whole hind limb is free of the body and the knee is halfway down the limb. This is undoubtedly the original and normal condition in land vertebrates; but in the more specialized mammals, such as carnivores and herbivores, especially the ungulates or hoofed animals, the knee is high up on the side of the body, in the middle of the *so-called thigh*, and the limb is free of the body only from the knee down.

3. *Position of the Heel.*—In man, in monkeys, in the bear, and several other mammals, and in all reptiles and amphibians, the tread is on the whole foot—i. e., *heel down*. This is undoubtedly the original and normal tread of the primal land vertebrate. But in all the more specialized mammals the heel is lifted high in the air—in the horse fifteen to eighteen inches above ground—and the tread is on the toes only. Therefore land vertebrates, as to their tread, may be divided into two groups, viz., *plantigrade* and *digitigrade*. Man, monkeys, bears, and some other mammals, and all reptiles and amphibians, are plantigrade, but all the more specialized and swifter mammals and all birds are digitigrade—tread only on their *toes*.

Again, in mammals there are two degrees of digitigradeness. The carnivores and all other clawed digitigrades and all birds tread on the whole length of the toes to the ball, while the hoofed mammals (ungulates) tread only on the tip of the last joint of the toes. The one treads tiptoe, the other on the *tip* of the *toe.* These may be called unguligrade. This becomes the more striking when, as in the horse, the tread is on the tip of the last joint of the *one* toe. We look with wonder and delight at the *danseuse* pirouetting on the tip of one toe. The horse is doing this all the time.

4. *Manus and Pes.*—There are two senses in which we may use the term *foot.* (1) We may use it as that part on which the animal treads. This is the functional or analogical sense. Or (2) we may use it as that part which corresponds to the foot of man, monkey, bear, reptile—*the original foot.* This is the morphological or homological sense. It is in this latter sense that we use it in comparative anatomy. In this sense the horse's foot is eighteen inches long, and the hand of the largest flying dragon (*Pteranodon ingens*) was fully seven or eight feet long (Fig. 164). In order, however, not to violate too flagrantly common usage, comparative anatomists use the Latin terms *manus* and *pes* to signify all that corresponds to the hand and foot of man and plantigrade animals.

FIG. 164.—Restoration of Rhamphorhynchus phyllurus (after Marsh). One seventh natural size.

5. *Classification of Ungulates by Foot Structure.*—The ungulates or hoofed animals are divided by foot struc-

ture into two groups, viz., *artiodactyle* or even-toed, and *perissodactyle* or odd-toed. The artiodactyles may have four toes, as in the hippopotamus and the hog, or two toes, as in ruminants. The perissodactyles may have three toes, as in the rhinoceros and tapir, or one toe only, as in the horse and zebra. Both of these groups have come from a five-toed ancestor by successive dropping of toes. There is also a regular order in the dropping. In the five-toed ancestor the two groups were not yet differentiated. The first toe to drop was the thumb, leaving the remaining four toes all functional, as in the hippopotamus. Then, if evolution is on the artiodactyle line, the two side toes gradually dwindle and shorten up, as in the hog, and finally disappear, as in ruminants, leaving only two greatly enlarged toes, which correspond to the middle and ring fingers of man. But if, on the other hand, the animal is on the perissodactyle line, then, of the four toes, the little finger first dwindles, as in the fore foot of the tapir, and then disappears, leaving *three.* Now, of these three, the side toes dwindle and shorten up and finally disappear, leaving only the greatly enlarged middle toe, as in the horse.

6. *Rudimentary Organs ; Useless Organs.*—All through the animal kingdom, especially in the more specialized forms of mammals, we find rudimentary and often wholly useless organs. These are evidently remnants of once useful organs, which have dwindled by disuse, but have not yet entirely disappeared. Examples meet us on every side. (*a*) The horse's toes are reduced to one, but not at once. It was a gradual process, every step of which may be traced. The first representative of the horse in the line of its descent had five toes on the fore foot, then, in later times, four, then three. Three-toed horses continued a long time, the two side toes meanwhile dwindling and shortening up and finally passing away.

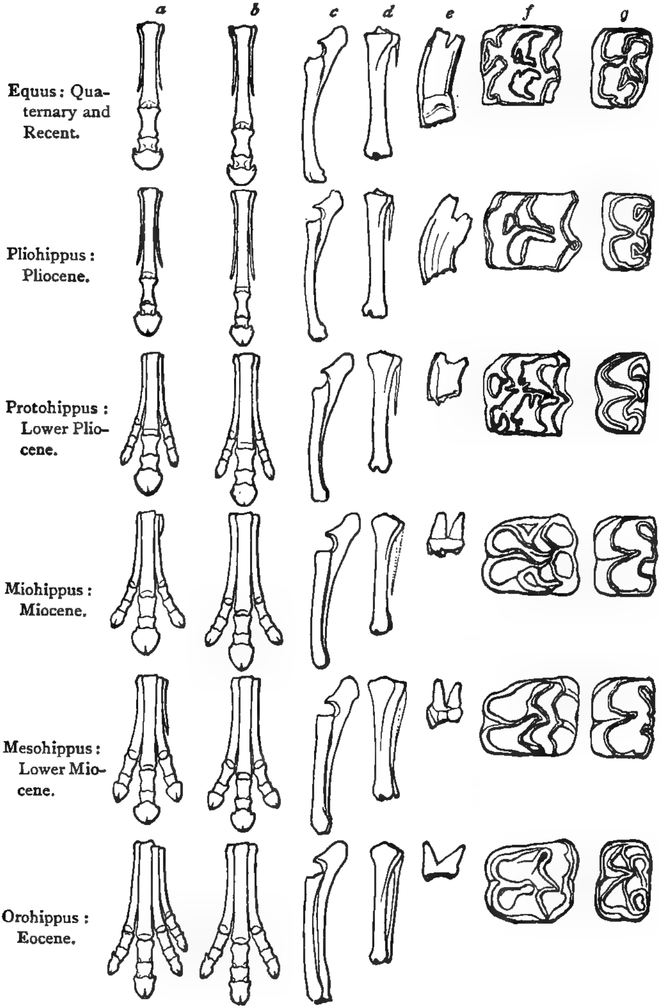

FIG. 165.—Diagram illustrating gradual changes in the horse family: Throughout *a* is fore foot; *b*, hind foot; *c*, forearm; *d*, shank; *e*, molar on side view; *f* and *g*, grinding surface of upper and lower molars. (After Marsh.)

But the two palm bones to which they were attached still remain as useless splints to attest the original three-toed condition. These and other changes are shown in diagram, Fig. 165. (*b*) In ruminants the toes are reduced to two, but we have already shown (page 253) that useless remnants of the other two are still found in most ruminants, showing their original four-toed condition. (*c*) Dewclaws in the dog and many other mammals reveal an original five-toed condition. (*d*) The whale is a very specialized mammal, and therefore full of useless remnants. Whales have no hair, but rudiments of hair in the skin show that their ancestors were hairy. They have no hind limbs, but rudiments are found buried in the flesh, and therefore useless. The baleen whales have no teeth, but rudiments of teeth are found buried in the jawbone, and are never cut. (*e*) We have already said (page 249) that snakes have lost their limbs by disuse. This is true, for rudiments of limbs are found buried in the flesh of some (the python), and, of course, useless. (*f*) Even in man, although he is far less specialized than most mammals, rudiments are found. Among these may be mentioned the muscles for moving the ears and for moving the scalp. Rudiments must be regarded as demonstrative proof of the derivative origin of organic forms.

Whole Skeleton.—We have taken only the limbs as best illustrating the principle, but the same is true of the whole skeleton. The skeleton, as a whole, is in all vertebrates the same machine, but modified in all its parts to adapt it for various purposes—viz., as a swimming machine, a walking and running machine, or a flying machine, and all without essential change of plan.

Other Systems.—The whole argument for derivative origin of organic forms is based on the equal balance of the two ideas—essential identity and adaptive modification. If the modification be too great, the essential identity and derivative origin of parts may be obscured or even obliterated. If, on the other hand, it be too small, then the identity may have come in some other way than by common origin—may have been made out of hand at once. Now, this equal balance is found in the skeleton, and especially in the limbs. In the *muscular system* the adaptive modification is too extreme; it obscures the derivative origin. In the case of the *visceral system*, on the contrary, there is scarcely enough modification to make any evidence. Next to the skeletal, the best evidences are found in the *nervous system*. Here the essential identity of parts in all vertebrates, and yet their modification in each class, is very striking, especially in the brain. We have already explained this (pages 76–78). In the case of the muscular system the modification in passing from the fish to the land vertebrates is so extreme that all hope of homology seems vain. But in land vertebrates, from the amphibia (frogs, etc.) to man, it may probably be traced by careful study, but this has not been attempted, except in a fragmentary way. Undoubtedly a rich field is open here.

III. SERIAL HOMOLOGY.

There is an evident correspondence in the several parts of the fore and hind limbs. The hip girdle corresponds with the shoulder girdle, and bone for bone, although the parts are more consolidated in the former; the femur corresponds to the humerus; the two bones of the leg to the two bones of the forearm, each to each; the seven bones of the ankle to the eight bones of the wrist, two of the former having been consolidated into one; the five bones of the instep (metatarsal) to the five bones of the palm (metacarpal) and the fourteen bones of the toes to the fourteen bones of the fingers. This introduces us to the idea of a *serial repetition* of similar parts—i. e., of *serial homology*. In general terms as applied to the whole skeleton, it may be stated thus: As the whole vertebrate kingdom is made up of a repetition of *individuals* constructed on the same plan, but modified according to the place and function in the vertebrate scale, so each individual vertebrate is made up of a repetition of *segments*, similar in plan but modified according to its place and function in the series of segments. This is, of course, best brought out in the skeleton.

Take any vertebrate, such as a fish or a man. Make a cross section of the body and look at the end. What we see is shown diagrammatically in Fig. 166. The section of the skeleton consists of three parts—centrum, *c*, an arch above (neural arch, *n*) surrounding nervous centers, and an arch below (visceral arch, *v*) surrounding the visceral cavity. The whole is enveloped in muscle and skin, with which we have no concern now. The three parts named above constitute one segment of the skeletal axis, and may be called a *vertebra*. Now the whole skeletal axis may be regarded as made up of a repetition of such skeletal segments or vertebræ modified according to place and function in the series (Fig. 167). The centrums repeated form the vertebral column, the neural arches repeated constitute the neural canal, in which are lodged the nervous centers, and the visceral arches repeated make the visceral cavity. But these segments are modified according to the place in

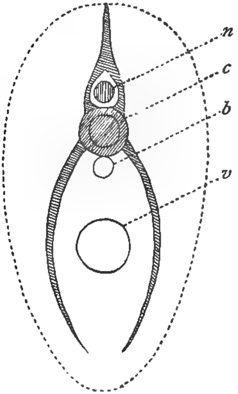

FIG. 166.—Cross section through a fish: *v*, visceral system; *c*, vertebra; *b*, blood system; *n*, nervous system.

the series, sometimes by enlargement, sometimes by diminution and even disappearance, sometimes by consolidation of several together. But throughout these modifications the essential identity, although obscured, is still discernible.

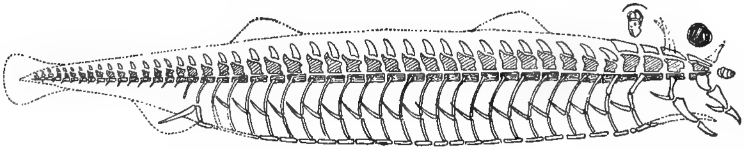

FIG. 167.—Owen's archetypal vertebrate, showing the successive segments but slightly modified. The olfactory capsule, the eye, and the ear are represented detached.

For example: In the dorsal region of the higher vertebrates the visceral arches are greatly enlarged to contain the thoracic viscera. Going forward, in the neck region in *man* and most vertebrates the visceral arches are wanting in order to give greater freedom of motion, but not in *all* vertebrates, nor in all stages of development. Ribs are borne by all the vertebræ up to the head in fishes, in serpents, and also in the embryos of mammals, and even of man. Going still forward, according to one view, the head is composed of several vertebræ consolidated and greatly modified (see Fig. 167). According to this view, the basilar portions of the occipital and sphenoid, and the ethmoid are the centrums of three successive vertebræ, the neural arches of which, greatly enlarged, form the skull, while the diminished and much modified visceral arches make up the face. There is, however, some doubt whether the vertebral theory of the skull is true in this strict sense; and, if so, of how many vertebræ it consists.

Going now backward, in the lumbar region, again, the ribs are wanting in man and mammals, but not in fishes, nor in serpents, nor in tailed amphibians, nor in the embryos of mammals, nor even in the embryo of man. So that their absence is only an extreme term of modification, all the steps of which may be found. Going still back, the sacrum may be regarded as five to six vertebræ with their bodies—neural arches and visceral arches—all consolidated. Indeed they are distinct, and have their ribs in many lower vertebrates and in the embryos of mammals and man.*

Signification of Limbs.—It will be observed that in this scheme we have left out the limbs. This seems a very great omission, but this is so only in the higher vertebrates. The primal vertebrates were probably limbless. And in all the earliest vertebrates and in the lowest vertebrates to-day limbs are comparatively insignificant appendages, which may be left out in any general scheme of skeletal structure. It is probable that limbs *can not* be brought into the original plan of homologous segments, but have been added afterward as a sort of afterthought.

Origin of Limbs.—Professor Owen † thought to bring limbs into this scheme of repeated segments by making them appendages to the visceral arches, and this view is expressed in his figure of the archetypal vertebrate (Fig. 167), where small appendages are seen on every arch. He believed that the shoulder girdle and hip girdle were formed by consolidation of several visceral arches, and that the limbs were greatly enlarged appendages to these arches, the appendages to the other arches being still rudimentary or wanting. But this view, though very suggestive, is not now generally

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* Cervical, lumbar, and sacral ribs are found in the embryo of mammals and of man. Wiedersheim, p. 51.

† Owen, "Homologies of Vertebrate Skeletons" and "Signification of Limbs."

accepted. The more probable view is that the same fold of the skin which formed the lower unpaired fin (anal fin) divided as it came forward into two *lateral* folds (Fig. 168, A), that these by local enlargements became the paired fins, anterior and posterior (Fig. 168, B), and by addition of skeletal framework were developed into limbs (Fig. 168, C) and finally became connected with the skeletal axis for more effective action. The subject is, however, still obscure.

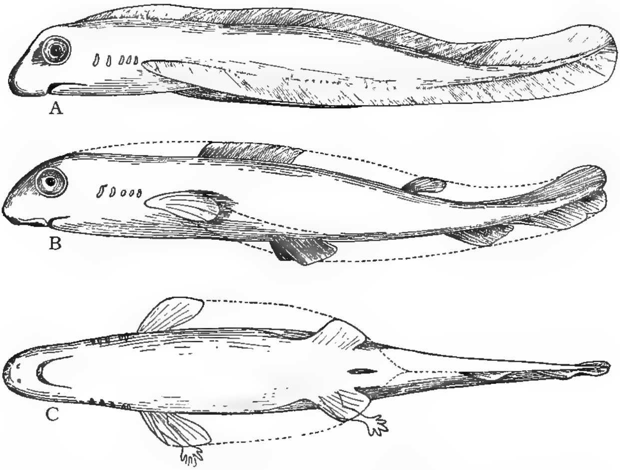

FIG. 168.—Diagrams showing probable origin of limbs: A, earliest stage, showing lateral folds; B, later stage, after paired fins were formed (from Wiedersheim); C, the formation of limbs from fins (from Parker).

Serial Homology of Other Systems.—Other systems show segmented structure, but not so clearly. Next to the skeletal in this regard comes the *nervous system*. Thus we may conceive the cerebro-spinal axis as a series of ganglia (fused, however, into a continuous tract) corresponding to the vertebræ, and giving off each a pair of nerves; and, according to the vertebral theory of the head, the successive lobes of the brain (cerebellum, optic lobes, cerebrum, and olfactory lobes) correspond to the successive cranial vertebræ.

The *muscular system* shows segmentation in a marked degree in fishes and some lizards. The flakes of a fish's flesh correspond to the vertebræ, and we have here literally body segments (*somites*). See also the so-called glass snake—really a limbless lizard. Under a sharp blow the tail breaks into segments right through between scales, flesh flakes, and vertebræ.

In the visceral system the segmentation is not discernible.

As a general law, the number of segments and their similarity is greater as we go down the scale of vertebrates, and, contrarily, as we go up the scale adaptive modification obscures more and more the homology.

SECTION III.

Invertebrates.

1. ARTICULATA.

Under *Articulata* we include arthropods and annelids or worms (see schedule, page 71), because, from the homological point of view (though not from any other), they are best united. What we propose to prove is that the structure of all these animals is exactly such as it would be if they all came by descent, with modifications, from one primal articulate animal; and, therefore, that we must conclude that they did all so come.

General Plan.—The general plan of structure is the same throughout, but wholly different from that of vertebrates. 1. The skeleton is *external*, instead of internal. 2. The nervous system lies along the ventral, instead of the dorsal, aspect of the body. 3. The body consists of *one* cavity, instead of two.

Of these two positions of the skeleton, which is best? For motion and locomotion they are probably equally good; but the external skeleton has the great advantage of being protective as well as locomotive, while the internal skeleton has the much greater advantage of leaving the surface sensitive to external impressions, and therefore an inlet to knowledge of external nature, and thus gives greater capacity for higher development.

So much for the general plan. Now the details of the homology.

Serial Homology.—In the case of vertebrates we took up first special homology, because this is by far the most distinct. In the case of *Articulata* we take up *only* serial homology, because not only is this the most distinct, but it includes the other also; for we may regard each articulate animal as consisting of a series of segments essentially similar, but modified according to its place and function in the series, and then the structure thus formed is again modified according to the place in

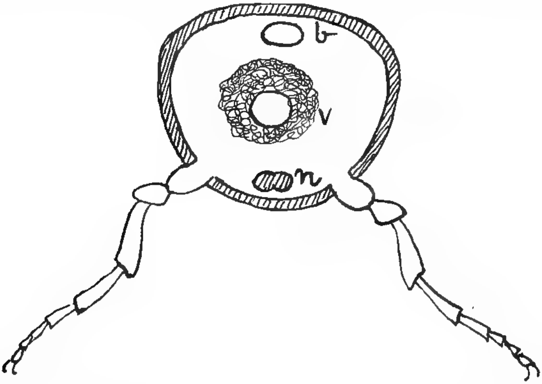

FIG. 169.—Diagram section across an arthropod, showing the inclosing skeleton ring and a pair of jointed appendages: *n*, nervous center; *v*, viscera; *b*, blood system.

the scale of *Articulata*, to make the infinite variety of forms constituting this department of animals.

Our object, then, is to show that the skeleton of an arthropod consists of naught else than a *series of similar* segments, modified according to the place and function in the series.

Take any articulate animal, say an arthropod, like an insect or crustacean. Make a cross section and view it on end (Fig. 169). We see an external bony ring inclosing everything, and attached to it a pair of jointed appendages, right and left. Now, the whole skeleton is made up of such rings and appendages, repeated and modified. The repetition of the rings gives rise to a hollow, many-jointed cylinder or barrel, and the repetition of the appendages to a continuous row of such on each side. Each ring, with its pair of appendages, is called a *somite*, or body segment. Such is the simple *idea* or archetype of an articulate animal; but, in fact, these ideal rings and appendages are very variously modified for function. Some are modified for swimming appendages, some for walking appendages or limbs, some as food-gathering appendages (jawfeet), some as biting appendages (jaws), some as sense appendages (eyes, ears, feelers), but all made on the same plan, only modified. The manner of modification is sometimes by enlargement, sometimes by diminution and even disappearance, sometimes by coalescence and consolidation of several into one piece.

For example, take one from about the middle of the scale—say, a crawfish or a lobster. This animal consists of about twenty-one rings and pairs of appendages (Fig. 170). In the tail region or abdomen the seven rings are all separate and but little modified, but their jointed appendages are greatly modified for swimming, D'; those of the last joint but one are enlarged and flattened, and, together with the flattened *last* joint, which

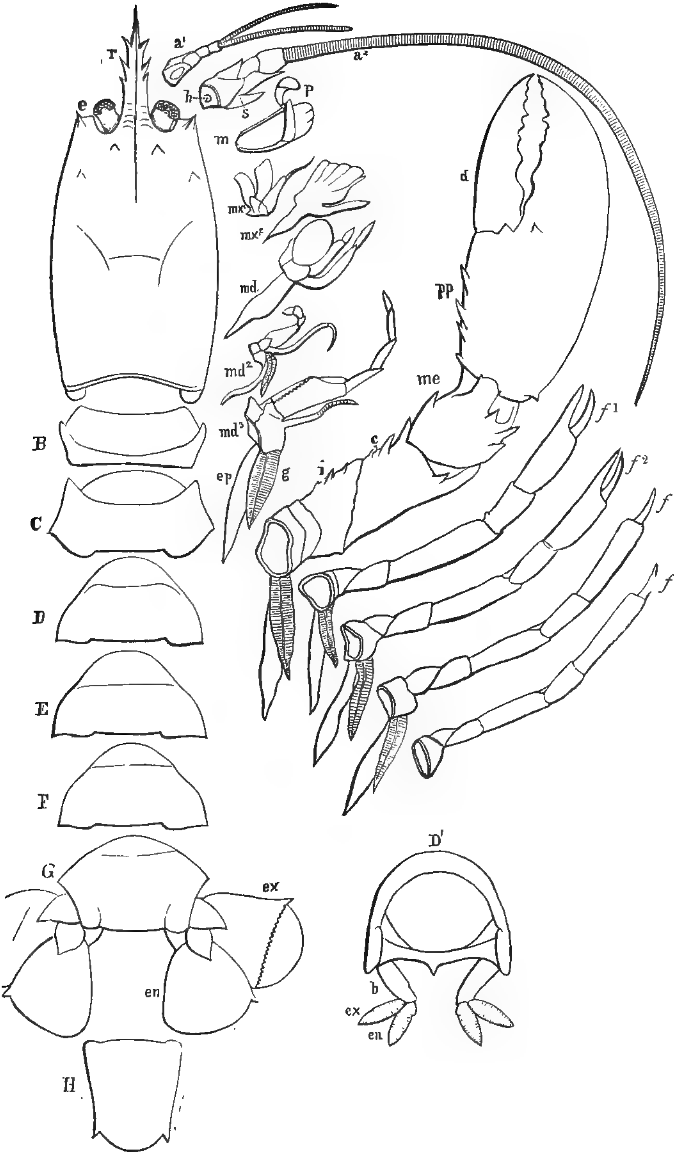

FIG. 170.—External anatomy of the lobster. (After Kingsley.)

is without appendages, form the powerful flipper at the end of the tail for backward darting. Going thence forward, we come to the cephalothorax. Here many joints in their dorsal parts are consolidated into a carapace, and their ringed structure is lost, but their entire distinctness is evident in the lower crustaceans and in the embryos of the higher. But observe that it is only the dorsal parts that are consolidated. In the ventral parts the separate rings are distinct, and each has its own pair of jointed appendages greatly enlarged for *walking*, p, f^1, f^2, f^3, f^4. These are the five pairs of limbs. Going still forward, we find next three or four pairs modified for the gathering of food. These are called *maxillipeds*, or jawfeet, md, md^2, md^3 The modification is not so great but that their resemblance to the limbs is obvious. Next come two or three pairs more modified, so as to adapt them for biting. These are the *maxillæ*, or *jaws*, mx. Next come two pairs of highly modified, greatly elongated, and many-jointed appendages, which are organs of touch and hearing. They are sense appendages. Lastly, a pair of jointed appendages, on the ends of which are placed the *eyes*. Some

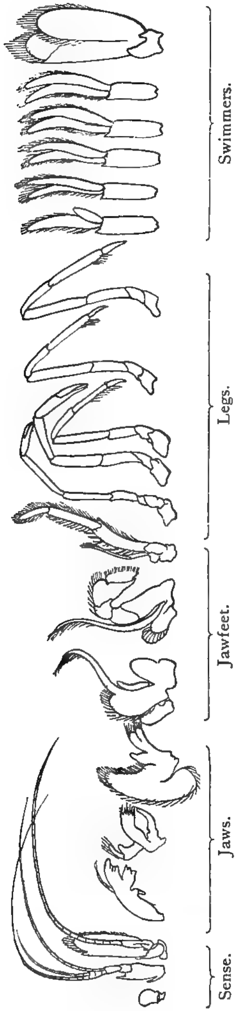

FIG. 171.—Appendages of a prawn. (After Cuvier.)

doubt whether these belong to the same category as the other appendages, but they are usually so regarded. In Fig. 171 we give the whole series of appendages in the crawfish:

The crab is much more modified, and the consolidation more complete. The tail seems to be absent, but is really only diminished in size and bent under and concealed beneath the body; but in the embryo the tail is similar to that of the crawfish (Fig. 172). The maxillipeds and sense appendages are also much reduced in size, but they are all present.

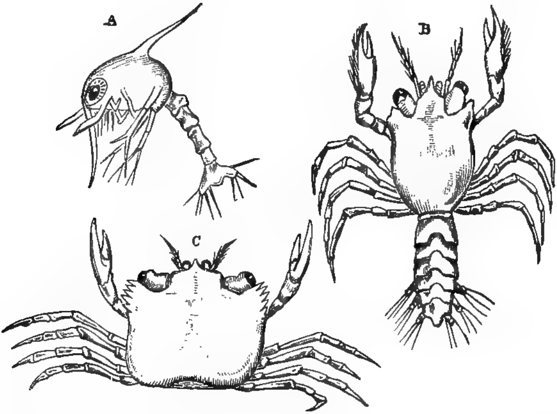

FIG. 172.—Development of Carcinus mœnas: A, zoæa stage; B, megalopa stage; C, final state. (After Couch.)

Going down the Scale.—We have taken a case from about the middle of the articulate scale, because there the essential identity and adaptive modification are evenly balanced and both conspicuous. But the evidence is completed by going down and up the scale. In the lower crustaceans the rings are all separate and the appendages less and less modified (Fig. 173). A series of appendages of a still lower form is given in Fig. 174. In this case the appendages are too much alike to be easily classified. Often, too—e. g., in the *Limulus*—the appendages which in the higher crustaceans are walking appendages become swimmers, while the maxillipeds become walkers. Finally, in the lowest crustaceans and, still better, in the centipede and in some marine worms, the rings and appendages are greatly increased in number, and are so similar that there is not modification enough to furnish argument for homology. There is only a slight modification of the head and tail joints (see Fig. 175). Indeed, some marine worms multiply by self-division. In such cases at the point of division some of the rings are consolidated and appendages modified to form a *new head* and a new tail (Fig. 176).

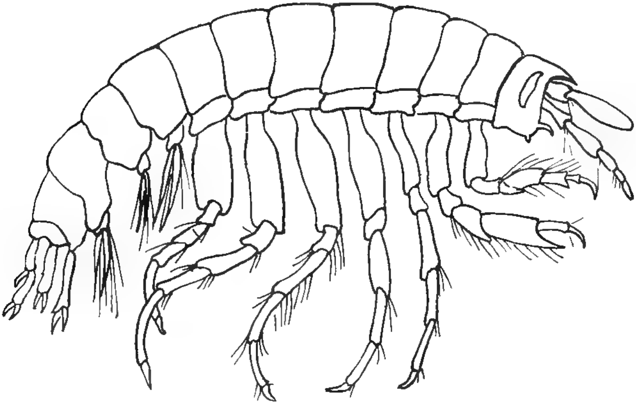

FIG. 173.—Vibilia, an amphibod crustacean. (After Milne Edwards.)

Going up the Scale.—Going up the scale to insects the modification is greater, but the elements—viz., rings and appendages—are the same. An insect consists ideally of about sixteen or seventeen segments and appendages (Fig. 177). In the abdomen the rings are perfect and movable, although the appendages are wanting; but they are present in the larval or caterpillar state. The thorax is a consolidation of three rings, each with its pair of appendages greatly enlarged for walking (legs). The head consists of three or four consolidated segments with appendages much modified—the first pair into antennæ, the second pair into mandibles, and the third pair into maxillæ and maxillary appendages or feelers, and the fourth pair into labium and labial appendages.

Origin of Insects' Wings.—The wings of insects are not homologous with legs or other appendages. There is some doubt as to their origin, but it is most probable that they are modifications of the trachi-branchiæ of the larvæ of aquatic forms. If so, insects sprang from aquatic species.

That insects are higher than crustaceans is shown by the *distinctness of the head.* The ring-series in crustaceans are grouped into two regions, the abdomen and the cephalothorax, the head being undistinguishable from the thorax. The same is true of spiders and scorpions. But in insects we have three distinct groups—the head, the thorax, and the abdomen. A distinct movable head is always a sign of the dominance of head functions.

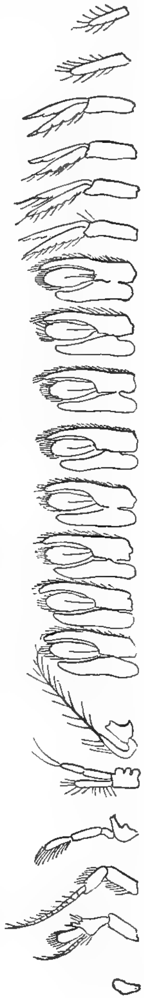

FIG. 174.—Appendages of Nebalia.

The higher position of insects is further shown by the number of their legs or appendages used for locomotion. It is a law in biology that a great number of parts, similar in form and function (vegetative repetition), indicates a low position in the scale of organisms. As we go up the scale the number of parts used for one function becomes less, and their efficiency becomes correspondingly greater. Legs are an admirable illustration of this law. In marine worms and in the lowest crustacea there is an indefinite but very great number of similar legs. As we rise among crustacea the number becomes definite, and countable as legs, when there are fourteen or seven pairs. These are called tetradecapods. In the higher crustacea—crabs, crawfish, etc.—they are reduced to five pairs. These are therefore called *decapods*. In spiders and scorpions there are only four pairs. These might be called *octopod insects*. In true insects they are reduced to three

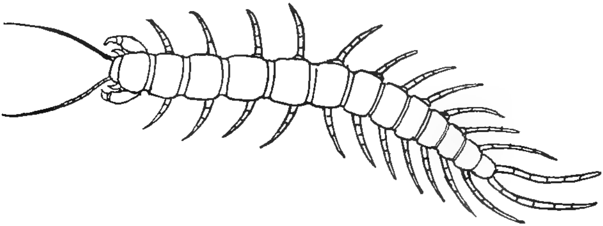

FIG. 175.—Lithobius forcipatus. (After Carpenter.)

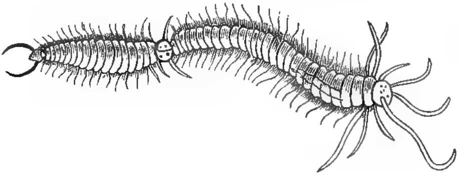

FIG. 176.—Syllis prolifera.

pairs, and these are called *hexapods*. If it be allowable to pass from one department to another, we might go

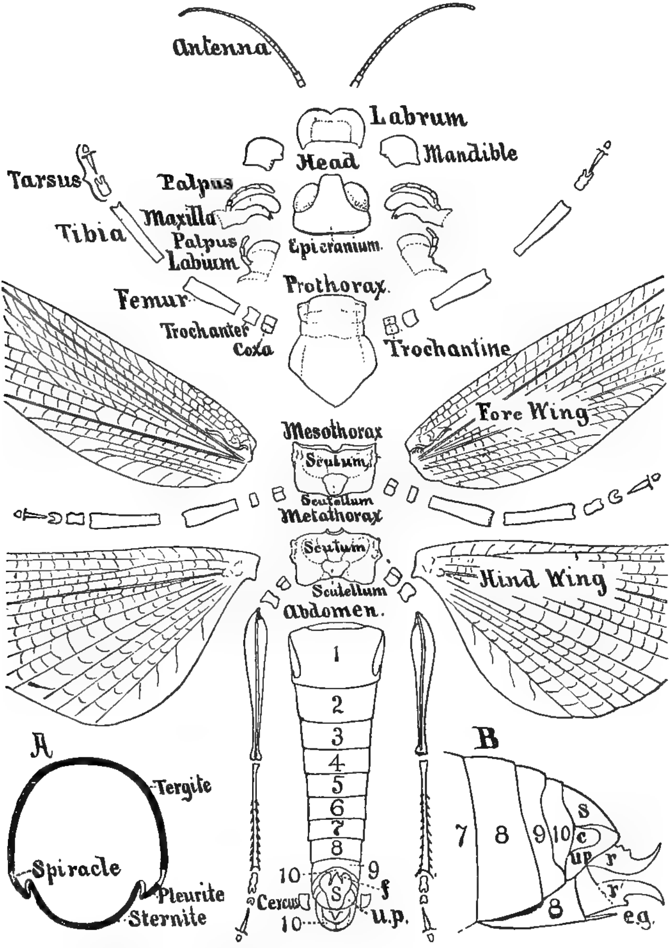

FIG. 177.—External anatomy of Caloptenus spretus, the head and thorax disjointed : *up*, uropatagium ; *f*, furcula ; *c*, cercus. (Drawn by J. T. Kingsley.)

on and say that in vertebrates the limbs are reduced to two pairs, and these are therefore *quadrupeds.* This is as far as reduction can go *for highest* locomotive efficiency on land. In birds locomotive efficiency on land is sacrificed for flight; and in man it is sacrificed for efficiency of another and still higher kind, and the reduction goes on to one pair, the other pair common to vertebrates being set free for higher uses as wings and hands.

Law of Differentiation.—We have already seen (page 23) that cells, commencing in the lowest animals and in the earliest embryonic condition, all alike, and performing each all the functions of life but very imperfectly, as we rise in the scale become differentiated in form and specialized in function, each doing its own work and doing it much better. So now we find the same law in the segments. In the earliest geological times, and in the lowest animals now, we find all the segments alike and performing similar functions, but imperfectly. But as we go up the scale the segments and their appendages are more and more differentiated in form and function, and by this division of labor the functions are better performed. The same law may be carried still a step further. Regarding a whole department, such as the vertebrata or articulata, as composed of a repetition of organisms made on the same plan; then in early geological times there was doubtless far more similarity than now. In the process of evolution these somewhat similar organisms were differentiated, each kind for its own place in the economy of Nature, and specially fitted for that place through the survival of the fittest. This law of differentiation, therefore, is the most fundamental and all-pervasive law of evolution.

Nervous System.—We have confined ourselves thus far to the skeletal system. Next to this, as illustrating serial repetition, would come the nervous system. Ideally the nervous system of articulata consists of a series of ganglia, one to each somite or body segment and presiding over that segment, but sympathetically connected by a continuous thread with one another, and all with the cephalic ganglion. But as we pass up the scale, modification and consolidation, differentiation and specialization, proceed *pari passu*, as already shown on page 87.

2. MOLLUSCA.

Here, again, we find an entirely different general plan of structure. In vertebrates we have an *internal* skeleton, the axis of which consists of segments modified according to place and function. In articulates we have an *external* skeleton still more obviously segmented and modified. In mollusca alone, among all the great departments, we have *no segmentation*, no serial repetition of ideally similar parts. This want of repeated segments is its most distinctive peculiarity. In mollusca, also, we have no true—i. e., locomotive—skeleton at all, either internal or external, but only a protective shell.

General Character.—The general characters of this type are mostly negative: 1. A want of a true locomotive skeleton. 2. A complete want of segmentation of any system. 3. The presence of a soft, mucous, sensitive surface wherever not covered with shell.

The most important of these is the complete absence of segmentation. It follows from this that there can be no serial homology. There is, of course, a special homology—i. e., a homology of part with part in different orders and classes of mollusks, but it is obscure and little studied. I shall not attempt its exposition.

Why there is no Segmentation in this Type.—It is seen that homology, especially serial homology, is mostly limited to the skeleton and nervous system—i. e., to the organs concerned with the distinctive *animal life*. Animal life and activity has to do specially with action and reaction between the animal and its environment. The limbs especially take hold on the environment and are modified by it. The vegetative organs, on the contrary, are little affected by the environment. Segmented structure is peculiarly adapted for diversified modification, showing homology. Now, in articulates the distinctive animal functions are very highly developed in proportion to the vegetative, and these are therefore the most perfectly segmented of all animals. In mollusks, on the contrary, the vegetative functions are very highly developed in proportion to the distinctively animal, and these do not lend themselves readily to homology. The vertebrates seem in this regard to combine the characters of both.

3. RADIATA.

In these, including echinoderms and cœlenterates, we again find an entirely different type of structure. We find, indeed, segmentation again, but of an entirely different kind. All these animals have an essentially *radiated* structure. Like the plugs of an orange arranged about the central pith, or like the spokes and fellies of a wheel about the central hub, so are the several segments of a radiated animal symmetrically arranged about its central mouth and stomach, and all the organs of the body are repeated in each segment. Thus, in a starfish, for example, the mouth and the stomach are in the center and surrounded by the nerve centers (œsophageal collar) and by the blood centers. From this center go to each arm or segment a branch of the stomach, a branch of the nervous system from a corresponding ganglion of the collar, and a great branch of the blood system. Each arm contains also its own *equal* part of the respiratory system and the reproductive system. The radial arrangement of the nervous system is shown in Fig 67, page 92. The other systems will be illustrated hereafter.

Comparison of this with Other Types.—Comparing this with other types, in both vertebrates and articulates we have segments repeated in a *linear series*, and therefore an *anterior* and *posterior* extremity; but in this we have segments repeated in a *circular* series, and therefore no beginning and no end, no anterior and no posterior extremity. Again, in all other types, including mollusca, we have all the organs, especially those of animal life, repeated on the two sides of a median plane —i. e., *bilateral symmetry;* in this one we have repetition of organs about a central column—i. e., *radial symmetry.* In the highest radiates alone are found the distinct beginnings of a bilateral symmetry.

In this also, as in the other two segmented types, the completeness of the segmentation, the number of repeated parts, and their similarity are greatest in the lower part of the scale; and as we rise the segments become more and more dissimilar by modification for various functions. But the obscuration by modification is less conspicuous in this type, because, taken as a whole, the animals of this are less highly organized.

4. PROTOZOA.

Among these, of course, there is as yet no distinct plan of structure (for they consist of a single cell), and structure such as we have been speaking of is produced by differentiation of the elements of a *cell aggregate.* These lowest animals may be regarded as the living stuff out of which the different types were constructed—the trunk from which diverged the four great branches (Fig. 158, page 248). There is no room for homology here.

GENERAL CONCLUSIONS.

The general conclusions of this chapter may be briefly summarized in several propositions.

1. There are at least four very distinct plans of structure among animals through which homology may be more or less clearly traced, but beyond which it can not be distinctly traced, although it doubtless exists. These are the vertebrata, articulata, mollusca, and radiata. The characteristic plan of vertebrates is that of an internal skeleton, the axis of which consists of segments ideally similar, but modified according to the place and function in the series of segments. The animal thus formed is again modified according to its place in the scale of vertebrates.

The characteristic plan of the articulata is that of an *external* skeleton, composed of segments and pairs of appendages, ideally similar, but modified according to the place in the series. The animal thus formed is again modified according to its place in the scale of articulata.

The characteristic plan of the mollusca is the total want of a true locomotive skeleton, and especially the entire absence of segmentation. There is therefore no room for serial homology. Even special homology is more obscure in this than in other departments. Nevertheless, there is enough to assure us that these also came by modification from some primal form of mollusk.

The characteristic plan of radiata is that of similar segments arranged symmetrically about a central mouth and stomach. In vertebrates and articulates we have segments repeated in a *linear* series; in radiates in a *circular* series. In all other types we have *bilateral* symmetry; in this we have *radial* symmetry.

2. In all plans the ideal similarity of the repeated parts in the animal and of the repeated animals in the department is clearest in the lower part of the scale, and adaptive modification for function becomes more conspicuous as we rise, until finally the essential identity may be wholly obscured by adaptive modification. This is the law of progressive differentiation so universal in Nature.

3. All these phenomena may be completely explained by the origin of organic forms by *derivation*—i. e., by "descent with modifications"; in a word, by the theory of evolution, and can not be explained in any other way.

PART II.

ORGANS AND FUNCTIONS OF ORGANIC LIFE.

We have explained (page 24) that all the functions of the animal body fall into two groups—one, distinctive of animals, and therefore called the functions of animal life; the other, possessed in common with plants, and called functions of vegetative or organic life. We have now treated of the distinctively animal functions. We come now to treat of the functions of organic life and their organs.

These are again subdivided into two very distinct groups—viz., the nutritive and the reproductive—the one including all that assemblage of functions which contribute to the conservation of the individual life; the other, all that assemblage of functions which insures the continuance of the species. We reproduce here, with slight addition, the schedule already used on page 24:

- Animal body
  - Functions of animal life..
    - Sensation and consciousness.
    - Volition and voluntary motion.
  - Functions of vegetative life
    - Nutritive
      - Nutrition proper.
      - Elimination.
    - Reproductive

CHAPTER I.

NUTRITIVE FUNCTIONS—METABOLISM, OR WASTE AND SUPPLY.

COEXTENSIVE with life and lying at the very basis of all life phenomena is a continuous change by waste and supply of the material of which the body is composed. This whole process of change is called *metabolism*, or transformation. It is not only coextensive with life, but it may be said to be life itself. It consists necessarily of two parts—viz., an *ascensive* change, by which new tissue is formed from crude material, and a *descensive* change, by which old tissue is decomposed and eliminated from the body. The former is called *anabolism*, the latter *katabolism*, or *waste*. This latter is apparently the active, initiative agent of the whole process.

Waste.—The process of waste is so fundamental that it must be thoroughly illustrated.

1. Suppose, then, we had a pair of scales of enormous size, and one of you (hearers or readers) were lying in a comfortable position in one pan and a weight for perfect counterpoise in the other. I shall suppose you at perfect rest physically and peace mentally, and, as contributing to this condition, perhaps smoking a cigar. The equilibrium would not continue indefinitely; if the scales were delicate, not even for a minute. On the contrary, even while we watch the experiment, your side of the

scale goes up. The body is *consuming* like the cigar—literally burning up and passing away as invisible gas through the nostrils. Probably about two pounds is thus consumed in twenty-four hours. This process of waste is more rapid in higher than in lower animals. It is continuous with life and in proportion to its grade. This may be expressed by the formula:

$$1.\ \textit{Waste} \propto \textit{Life}.$$

2. We have taken the case of absolute rest of body and mind. But suppose next that the subject of this experiment is in violent activity, physical, mental, or moral, perhaps dancing a hornpipe, perhaps wrestling with a mathematical problem, perhaps in intense anxiety, remorse, or grief. Under these conditions the wasting, as measured by pounds, is more rapid. This is expressed by formula 2:

$$2.\ \textit{Waste} \propto \textit{Work}.$$

3. We will next suppose the subject to be inclosed in a large *calorimeter*, or instrument for measuring *heat* by melting of ice. In such case there would be a constant stream of water from the instrument, indicating a constant evolution of heat generated by the combustion of waste. Furthermore, the formation of water, and therefore the generation of heat, would be in proportion to the grade of life and the amount of activity. All this is expressed by formula 3:

$$3.\ \textit{Heat} \propto \textit{Waste} \propto \textit{Life} \propto \textit{Work}.$$

4. *Supply.*—Now it is evident that this can not go on continuously without a contrary process, otherwise the body would completely consume itself and exhale in smoke, like the cigar. There must be a *supply exactly proportioned to the waste.* It is this that creates the necessity for *food.* Food, therefore, must be proportioned to

waste, and therefore to grade of life and intensity of work. This is expressed in formula 4:

4. *Food* $\propto$ *Waste* $\propto$ *Life and Work.*

Therefore life in a scale pan would show a continual oscillation of level—i. e., of weight of body. In adults, whose supply is only equal to waste, the average weight is maintained; in a child the supply is a little greater than the waste, and the average weight increases.

Observe that the most fundamental of these two opposite processes is the *waste*. This is continuous with life and apparently its cause; the other (supply) is occasional. The waste goes on continuously, whether there be supply or not, as long as life lasts. The supply may be regarded as a secondary consequence of the waste.

Illustrations.—1. Thus the living animal body may be compared to a burning lamp—ever consuming and ever resupplied. In both cases there is waste and supply, and in both cases there is continual oscillation of weight. In both cases heat is produced by the consumption of material. Moreover, the amount of heat produced by the burning of a pound of material is substantially the same in the two cases, only in the one case the heat is concentrated on a given point and compressed into a short time, and is therefore intense, while in the other it is spread over the whole body and stretched over twenty-four hours, and is therefore less intense at one time and place.

2. Again, the living body may be compared to a temple on which are constantly engaged two opposite forces—the one tearing down, the other repairing; the one *de*structive, the other *con*structive; the more rapid the destruction, the more active the construction. These two go on with varying success until at last the de-

structive forces prevail and the struggle terminates in death.

3. Or, again, the living body may be compared to a *pool*, with its *inlet* and *outlet.* The form remains the same, but the matter is continually changing. The more rapid the change, the quicker and fresher is the water.

Waste Removal.—It is seen, then, that one necessity arising from waste is food. But there is another and far more urgent necessity—viz., the *quick removal of waste* from the body. The reason is that the waste is *poisonous* to the blood. Food-taking may be delayed for a day or several days, or even perhaps for forty days; but waste removal, suspended for five to ten minutes, destroys life.

For the removal of waste there are two main pipes—viz., the *lungs* and the *kidneys.* In the one case the removal is by *combustion*, in the other by *solution.* In the one the final product is gaseous, in the other liquid. By far the largest amount—seven eighths of the whole * —is removed by the lungs, and the urgency of this removal is also the greatest. Stop the removal by the lungs, and death occurs in five minutes; stop the elimination by the kidneys, and death occurs by blood poisoning in about forty-eight hours.

Thus, to summarize, there are going on continually in the living body two opposite processes—the one gathering and *constructive*, the other *destructive* and removing; the one *ascensive* from *food* to *tissue*, the other *descensive* from *tissue* to *waste* removed. The one is called *anabolism*, the other *katabolism.* The one is *nutrition* proper, the other is *decomposition* and elimination. The latter—i. e., katabolism—is that which is most closely connected with life; it is that which starts the whole process, that

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* Berthelot, Rev. Sci., viii, 134, 1897.

which *generates life force itself.* Even the force necessary for anabolism seems to be generated by katabolism. The truth of this proposition we are not yet prepared to prove, but will do so hereafter.

The whole subject of the nutritive functions—i. e., all the functions concerned in the conservation of the life and health of the individual—divides itself naturally into three parts, viz., *ascensive*, *distributive*, and *descensive.* The first is anabolic, the second intermediate, and the third katobolic. The first includes all the processes from crude food to finished tissue; the third, all the processes from perfect tissue through all its changes by decomposition to final elimination from the body as waste; the second, or intermediate, all the processes whereby food is distributed to all parts of the body and also all waste is distributed, each kind to its appropriate organ of elimination. Briefly, they may be called food preparation, food and waste distribution, and waste removal. Each is concerned with a distinct system of organs—the first with the *digestive system*, the second with the *blood system*, and the third with the *excretory system.*

CHAPTER II.

NUTRITION PROPER—ANABOLISM—FOOD PREPARATION—DIGESTIVE SYSTEM.

THIS includes all the changes from crude *food* to finished *tissue.*

SECTION I.

Food: its Kinds and Uses.

Definition.—The word food is used in a wider and a narrower sense. In the wider sense it includes all substances the ingestion of which is necessary to life. In this sense it includes water and air and many salts. In a narrower sense it means such substances as are used for *tissue building* and for *force making*. It is in the narrow sense that we shall use it here.

Kinds.—In this sense there are three kinds of food, viz., *albuminoids*, *amyloids*, and *fats*. The first are composed of C, H, O, N, and sometimes a little P and S, and are therefore called quaternary compounds, or often nitrogenous compounds; the second, of C, H, and O, the two latter in proportions forming water, and are therefore called *carbohydrates;* and the third, also of C, H, and O, but the C in excess and the O in deficit. The last two are called ternary compounds. Examples of the first are found in *albumen* (white of egg), *fibrin* (lean meat), *gluten* of wheat and other grains, *legumin* of peas, beans, etc., and *protoplasm*, or living substance of animals and plants. Examples of the second are the sugars and starches, and of the third all the animal and vegetable fats and oils. The following schedule expresses most of these facts:

Name.		Composition.	Examples.
Food	Albuminoids	C, H, O, N, etc., Quaternary	Fibrin, albumen, protein, gluten, protoplasm.
	Amyloids....	C, H, O, Ternary	Starches and sugars
	Fats........	$\overset{+}{C}$, H, $\overset{-}{O}$, Ternary	Fats and oils.

Milk.—The material prepared by Nature as the food of the young of mammals must contain all these. Albuminoids are represented by the *casein*, or curd; amyloids, by the milk-sugar; and fats by the butter.

Uses of Food.—The uses of food are twofold, viz., (1) for tissue-building—i. e., repair of waste in the adult and repair and growth in the young; (2) for *force and heat making* by combustion, or, we may say briefly, *tissue* food and *fuel* food. This is expressed by schedule:

Food	Tissue........	Repair. Growth.
	Fuel..........	Force. Heat.

We say fuel for force and *heat*, but the real object in the animal body, as in the steam engine, is *force*, although, in both, heat is a necessary concomitant. In the case of the body it is sometimes an indifferent concomitant, as in a moderate temperature; sometimes a very comfortable concomitant, as in cold weather; and sometimes a distressing concomitant, as in very hot weather. We will explain this more fully hereafter.

Distinctive Uses of the Kinds.—The albuminoids are used mainly for tissue-building, and they *alone* can be used for this purpose, for the tissues are themselves albuminoid. But whatever of albuminoids is left over from tissue-building is used for fuel also—i. e., for force and heat making. The amyloids and fats can be used only for force and heat, for these do not contain the nitrogen necessary for the formation of tissue. Thus an animal fed on amyloids and fats alone can not continue to live indefinitely for want of the necessary repair of the tissues. This is called *nitrogen starvation.* Therefore tissue-making can be done only by albuminoids, but force and heat making by all three kinds.

ILLUSTRATIONS.—*Carnivores* fed on lean meats consume only albuminoids. They use first whatever is necessary for repair of tissues, and whatever is left over is burned for force and heat. *Herbivores* take albuminoids in, relatively, small quantity; their food is mostly amyloids. They probably use the whole of their albuminoids for repair, and their amyloids for force and heat. *Man* is an *omnivore*, but, except the livers on rice or potatoes, he probably takes more albuminoid than is necessary for repair. What is left over, which we shall call albuminoid *excess*, he uses for force and heat. All the amyloids and fats are used for the latter purpose.

Waste Tissue.—But the waste is not *wasted.* This also is burned as fuel. But since in the adult the *waste* is exactly equal to the *repair*, it is evident that the equivalent of the whole * albuminoid food is burned as fuel for force. But since amyloid and fats are also burned, it is evident that the equivalent of the whole food is burned for force and heat.

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* Except an incombustible part, as explained hereafter.

PREPARATION OF FOOD.

Food must be *prepared* before it can be absorbed into the blood, because it is nearly always solid and must be reduced to a liquid condition before it can be taken up—it must be able to *soak** through membranes. The food of plants is already dissolved, as gases in the air bathing the leaves, or as liquids bathing the roots. It is therefore absorbed at once without further preparation. It is already prepared by Nature. But in animals there must be a reservoir in which the solid food is stored and dissolved. This reservoir is the *stomach*, and the process of solution is *digestion*. But if we compare the lower with the higher animals, we find, in accordance with the law of differentiation, a gradually increasing complexity in the process. In the lowest protozoa—amœba—the living protoplasm flows around the prey, dissolves, and appropriates it at once into the tissues. The captured prey passes at *one step* from crude food to living tissue, but the tissue thus summarily made is a *poor article*. In the highest animals, on the contrary, this simple process is differentiated into many consecutive processes, and the finished article of tissue is far more perfect. In man and the higher animals the steps are:

	Mechanical process.	Chemical process.
1. Mouth digestion............	Insalivation.	Saccharization.
2. Stomach digestion..........	Chymification.	Peptonization.
3. Intestinal digestion.........	Chylification.	Emulsification.
4. Absorption	By capillaries and lacteals.	
5. Sanguification..............	By liver and mesenteric glands.	
6. Circulation............		
7. Assimilation		

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* We say *soak*, but it is necessary to remember that absorption is not a purely *physical* process, for it is *selective*.

Our plan will be to take up each of these and carry the process through the vertebrates; and then in the invertebrates to take up the whole process together in each department.

SECTION II.

Mouth Digestion in Vertebrates.

This includes the gathering (prehension), the mastication, and the insalivation of food. Prehension in man, monkeys, and some other mammals is done by the hands or paws. In some, as the elephant, by the snout, but in most vertebrates directly by the teeth. The object of *mastication* is trituration of the food for more perfect insalivation, and is done by the teeth. We shall have much to say about this process in connection with the comparative morphology of the teeth and physiology of mouth digestion. For the present we dwell only on the process of *insalivation* and its effect on digestion of the food.

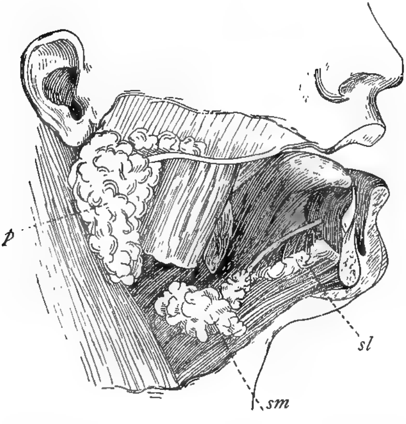

FIG. 178.—Lower jaw on right side and some adjacent parts cut away so as to show the salivary glands: *p*, parotid; *sm*, submaxillary; *sl*, sublingual. (After Cleland.)

Salivary Glands.—There are three pairs of these, viz., the *parotids*, *p* (Fig. 178), on the side of the face just below and a little in front of the ear; the *submax-*

illaries, *sm*, just within the angle of the lower jaw on each side; and the *sublinguals*, *sl*, just behind the chin on each side. Every gland has its excretory duct. That of the parotids runs forward and opens into the mouth between the cheek and the upper jaw teeth on each side; that of the submaxillaries runs upward and opens on each side of the back part of the tongue; while that of the sublingual opens on each side of the frenum near the tip of the tongue.

Structure.—Imagine a slender tube the size of a knitting needle branching and rebranching to capillary fineness, each capillary branch terminating in a saccule, the whole, even to the minutest branch and saccule, lined with a pavement of living nucleated cells, an extension of the epithelium which lines the mouth cavity, then the whole system of tubes webbed together by loose connective tissue and invested with a membrane of fibrous, or condensed connective tissue, and we have a tolerably good general idea of the structure of a salivary gland, which may indeed be taken as a type of a

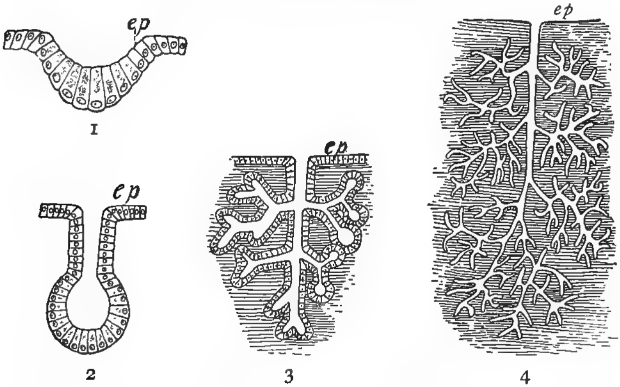

FIG. 179.—Structure of a gland: 1, 2, 3, 4, different stages in the process of infolding of the epithelial surface, *ep*; 4, fully formed gland.

secreting gland. It is evidently only a device to bring as large a surface as possible of epithelial cells into a small space; for the secretion is a product of epithelial action. Fig. 179 shows the different stages of infolding.

Excitant.—Any stimulation of the tongue and interior of the mouth, even mechanical, will excite the secretion, but especially any strong taste. Even the sight of food or the idea of food will often cause it to flow. The first effect of excitement is the rush of blood to the gland, and then follows a flow of secretion. Evidently the secretion is manufactured out of materials in the blood. This preliminary rush of blood and consequent swelling of the gland is the cause of the pain produced by food or even the sight of food in *mumps*, which is a disease of the parotid gland.

Composition and Use of Saliva.—It is easy to collect the salivary secretion in considerable quantity, and thus to determine its composition. In a horse the duct of the parotid gland runs just beneath the skin over the broad, flat surface of the jaw and may be easily taken up, a metallic tube introduced and turned outward. If, now, food be given, or even a sheaf of hay be shown, immediately the liquid secretion begins to pour from the tube, and continues to pour as long as the food is masticated. In this way half a pint or a pint of the clear liquid may be collected.

Saliva is a watery liquid, consisting mainly of mucus (water and broken-down epithelial cells), but containing a peculiar ferment called *ptyalin*, which is its active principle ; its composition and its chemical properties seem to be identical with *diastase* of sprouting seeds. Like diastase, it changes the insoluble forms of amyloids (starch) into the soluble forms (sugar). It does so by hydration of the starch.

$$\overset{\text{Starch.}}{C_6H_{10}O_5} + \overset{\text{Water.}}{H_2O} = \overset{\text{Sugar (glucose).}}{C_6H_{12}O_6}$$

Its function, then, is the digestion of amyloids. This, of course, takes time. Starches, therefore, are dissolved in the stomach, although the digestive juice is made in the mouth. Ptyalin is far more important in herbivores than in carnivores.

Ferments.—Ferments are of two general kinds—viz., those, like yeast, that contain living microbes which determine decomposition in the fermenting substance, and those, like diastase, that contain no microbes and determine change, but not decomposition. All the digestive ferments are of this latter kind. They are called *enzymes.*

After mastication and thorough insalivation the food is gathered into a bolus, pressed by the tongue into the throat, and *swallowed*—i. e., it is there seized by the involuntary muscles and hurried into the stomach. There we leave it for the present to take up the

COMPARATIVE PHYSIOLOGY OF MOUTH DIGESTION IN VERTEBRATES.

The chemical process of saccharization is precisely the same in all vertebrates and probably in all animals. The only important variation is in the mechanical processes of food-taking and *mastication*, especially the latter. This brings us to the important subject of

Teeth in Vertebrates.—We take up this somewhat fully on account of its important bearing on *classification*, especially of mammals. The character of the teeth is determined by the food, and the nature of the food determines the habits, and therefore the whole structure of the animal. All the parts of an animal are in harmonic relation with one another. The keynote of this complex harmony is the *teeth*. Next to the teeth, foot structure is most important in classification.

Mammalian Teeth.—1. *Origin and Development.*—In speaking of the skeleton we said (page 224) that teeth do not belong to the true internal skeleton, but are an

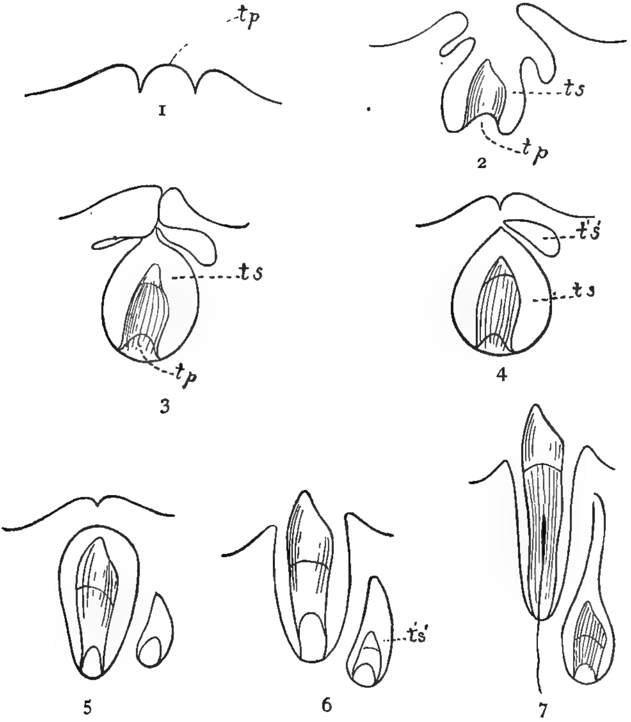

FIG. 180.—1, 2, 3, 4, 5, 6, 7, showing successive stages in the development of a human incisor: *tp*, tooth pulp; *ts*, tooth sac.

epidermal structure, or, more specifically, an epithelial, a gum structure. The evidence of this is found in their embryonic development. The following figures (Fig.

180, 1, 2, 3, etc.) show the embryonic development of teeth in man. The same process is true of all mammals.

At first there is a little papilla on the gum, which is the pulp of the future tooth (1). Then this is sunk more and more into the gum, to become the future socket (2). Then the pulp begins to secrete the tooth, and the socket closes up above, forming the tooth (sac 3, 4, and 5), and the tooth is now entirely inclosed in the gum and in the jawbone. Then by continued growth it breaks through the jaw and the gum and the tooth is *cut*, and thence continues to grow to its full size (6 and 7). But some teeth—milk teeth—are shed and replaced by permanent. Are these also gum structures? Yes. It is seen that the tooth sac has a saccule on each side. One of these continues to develop, and a tooth is formed in it. This grows, and finally pushes out the first tooth and takes its place (5, 6, 7). In some rare cases the other saccule also forms a tooth, which may develop. It is in this way that we account for those rare cases of a third set of teeth. But what is exceptional in man is the rule in many reptiles and in sharks, as we shall see hereafter.

2. *Composition of Teeth.*—Mammalian teeth consist usually of three kinds of substance—viz., *dentine*, *enamel*, and *cement*. The dentine is a denser kind of bone, already described, and forms the principal part; the enamel is a still denser variety, and covers the crown or exposed part; and the whole is covered and the inequalities filled up with cement, which is a more structureless variety than either. The cement is almost wanting in many teeth, as man's, and in such cases is quickly worn off and disappears, but is an important part of the more specialized teeth of many mammals.

3. *Kinds of Teeth.*—There are four kinds of teeth in the jaws of mammals—viz., (1) the incisors, or front

teeth, (2) the canines (tusks of carnivores, eye teeth of man), (3) *premolars*, or deciduous molars or bicuspids of man, and (4) the permanent or *true molars.* The function of the first is the *cutting* off of morsels of food, of the second is *seizing* and *holding* the prey. The jaw teeth —i. e., the molars and premolars—are the true *masticating* teeth. This grouping of the teeth into kinds having different functions is very characteristic of *mammals.*

4. *Variation of the Teeth.*—The teeth of different orders and families of mammals vary in relative *size* and relative *number* of *the kinds*, and in the *structure* of the *molars.*

(*a*) *Relative Size.*—In man all the teeth are of similar size, forming thus a continuous *even arch;* but in the more specialized mammals some of the teeth may be enormously developed—for example, the canines in carnivores, and especially the walrus; the incisors in rodents, and especially in proboscidians (elephants). In cases of enormous development, such as the incisors of rodents and the tusks of the walrus, the boar, and the elephant, the pulp is *permanent*, and the tooth grows continuously. Such teeth have a hollow at the base. Thus, teeth are sometimes of *definite* and sometimes of *indefinite growth.*

(*b*) *Number of Teeth and Relative Number of the Kinds.* —The normal number of mammalian teeth seems to be forty-four, and any less number must be regarded as the result of gradual loss; precisely as in the case of toes of less number than the normal five. But the whole number, and especially the relative number of the several kinds, vary in a way which is very characteristic of the different *orders* and *families* of mammals. This introduces the subject of the *dental formula*, which is a compendious way of expressing the number of different kinds of teeth in mammals, very necessary in description of mammals, and therefore universally used by naturalists. A number of these are given below:

Type	i, $\frac{3-3}{3-3}$;	c., $\frac{1-1}{1-1}$;	pm., $\frac{4-4}{4-4}$;	m., $\frac{3-3}{3-3}$	= 44.
Man...............	i., $\frac{2-2}{2-2}$;	c., $\frac{1-1}{1-1}$;	pm., $\frac{2-2}{2-2}$;	m., $\frac{3-3}{3-3}$	= 32.
Bear...............	i., $\frac{3}{3}$;	c., $\frac{1}{1}$;	pm., $\frac{4}{4}$;	m., $\frac{3}{2}$	= 42.
Cat................	i., $\frac{3}{3}$;	c., $\frac{1}{1}$;	pm., $\frac{3}{2}$;	m., $\frac{1}{1}$	= 30.
Ruminant	i., $\frac{0}{3}$;	c., $\frac{0}{1}$;	pm., $\frac{3}{3}$;	m., $\frac{3}{3}$	= 32.
Rodent.............	i., $\frac{2}{1}$;	c., $\frac{0}{0}$;	pm., $\frac{3}{2}$;	m., $\frac{3}{3}$	= 28.
Sloth..............	i., $\frac{0}{0}$;	c., $\frac{1}{1}$;	....	m., $\frac{4}{3}$	= 18.
Ant-eater..........	i., $\frac{0}{0}$;	c., $\frac{0}{0}$;	..... $\frac{0}{0}$	..... $\frac{0}{0}$	= 0.
Ornithorhynchus	....	....	....	....	0.

To explain: In the type mammal, probably in all the early Tertiary mammals and in the most generalized mammals, like the hog *now* (Fig. 183), there are forty-four teeth in all, of which twelve are incisors—i. e., three on each side above and below, i. $= \frac{3-3}{3-3}$; four are canines—i. e., one on each side above and below, c. $= \frac{1-1}{1-1}$; sixteen are premolars—i. e., four on each side above and below, pm. $= \frac{4-4}{4-4}$; and twelve are molars—i. e., three on each side above and below, m. $= \frac{3-3}{3-3}$. But, as the bilateral symmetry is always perfect in the teeth, there is no necessity to express but one side—i. e., all the teeth as seen from one side, as in all the formulæ, except the first two.

The normal number, we have said, is forty-four.

This was probably the number in the early Tertiary mammals; any less number is the result of gradual abortion. Thus ruminants have no front teeth in the upper jaw, but the rudiments of these buried in the jawbone unborn show that they came from animals having a full set. The same is true, as already explained (page 260), of whales, and also of edentates, etc.

(*c*) *Structure of Molars.*—Molars are the *masticatory* teeth, and are therefore, more than all others, subject to variation according to the character of the food. In this regard there are three main kinds, viz., *omnivorous*, *carnivorous*, and *herbivorous*. Omnivorous molars are simply tuberculated, and are equally adapted to all kinds of food, but not specially and perfectly adapted to any one kind. Such are the teeth of man, of monkeys, of bears, and the hog (Figs. 181, 182, 183).

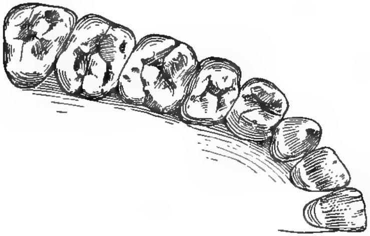

FIG. 181.—View of teeth of the right side of the upper jaw of man.

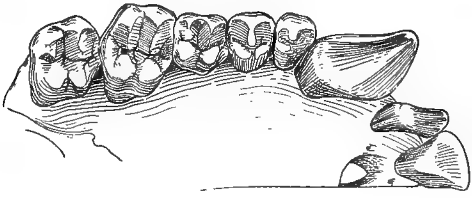

FIG. 182.—Teeth of the right side of the upper jaw of a monkey.

Carnivorous molars are specially adapted for flesh eating. They only *crush* and divide the food sufficiently for swallowing, but do not grind or triturate it. This is not necessary, because thorough insalivation is not required for flesh-food (Fig. 184).

Herbivorous molars are by far the most specialized and complex, because their food requires the most complete trituration and insalivation (Fig. 185).

Undoubtedly the primal mammal was omnivorous and had simple tuberculated molars. From this generalized form, as time went on, mammals were specialized in two main directions—the one more and more adapted to flesh eating, the other to herb eating. The extreme forms are represented now by the cat tribe on the one hand and the ruminants on the other. In the meanwhile

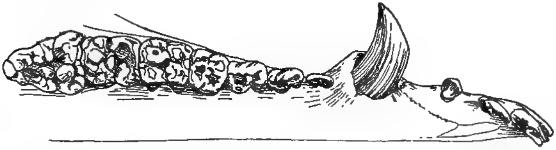

FIG. 183.—Teeth of the right side of the upper jaw of a hog.

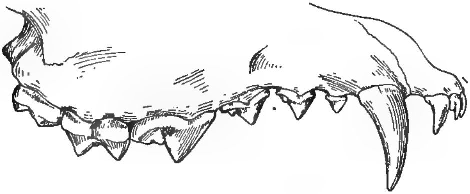

FIG. 184.—Side view of the upper jaw of a dog.

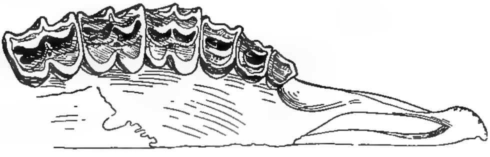

FIG. 185.—Face view of the upper jaw of a sheep.

an intermediate type continued in a more generalized form, including *man*. The diagram shows these facts:

Carnivorous.
Omnivorous . . . Monkey, man, etc.
Herbivorous.

Structure of Herbivorous Molars.—The most interesting examples of masticatory teeth are found in herbivores. In these we have veritable upper and nether millstones. Fig. 186 is a face view of a molar of a horse. The double lines are enamel, the shaded spaces dentine, and the unshaded cement. On account of its greater hardness, the enamel stands out as ridges above the softer dentine and cement, and continues to do so however much the tooth wears.

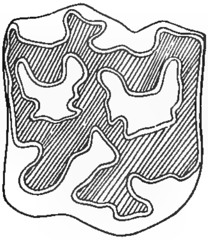

Fig. 186.—Grinding face of a horse's molar.

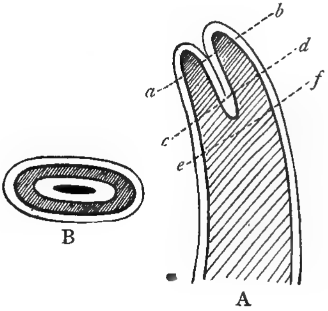

Fig. 187.—Incisor of a horse: A, vertical; B, cross section.

Origin of this Structure.—The dentine is secreted by the tooth pulp, the enamel by the membranes of the tooth sac. Therefore the tooth sac must have followed the enamel in all its windings. The complexity of structure is therefore the result of *infoldings* of the sac on the side and *down-dippings* of the same from above. The cement is afterward formed on the outside, and, as it were, poured over all, filling up the inequalities. A simple case of the down-dipping is seen in the front teeth of the horse. In this case the down-dipping (Fig. 187, A) determines on cross section a concentric arrangement of the enamel and cement (Fig. 187, B), which successively disappear as, by use, the tooth wears to lower and lower level (*a b*, *c d*, *e f*), first the cement, and then the enamel, until only the dentine remains. These changes occur first in the middle front teeth, and then in the side teeth. On this fact is founded the mode of estimating the age of horses by the teeth.

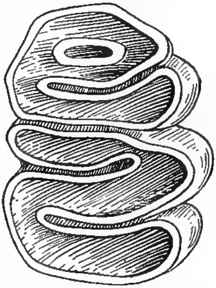

FIG. 188.—The grinding face of a molar of a paca (*Cœlogenys*) of South America, enlarged.

In the horse and cow the arrangement of the enamel plates among the dentine and cement is adapted for *side-to-side* grinding, but some mammals have *fore-and-aft* grinding. In these the enamel plates are *transverse.* This is well seen in rodents (Fig. 188), and especially in the elephant. The molar of an

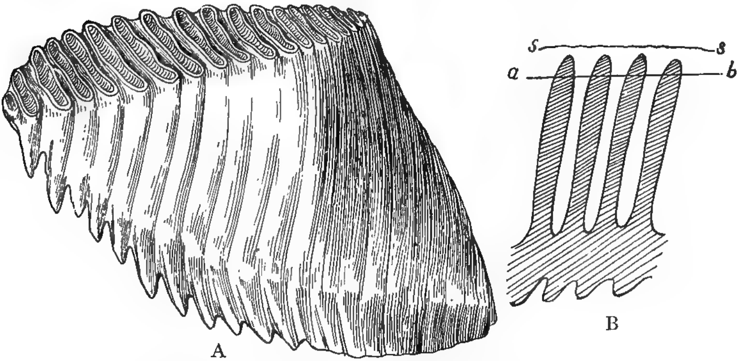

FIG. 189.—Elephant's molar: A, showing side and grinding face; B, section showing the plates; *s s*, original surface; *a b*, worn to a face as in A.

elephant is the most efficient fore-and-aft grinder imaginable. The whole tooth, as seen (Fig. 189), is composed of narrow transverse islands of dentine, surrounded by ridges or plates of enamel separated by cement. The section shows how this has been formed. Imagine a mass of dentine from which spring many thin plates of the same, each plate sheathed with enamel, and then cement poured over the whole, and finally the tooth subjected to wear.

Mouth Armature of Whales.—Many cetaceans—e. g., the sperm whales, porpoises, etc.—have teeth, but these are conical, prehensile, not masticatory, teeth. But the baleen (whalebone) whales have no teeth, but in their stead have the most efficient food-taking apparatus known. These animals have enormous heads (nearly half the whole body), fifteen to twenty feet long and ten to fifteen feet deep, and nearly the whole of this great head is mouth. This huge cavern is largely occupied with whalebone plates (Fig. 190).

Fig. 190.—Head of a whale: A, side view; B, section.

These horny plates, hundreds in number, are attached above to the roof of the mouth, hang down, and are split up into fibers at their edges, so that the open mouth is like a moss-roofed cavern. The hollow space beneath is filled up by the enormous tongue.

Mode of Feeding.—The baleen whales feed on squids, cuttlefish, medusæ, and small crustaceans, which exist in enormous numbers in arctic seas, usually near the surface. The whale rushes forward at great speed with mouth open, so the water pours like a torrent into the mouth and out at the sides between the plates. All the surface animals are caught on the mossy roof and sides. When a sufficient quantity is gathered the mouth is closed, the superfluous water is spouted through the blowhole (nostril), and the prey is swept up by the tongue and swallowed.

Homology of Baleen Plates.—These plates are a substitute for, not a modification of, teeth. They are therefore analogous, but not homologous with teeth. As already explained, these whales have rudiments of teeth, which are never cut. What, then, are the plates homologous with? They are probably extreme modifications of *gum ridges*—such, e. g., as those found on the mouth-roof of a horse. If each of such ridges produced a downward growth of horny tissue we should have something like the baleen plates of the whale.

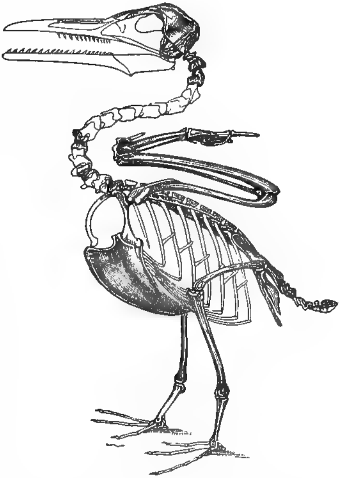
FIG. 191.—Ichthyornis victor, × ¼. (Restored by Marsh.)

Birds.—Existing birds have no teeth, yet in the embryo of some birds rudimentary teeth are found which are never developed. This is, of course, strong presumptive evidence that birds once had teeth, but they have gradually dwindled and passed away, because another apparatus —viz., a horny beak—was used in its place. This presumption is confirmed by the finding of Jurassic and Cretaceous birds with the mouth full of teeth—true *socketed* teeth (Fig. 191). These, however, were conical, prehensile, not masticatory teeth.

Reptiles.—There is great variety among reptiles in this regard. This was to be expected, for they are the ancestors of both birds and mammals. Some, as the turtles, have no teeth, but, like birds, a horny, nipping beak in their place. Some, like serpents, have teeth not only in the jaws, but on other bones of the mouth, as, e. g., the palatal. But in all reptiles which have teeth these are conical, prehensile, and not masticatory teeth. Also, with the exception of crocodilians, the teeth are not socketed. They are formed in a fold of the gum, and afterward fixed to, but not sunk into and inclosed by the jawbone. Among extinct reptiles socketed teeth were more common. In serpents the teeth all point backward. This is necessary in swallowing large prey, which, by a peculiar movableness of the bones of the head, are thus dragged by main force down the throat.

Fangs of Serpents.—These are worthy of brief notice as an example of admirable adaptive modification. *First*, observe that the canal in the tooth which conveys the poison does not go to the end, for that would interfere with the keenness of the point, but comes out a little short of the extreme end. The same device is used in the subcutaneous injector of the surgeon. Observe, *second*, that the formation of the poison canal is not in violation of the ordinary structure of teeth, but a curious modification of it. It is not along the tooth cavity, but is really *outside* of the tooth. Fig. 192, *a*, represents a section of a flat tooth. Suppose such a tooth bent upward (*b* and *c*) until the edges meet above and are soldered; *pt* is the poison tube. That this peculiar structure was gradually formed is shown by the fact that all the steps of the process may be found among living serpents — viz., teeth slightly grooved, deeply grooved, and tubulated. All degrees of virulence of the poison may be found. The poison gland is probably an extreme modification of a salivary gland, and the poison of saliva. The saliva is slightly poisonous in many animals.

Observe again, *third*, that the fang is formed in a fold in the gum, and at first loose, but afterward fixed to the jawbone. Also that in the fold there are many subordinate folds, in each of which

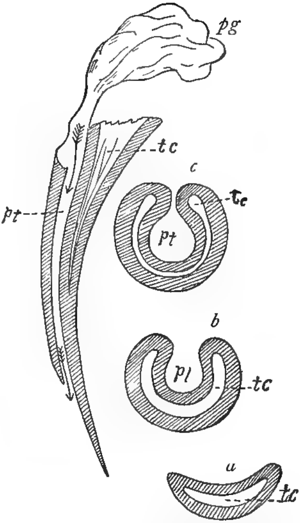

FIG. 192.—A longitudinal section of the fang of a serpent: the cross sections show mode of formation of the poison tube; *pt*, poison tube; *tc*, tooth cavity; *pg*, poison gland.

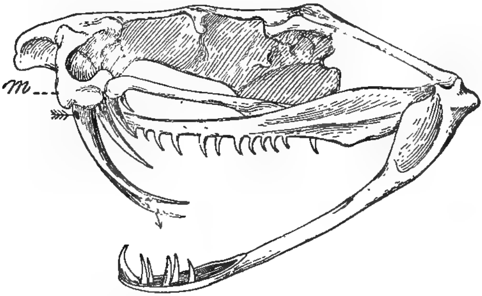

FIG. 193.—Head of a rattlesnake, showing several fangs in different stages of development. The arrow shows the poison tube; *m*, maxillary bone.

is formed a tooth, and thus there is a magazine of teeth of all sizes, which are successively brought forward and attached as the old tooth drops off (Fig. 193).

Origin of Mammalian Teeth.—A characteristic of mammalian teeth is that they are differentiated into three groups, distinct in form and in function, viz., *incisors* for cutting, *canines* for seizing, and *molars* and *premolars* for masticating. The complex structure of these last is especially significant. Now in some early extinct reptiles of the Permian and Triassic periods, immediately before the appearance of mammals, the teeth were already differentiated into the three groups, and the jaw teeth were already become molariform (Fig. 194). Indeed, a complete series may be traced from the simple conical prehensile teeth of ordinary reptiles to the most complex grinders of ruminants. It is certain, therefore, that mammalian teeth have come by gradual modification from simple prehensile teeth of reptiles.

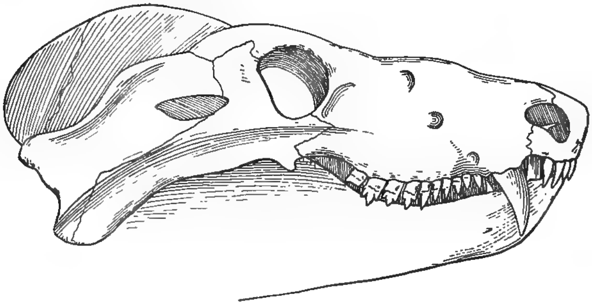

FIG. 194.—Head of Cynognathus, a Triassic reptile, showing teeth similar to those of mammals. (From Woodward.)

Fishes.—The teeth of fishes are of three kinds—viz., *conical*, *lancet-shaped*, and *pavement* teeth. The *conical* are the commonest; they are prehensile only. The *lancet-shaped* teeth are very characteristic of sharks. They are interesting as examples of magazines of teeth of all sizes, and a successive dropping of old and a coming forward of new to their place. In a shark's jaw there is a magazine of many hundreds of teeth, growing smaller as we pass inward from the edge of the jaw (Fig. 195). Only the large teeth of the outer rows are in use at one time; but there is a continual growing outward of the gum, carrying the teeth with it in the direction of the arrow. Sharks' teeth are very interesting in another respect—viz., as showing their homology with scales, which are, of course, a skin structure. Every gradation from one to the other can be traced over the edge of the jaw of some sharks.

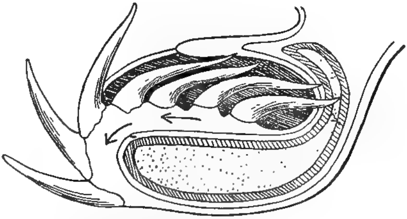

FIG. 195.—Section of lower jaw of a shark, showing the magazine of teeth. The arrows show the direction of replacement.

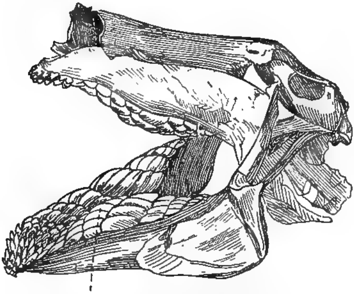

FIG. 196.—Jaw of Port Jackson shark (*Cestraceon*), showing pavement of rounded teeth. (Owen.)

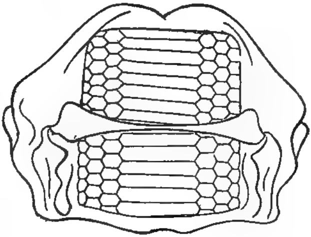

FIG. 197.—Jaw of a skate (*Hylobates*), showing tesselated pavement of teeth. (From Owen.)

Pavement teeth also may be of several kinds, notably what might be called *cobble-stone* pavement (Fig. 196) and *tessellated* pavement (Fig. 197), such as are found in skates. Pavement teeth are used for crushing shells before swallowing. They are interesting as the simplest form of teeth, and as showing their origin from the gum. They are a secretion on the surface of the gum, and afterward fixed to the subjacent bone.

SECTION III.

Stomach Digestion; Chymification, Peptonization.

As already seen, after mastication and insalivation, the food is gathered by the tongue into a bolus and pressed into the throat (so much is voluntary); then seized by the involuntary muscles and rushed down through the gullet (œsophagus) into the stomach, to undergo there the second stage of preparation. The œsophagus is a muscular tube about ten inches long and nearly an inch in diameter. The muscular fibers are mostly circular or ring fibers. We have already said that a characteristic of involuntary muscles is a consecutive contraction of fibers, producing propagated waves of contraction in one direction. Such a wave of contraction propagated downward carries the food before it to the stomach. It is a strong, water-tight contraction, as shown by the fact that long-necked animals, like the horse, swallow water upward from the ground in drinking. The normal direction of waves is downward or stomachward. These are called *peristaltic*. Sometimes—abnormally in man, as in vomiting, but normally in ruminants, as in bringing up the cud—the waves may run in the contrary direction. These are called *antiperistaltic*.

Saccharization of the Food.—This belongs to mouth digestion, for the saliva is the digestive juice for starch. If the food remained long enough in the mouth the saccharization would take place there, but in fact it takes place in the stomach, although the stomach has really nothing to do with the process. On the contrary, the gastric juice by its acidity rather checks the saccharization of starch, so that this change takes place mainly in the early stages of stomach digestion before gastric juice is yet formed in large quantities.

The Stomach.—The *position* is just below the diaphragm and behind the triangular space in front called the *pit* of the stomach, but a little more to the left side. Its shape is seen in Fig. 198. Of its two openings, that leading into the œsophagus is called the cardiac, and that leading into the intestines the *pyloric* orifice.

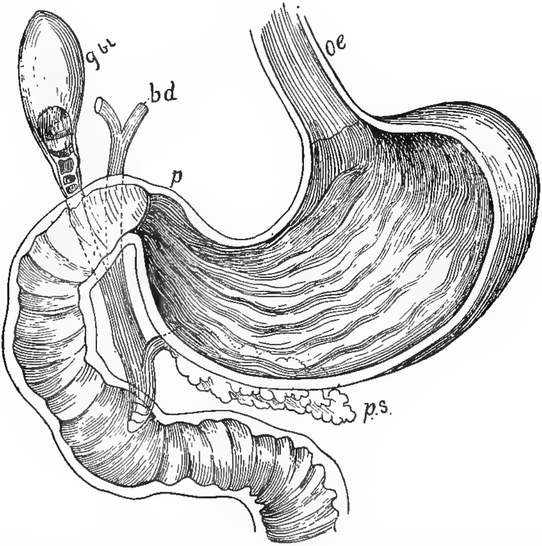

FIG. 198.—Stomach of man ; a section showing form and interior surface : *oe*, œsophagus ; *p*, pylorus ; *bd*, bile duct ; *gbl*, gall bladder ; *ps*, pancreas.

Coats.—The stomach consists of three coats—an *investing serous* coat, very smooth, thin, and tough; a *middle muscular* coat; and a *lining mucous* coat. The muscular coat is by far the thickest, so that the organ may be called a hollow muscle, invested with serous membrane and lined with mucous membrane. The function of the serous coat is to give toughness and easy gliding without friction over other organs in the abdomen. The function of the muscular coat is to do the *mechanical* work, and of the mucous coat the *chemical* work of digestion.

Mechanical Work; Chymification.—The mechanical work of mixing the food with the gastric juice is done by the muscular coat. This consists of several sheets of parallel fibers running in different directions, longitudinal, transverse or ring, and oblique fibers. Under the contraction of these the stomach is seen to squirm, and especially to transmit light waves of annular contraction, chasing one another from the cardiac to the pyloric end. By these contractions the food is gently urged along the *greater* curvature to the pylorus and back along the lesser curvature to the cardiac orifice, and so on repeatedly until the digestion is complete.

The *pylorus* (gate keeper) is a strong collection of circular fibers at the outgoing orifice of the stomach. During digestion it is completely closed. After two to five hours, depending on the nature of the food and the digestive power of the stomach, the digested food is allowed to pass the pylorus; but if any undigested portions appear the pylorus closes, and sends it on its way round again until in a proper condition. But sometimes, by repeated application, the gate keeper is, as it were, *teased into compliance*, and even undigested matter may be allowed to pass, and may create trouble farther on. The final result of this process is a grayish, slightly acid, semiliquid mass, about the consistence and somewhat the appearance of pea soup, and called *chyme.* This is passed on to the intestines, to undergo the next stage.

Chemical Work; Peptonization.—The gastric juice is elaborated by the whole mucous membrane of the stomach, but especially by the peptic glands. Glands, as already explained (page 294), are a device for increasing the extent of the epithelial surface. In this case the device is of the simplest sort. The interior of the stomach is thickly strewed with deep *pits* lined with epithelium (Fig. 199). Some of these pitlike tubes are branched, but only simply. The epithelial surface is thus many times greater than the interior surface of the stomach. The gastric juice is secreted mainly in these pits, both simple and branched. As soon as the food touches the stomach the mucous membrane becomes engorged with blood and reddened, and the gastric secretion commences.

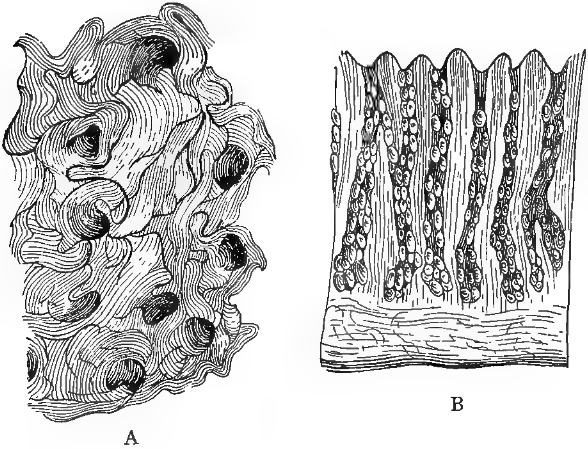

FIG. 199.—A, interior of stomach, showing the openings of the peptic glands; B, section through the walls.

Composition and Uses of Gastric Juice.—Accidental woundings of the stomach have afforded means of collecting the gastric juice of man in considerable quantity; that of animals has been collected in vivisection experiments. The secretion, therefore, has been analyzed. It consists of mucus, with a little free acid, hydrochloric and lactic, and a peculiar ferment, an enzyme called *pepsin*, which has the property of dissolving albuminoids. This it does by hydration. The soluble forms of albuminoids thus formed are called *peptones*, and the process of change peptonization. In some cases of weak digestion pepsin made from a calf's stomach may be used as medicine with good effect.

In both saccharization and peptonization the process is purely chemical, and takes place just as well in a warm *flask* as in the stomach. The true vital process is the formation of the ferment, not the change effected by it on the food.

Effect on Milk.—The effect of pepsin on *milk* is very characteristic. It first curdles, and then dissolves it. The albuminoid—casein—in milk is in a liquid state and apparently suitable for direct absorption. But albuminoids in their natural state are unstable and liable to pass into a solid. Therefore the casein is first solidified and then changed into peptones, in which state it is no longer liable to solidification. Advantage is taken of this property of curdling milk in the manufacture of cheese. Fresh milk is treated with a small quantity of an extract of rennet (calf stomach); the quantity used is sufficient to curdle, but not enough to dissolve the casein.

Absorption.—Water, alcohol, perhaps to some extent sugar, may be taken up directly by the capillaries of the stomach into the blood. But *absorption* is the special function of the *intestines*. The chyme is therefore passed on into the intestines to undergo the third stage of food preparation. There we leave it for the present while we take up the

Comparative Physiology of the Stomach.—The *chemical* process of digestion is the same, and the apparatus nearly the same in all vertebrates. There are only two modifications sufficiently important to arrest our attention—viz., that of *ruminant mammals* and that of *granivorous birds.*

Ruminants.—The stomach of ruminants (Fig. 200) is very complex, and the whole digestive process very elaborate. The stomach consists of four parts—viz.: (1) the *rumen* or paunch; (2) the *reticulum* or honeycomb; (3) the *psalterium* or *omasum* (psalter, or book, or manyplies); and (4) the *abomasum* or rennet. The rumen or paunch (1) is of immense size, and its function is to store the half-chewed food and soften it by maceration. It is thick and muscular, and constitutes what is called the *tripe.* The reticulum (2) may be regarded as an appendage of the paunch, and its function is probably to prepare a macerating liquid and perhaps also to make up the cud-balls. It is full of deep pits,

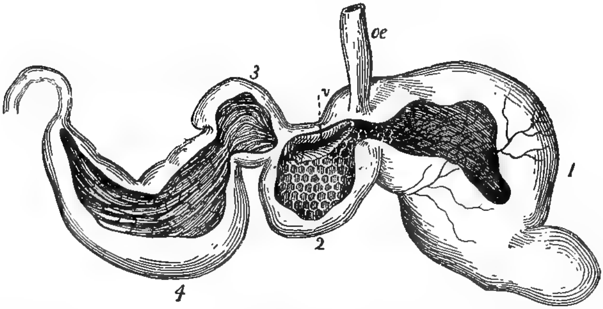

FIG. 200.—Stomach of a sheep, partly cut open so as to show the interior: *oe*, œsophagus; *v*, valvular opening from the œsophagus to the omasum.

like a honeycomb. The *psalter* or manyplies (3), as its name indicates, has its mucous membrane thrown into many wide and thin folds, like the leaves of a book. It is probable that the digestion of starch (saccharization) takes place here, and is all the more complete because the acid gastric juice is not secreted until we reach the last compartment. Finally, the abomasum or rennet (4) is the true and final digestive stomach, where pepsin is formed and peptonization takes place.

We see, then, that several functions which are combined in the same organ in most animals are here differentiated with more perfect results. The reason of this is found in the *nature* of the food and the habits of the animals. The food consists of grasses and herbage, in which the amount of nutritious matter is so small that they must take a very large quantity, and therefore the stomach must be correspondingly large. But again, on account of the small percentage of nutritious matter, the food must be very thoroughly triturated and the digestive process very complete so as to extract it all. We have already seen how well their teeth are adapted to thorough trituration; we see also how the stomach is adapted to perfect digestion. But perfect trituration of so large an amount of food would take much time, and these animals are timid and preyed upon by carnivores. Therefore they are compelled to take their food rapidly, imperfectly chewing and hastily packing it away in the paunch, where it is soaked and softened. Then at their leisure they lie in some concealed place and *ruminate*, or chew the cud. Every one must have observed the process in domestic animals, and perhaps envied their placidity of mind. If we observe closely we see the chewing stop a while; the bolus goes down the gullet by peristalsis, then another comes up by antiperistalsis, and the chewing recommences and continues until the cud is reduced to a fine, smooth paste, and again swallowed.

Now, when the imperfectly chewed food is swallowed the first time it finds a broad open way to the paunch; but when, after perfect chewing, it is swallowed the second time the powerful muscles about the œsophageal orifice of the stomach, by a reflex action little understood, contract in such wise as to bring the orifice of the œsophagus directly into contact with the opening into the manyplies, and the food passes into this compartment.

Evolution of Ruminant Stomach.—We have already seen that the teeth of ruminants were only gradually developed in geologic times from a simple tuberculated structure into the complex grinders which we now find. The same is true of the complex stomach, but the evidence is less complete, because the stomachs of extinct animals are not preserved. Nevertheless, some stages are still found in existing animals. In all mammals, even in man, there is a slight difference of function in the cardiac and pyloric ends of the stomach. In many, as the horse, there is a strong line of demarcation between them. In others, as rodents (Fig. 201), there is a strong hourglass contraction between; but nowhere is the differentiation so marked as in ruminants.

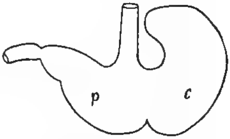

FIG. 201.—Stomach of a rat: *c*, cardiac; *p*, pyloric portion.

Granivorous Birds.—The food of grain-eating birds is hard and requires thorough trituration, yet birds have no teeth, and therefore mastication and insalivation can not take place in the mouth. Their food is swallowed whole and insalivated in the crop, and masticated in the gizzard. Fig. 202 gives the whole apparatus. It consists of three parts—viz., (1) the *crop* (*inglu-*

vies), a reservoir for storing and softening the food by the saliva; (2) the *proventriculus*, which furnishes the peptic juice; and (3) the *gizzard*, or *ventriculus*, or *gigerium*, which triturates the food and mixes it thoroughly with saliva and gastric juice furnished in the parts above. The gizzard consists of two very powerful muscles, provided each with a cushion or pad, which rub against one another (Fig. 203). The cavity is small and lined with a hard, almost horny skin. Gravel is taken as grinders to this mill, and renewed as required. The whole process is briefly as follows: The food is first stored and insalivated and softened in the crop. The crop acts as a hopper to the *gizzard mill*, dropping little by little as required. The digestive juice secreted by the *proventriculus* is also added little by little as required. The triturated and digested material finally passes on to the intestines.

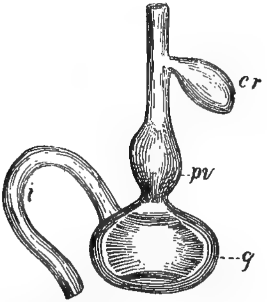

FIG. 202.—Digestive apparatus of a granivorous bird: *cr*, crop; *pv*, proventriculus; *g*, gizzard; *i*, intestine.

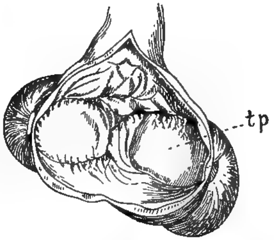

FIG. 203.—The gizzard of a goose cut open: *tp*, triturating pad. (After Owen.)

Evolution of this Apparatus.—This elaborate apparatus is most perfect in grain-eating birds; but all grades approaching it may be found in birds from the simple thin sac of the flesh-eating to the powerful mill of the grain-eating.

SECTION IV.

Intestinal Digestion: Chylification; Emulsification.

Intestines; Form, Structure, and Relations to the Abdominal Cavity.—The intestines consist of a long, slender tube—in man about thirty-five feet long and one inch to two inches in diameter. It is divided into two very distinct parts—viz., the small and large intestines. These differ in *size*, the small being about one inch, the large two inches in diameter. They differ also in *appearance*, the first being smooth, cylindrical, the second puckered and sacculated by a strong muscular band (Fig. 204). The true process of digestion is substantially completed in the former. The function of the latter is not well understood, but both the characteristic color and odor of excrements are taken on here. Also the peculiar shape of the balls in the horse or pellets of sheep and goats are given here.

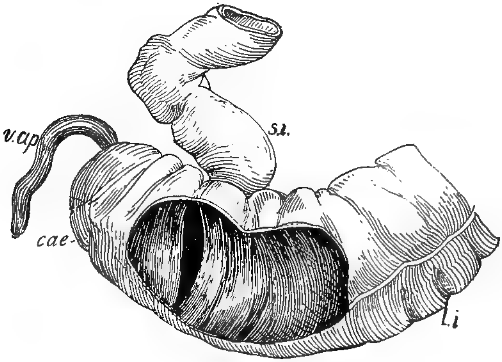

FIG. 204.—The junction of the small and large intestines: *si*, small intestines; *li*, large intestines; *cae*, cæcum; *vap*, vermiform appendage.

The two parts do not grade continuously the one into the other. On the contrary, the small open into the large on one side a little way from the end by a valve (ileocæcal valve; Fig. 204). Each of these two parts are again subdivided into three, as shown in the schedule:

Small…….	Duodenum.	Large ……	Cæcum.
	Jejunum.		Colon.
	Ileum.		Rectum.

The duodenum is the part next the stomach, seen in Fig. 198, into which are poured the digestive juices from the liver and pancreas. It is the largest and shortest part of the small intestines, being about ten inches long and two inches in diameter. The jejunum and ileum grade completely into one another both in structure and function. Of the large intestines, the cæcum is the somewhat enlarged blind extremity into the side of which the ileum opens (Fig. 204) by the ileocæcal valve. Attached to the blind extremity there is a curious, wormlike appendage, which by inflammation gives rise to the grave disease (appendicitis) which is now attracting so much attention. The rectum is the last or lower part, about six inches long, and cylindrical in form, opening through the anus. The colon is the sacculated part between the cæcum on the one hand and the rectum on the other, and constitutes the principal part of the large intestines. The cæcum is in the lower right-hand part of the abdomen. The colon runs from it upward on the right side to the region of the stomach, then across to the left, and then down the left side to the rectum.

Relations to the Abdominal Walls.—So long and so slender a tube must be so held in place that it be not tangled; and also it must be in easy reach of the great vessels which supply it with blood, and which take away the digested food. This is done by a thin, transparent membrane which is attached by one edge to the backbone, and by the other to the whole length of the intestine, following all its complex windings. This is called the *mesentery* (Fig. 205). From this arrangement

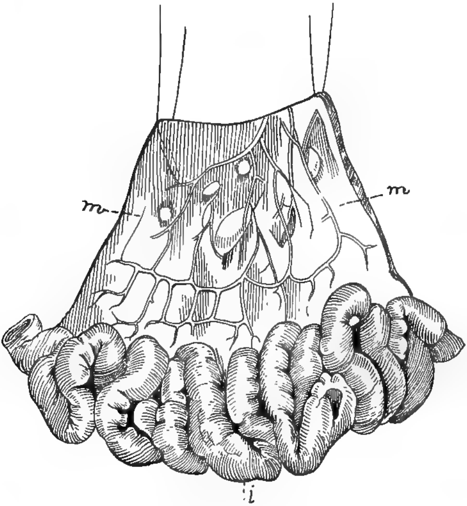

FIG. 205.—Small intestines attached to the mesentery.

it follows that the intestines are nowhere more than six inches away from the great vessels lying along the backbone.

Peritonæum.—It may seem paradoxical, but is nevertheless in some sense true, that the intestines, and indeed all the abdominal viscera, are outside the abdominal cavity. The whole abdominal cavity (*vc*, Fig. 206) is lined with smooth, shining, serous membrane called the *peritonæum* (*per*). This, on reaching the backbone, is reflected forward as a double membrane, the mesentery, and then over the intestine as its investing coat. If this serous membrane could be dissected off completely it would form a complete sac without opening.

What we mean by saying that the intestines are outside of the peritoneal cavity is shown in Fig. 206.

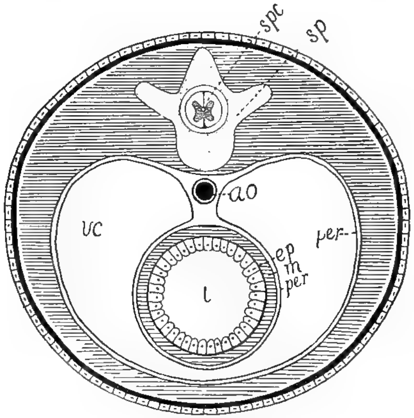

FIG. 206.—Diagram showing the relation of the intestines to the abdominal cavity: *i*, intestine; *vc*, visceral cavity; *per*, peritonæum; *m*, muscular coat; *ep*, epithelial coat; *sp*, spinal column; *ao*, aorta; *spc*, spinal cord. (After Wiedersheim.)

Coats of the Intestines.—Like the stomach, the intestines have three coats—the outer, *peritoneal;* the middle, *muscular;* and the inner, *epithelial.* In other words, it is a hollow, muscular tube, invested with the peritoneal coat and lined with epithelial or mucous membrane. The peritoneal coat gives smoothness, the muscular coat does the mechanical work, and the epithelial the chemical work of digestion.

Mechanical Work.—The muscular coat consists mainly of two sheets of parallel fibers. In the outer one the fibers run lengthwise, in the inner ringwise. Under the contraction of these the intestines may be seen to squirm wormlike from side to side, and *light* waves of contraction may be seen running always in one direction—downward. This is the peristaltic action of the intestines. The waves must be light, otherwise the food would be too much hurried along its way. Slowly, therefore, the digested food is urged along. In the meantime the absorbents are taking up the liquid parts. The percentage of liquids decreases, until finally only solid, indigestible parts remain. This is finally pushed through the ileocoæal valve (Fig. 204) into the large intestines, and the digestion is substantially done. There are changes of an obscure kind which go on there, but these are too little known to detain us.

Chemical Work.—The digestive juices of intestinal digestion are three—viz., the bile, the pancreatic juice, and the intestinal secretion. The general effect of these is to produce a milky liquid called *chyle.*

(*a*) The *bile* is secreted by the liver, and during digestion is poured out in large quantities into the duodenum a little way below the stomach through a common duct made up of the union of the bile duct with the pancreatic duct (Fig. 198). The digestive effect of the bile is manifold. 1. It will be remembered that the chyme is acid, and that acidity is unfavorable to the saccharization of starch. Thus it happens that some starch may escape solution in the stomach. Now, the bile is alkaline, and therefore neutralizes the acidity of the chyme, and thus revives the activity of the ptyalin on the starches. 2. It will be remembered, again, that of the three kinds of food we have had digestive juices for two, viz., ptyalin for starches and pepsin for albuminoids; but the fats have not yet been touched. Now, the alkalinity of bile partially saponifies the fats, and thus prepares them for emulsification by the pancreatic and intestinal juices. 3. It is found, too, that in order to be absorbed easily a liquid must be either neutral or a little alkaline. Thus the bile, by neutralizing the acidity of the chyme, prepares it for easy absorption.

(*b*) The pancreas (*sweetbread*) lies just below the stomach, and its excretory duct unites with the bile duct to open by a common duct into the duodenum. Its structure is similar to that already described in the salivary gland. Its secretion is perhaps the most important of all the digestive juices. It performs the function of all previously mentioned, and supplements them all. It saccharizes starch, like the saliva. It peptonizes albuminoids, like the gastric juice. It is slightly alkaline, like the bile, and it is a powerful emulsifier of fat, like the intestinal mucus. These properties are the result of several ferments, among which may be mentioned *pancreatin* or *amylopsin* and *trypsin*, the former a solvent of *starch* and the latter of *albuminoids*. Whatever of albuminoids or amyloids escape digestion in the stomach are dissolved here.* It also forms still another ferment which splits fats into glycerin and fatty acids.† In addition to all these the pancreas has still other functions, which will be discussed later. Suffice it to say now that it apparently delivers a peculiar ferment directly to the blood.

(*c*) The *intestinal secretion* probably has other digestive properties little known, but certainly by its slimy viscidity it is very efficient in the emulsification of fats.

Emulsion.—We have said that chyle is a milky liquid. Its whiteness is wholly due to emulsified fats. We explain this as follows: Ice is transparent, but break it up into fine particles like snow and it is intensely white. Glass is transparent, but grind it to fine powder and it is white. Water is transparent, but spray and foam are white. And so in all cases of whiteness. Oils

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* Recently shown (Archives des Sciences, iv, 490, 1897) that the spleen furnishes a product necessary to the formation of trypsin.

† Am. Nat. xxxi, 1040, 1897.

and fats are transparent, but broken up into microscopic globules they are also white. Now, what is called an emulsion consists of millions of microscopic globules of oil swimming in a transparent liquid, but, in order that the globules do not run together and unite, the liquid must be *viscid.*

EXPERIMENT.—Take a small bottle, fill it partly with a viscid liquid like gum water or mucus, and then pour in a little oil of some kind, as turpentine or sweet oil. We see them as two equally transparent layers one atop the other. Now, putting the thumb on the mouth of the bottle, shake it violently. The result is an intensely white fluid, which, examined by microscope, shows nothing but transparent globules floating in a transparent liquid. This is an *emulsion.* Milk is also an emulsion, and its whiteness is due to the same cause. Chyle is an emulsion, and its whiteness is due to the presence of microscopic fat globules. If there be no fat in the food, the chyle will be transparent. In the process of digestion the fats and oils are broken up by the constant pressing and kneading action of the intestines in the presence of a viscid liquid.

Absorption.—The three kinds of food are now all become absorbable. The starches have become sugars, the albuminoids peptones, and the fats emulsions. The food is now ready for absorption. But for rapid absorption we must have a large surface. This condition is supplied partly

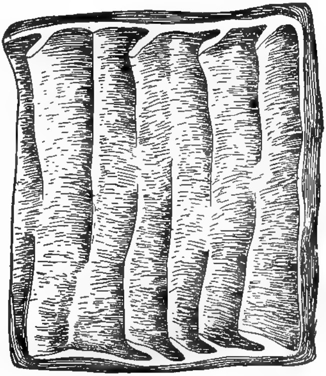

FIG. 207.—Interior of the intestines, showing the valvulæ conniventes.

by the great length of the intestines, still more by the many folds of the mucous membrane (*valvulæ conniventes*) (Fig. 207), but most of all by the *villi.* These microscopic hairlike projections cover the surface as thickly as the pile of velvet or the tufts of Brussels carpet. They give a velvety feel to the mucous membrane (Fig. 208). Each villus contains two kinds of absorbent vessels—viz., capillary blood vessels and lacteals. These, though separated in the figure, are both of them in each villus.

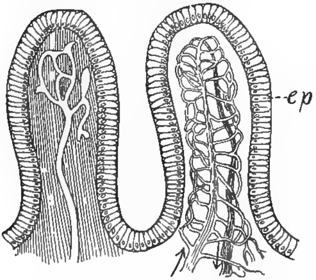

FIG. 208.—Two of the villi, greatly enlarged; one showing blood capillaries, the other, the lacteals: *ep*, epithelium.

Two Modes of Absorption.—The food is absorbed in two ways—viz., by blood *capillaries* and by *lacteals.* The blood capillaries contain a *circulating current,* and therefore take up the food and carry it along with the blood. The lacteals, on the contrary, are purely absorbent, and they end in blind, fingerlike extremities, and therefore *suck up* the liquid food. Whatever of food is absorbed by the stomach is wholly by blood capillaries. But the intestines are specially organized for absorption in both ways. The food is divided between these two modes. The sugars are absorbed mainly by the capillaries, the fats by the lacteals, while the peptones are divided between them.

Course of Each to the General Circulation.—That taken up by the capillaries is carried to the portal vein; thence it passes through the *liver,* and by the hepatic vein it reaches the vena cava ascendens and by it is carried to the heart, and is thence distributed everywhere. That taken up by the lacteals is carried by the lacteal or lymphatic vessels of the mesentery through the mesenteric glands into the receptaculum chyli, and thence up to the thoracic duct, the lymphatic trunk lying along the backbone on the left side (Fig. 209). This duct rises to the collar bone, then turns downward and empties into the angle formed by the junction of the subclavian vein from the left arm and the jugular coming from the head, and thence it passes by the vena cava descendens directly to the heart, to be distributed to the whole body. This will be explained more fully hereafter.

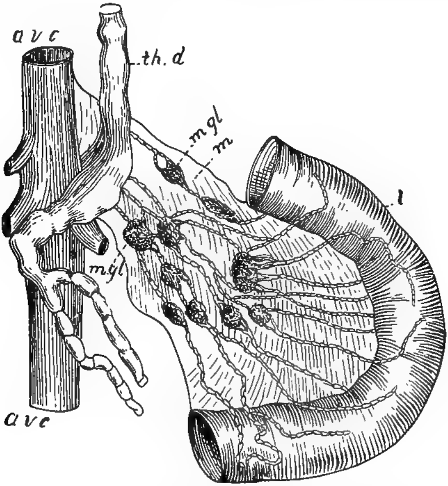

FIG. 209.—A segment of the intestines (*i*), showing the lacteal vessels passing along the mesentery (*m*), through the mesenteric glands (*mgl*), and into the thoracic duct (*thd*): *avc*, ascending vena cava.

Sanguification.

In the course of each of these to the general circulation there are certain changes which assimilate it to the character of the blood. (1) We have said that that which is taken up by the capillaries passes into the vena porta. Now this is a quite unique and exceptional vein. All other veins ramify at one end only; this at both ends. All other veins, after receiving their supply by the capillaries from the tissues, empty by an open mouth into the general circulation. This one receives its supply from the capillaries of the intestines, the stomach, and the spleen, and then, instead of emptying into the vena cava, close at hand, goes to the liver, to be *again distributed* by inverse capillary ramification through that organ, and gathered a second time by the capillaries of the hepatic vein, and so delivered to the general circulation. Thus there is a mesenteric artery, but no corresponding mesenteric vein. There is a splenic artery, but no splenic vein. The vena porta takes the blood of both these, and carries it to the liver, to be again distributed there. This is shown in the diagram (Fig. 210). Now, during the passage of the digested food through the liver it undergoes an important change, preparing it for immediate use in the generation of force and heat. In other words, it is sanguified—i. e., made into material suitable for circulation in the blood. The nature of this important change we will explain more fully when we come to speak of the functions of the liver (page 446).

That part of the dissolved food which is taken up by the lacteals, as we have seen, is carried through the mesenteric glands before reaching the thoracic duct. In these glands an important change takes place. After passing through these it is no longer mere dissolved food—i. e., peptones and fats—but apparently a living fluid like the blood, although not yet red. Before passing through the glands it is noncoagulable; after passing it is coagulable, like the blood. Before passing it contains no globules except fat globules. After passing it contains also living nucleated cells like the white corpuscles of the blood, contributed to it by the glands. In a word, before passing, it is *chyle;* after passing, it is

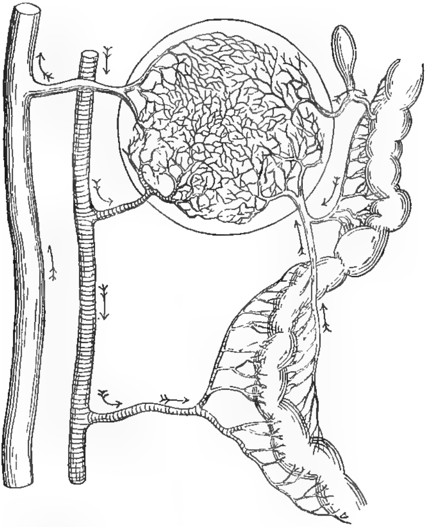

FIG. 210.—Diagram showing the distribution of the blood through the liver. The arrows show the direction of the current.

at least partly converted into blood. The change is completed in the blood itself.

The last stage—i. e., the actual *assimilation* into *tissue*—will be spoken of in connection with the circulation.

MODIFICATION OF THE PROCESS OF INTESTINAL DIGESTION IN VERTEBRATES.

There is little to be said on this subject, because the modification of the process, as already given, is unimportant. The whole process of digestion—mouth digestion, stomach digestion, and intestinal digestion—is simpler in carnivores and more elaborate in herbivores. Man in this regard, as in so many others, may be regarded as a generalized mean. The intestinal canal is shorter in carnivores and much longer in herbivores than in man. It may be well, however, to mention one or two interesting points. The cæcum, which in man is but a slight enlargement of the blind end of the large intestine (see Fig. 204), is greatly enlarged in the horse, and in the rat is indeed a sort of second stomach as big as the true stomach (Fig. 211). The most interesting thing in this connection is the origin of the strange wormlike appendix. It is probably the remnant of the shriveling of the extreme end of a much longer cæcum. It is an example of a useless remnant of a once useful organ.

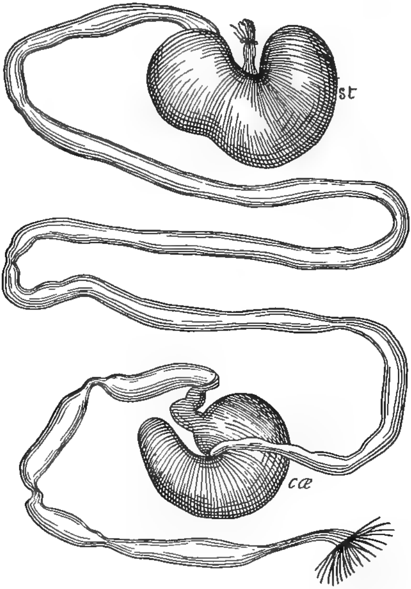

FIG. 211.—The alimentary canal of a rat: *st*, stomach; *cæ*, cæcum. (From Owen.)

One more example: In fishes the whole digestive process is very simple, and the intestines are correspondingly short. But in the shark, although externally the intestine is almost a straight tube running through the body, yet *internally* its surface of absorption is made very large by means of a curious spiral valve. This gives the peculiar spiral marking on the dung of these and of some other lower vertebrates, both living and extinct, for fossil dung of sharks and reptiles is not uncommon.

SECTION V.

Digestive System in Invertebrates.

General Remarks.—1. As already explained, we shall pursue a different plan here. Instead of following each stage of digestion through the different classes, we shall run through the whole digestive process in each class as taken up.

2. The complexity, and especially the diversity, among invertebrates is so great that if we took them up with anything like the fullness that we have taken up vertebrates, our object—viz., to make a small volume, giving only an outline of the most interesting points—would be defeated. We will, therefore, only give a few very striking examples from different departments.

ARTHROPODS.

Insects: Mouth Parts.—Insects are wonderfully specialized animals. This is especially true of their *mouth parts*. From this point of view insects may be divided into two groups—viz., the biting and the sucking insects, or the *mandibulate* and the *haustellate*. The former include the orthopters (grasshoppers), the neuropters (dragon flies), and the coleopters (beetles). The latter include the lepidopters (butterflies and moths), the dipters (flies), and the hymenopters (bees and ants), although these last are intermediate. Of these two kinds of mouth parts the former is undoubtedly the original and normal, of which the latter must be regarded as an extreme modification, for the mandibulate form alone is found in the larval state (e. g., caterpillars) and in early geological times.

Normal Mouth Parts.—Taking, then, the orthopter, or grasshopper, or else a beetle, as example, there are six movable mouth parts; but as four of these are in pairs, we may say there are four *kinds*. These are the *labrum* (so-called upper lip), the two *mandibles*, the two *maxillæ*, with their jointed appendages, and the *labium* (lower lip), with its jointed appendages. Sometimes there is an elongation of this last called the tongue. These are seen in place in the beetle (Fig. 212), and the same parts in a grasshopper separated to display their forms and position in Fig. 213. Looking directly at the mouth of the grasshopper or beetle, their relative position and direction of motion is shown in the diagram (Fig. 214). The food is gathered by the maxillary and labial palpi, is placed between the jaws (mandibles and maxillæ), pressed together between the upper and lower lips, and

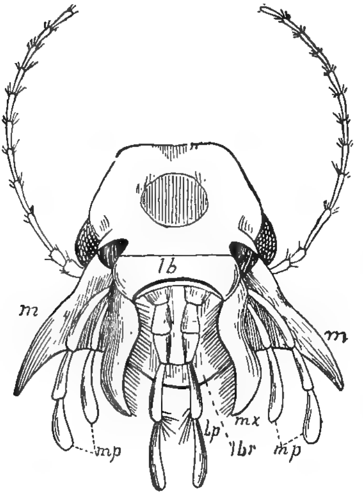

FIG. 212.—Head of a beetle seen from behind: *lb*, labium; *lp*, labial palpi; *m m*, mandibles; *mx*, maxillæ; *mp*, maxillary palpi; *lbr*, labrum.

divided and masticated by the jaws working toward one another *laterally* (not vertically, as in vertebrates).

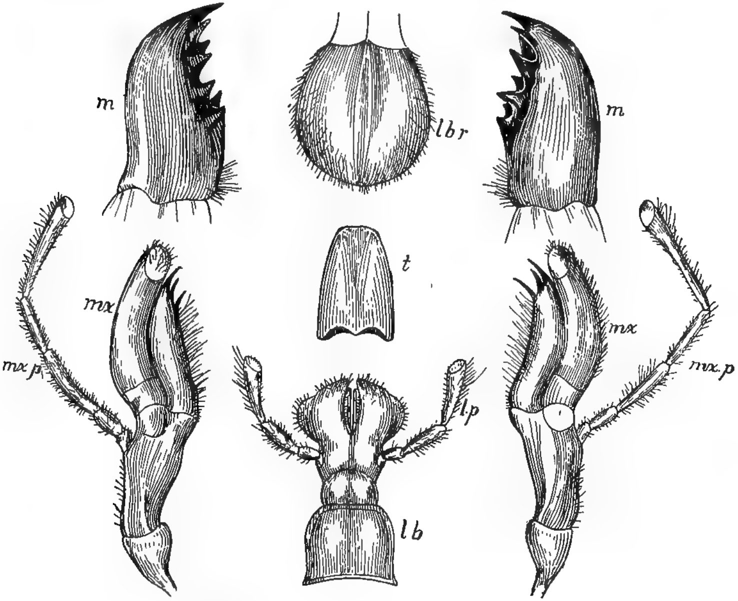

FIG. 213.—The mouth parts of a grasshopper enlarged: *lbr*, labrum; *m m*, mandibles; *lb*, labium; *lp*, labial palpi; *t*, tongue; *mx mx*, maxillæ; *mxp mxp*, maxillary palpi.

Serial Homology of these Parts.—As already said (page 273), the insect head consists of four segments with their paired appendages. The labrum is an extension downward of the first segment, and the antennæ are the jointed appendages; the mandibles are the paired appendages of the second segment; the maxillæ, the paired appendages of the third segment; while the labium and its paired appendages belong to the fourth segment (Fig. 215).

Special Homology.—In *suctorial* insects the mouth parts are an extreme adaptive modification—so extreme in some cases that their homology with those of masticatory insects is somewhat doubtful. We give what seems the most probable view in two extreme forms:

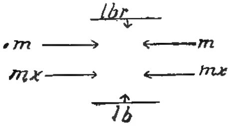

FIG. 214. — Diagram showing the relative positions and direction of motion in mastication. The arrows show the direction of motion.

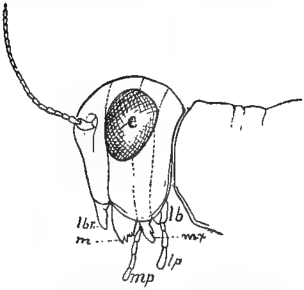

FIG. 215.—Side view of the head of a grasshopper: *e*, eye; other letters are the same as in Figs. 212, 213, and 214.

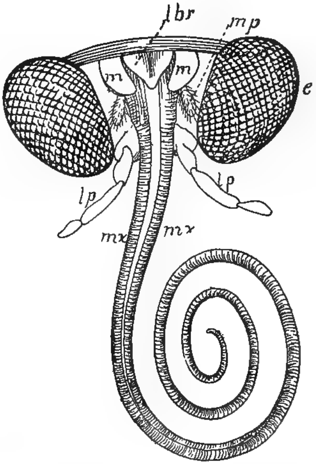

FIG. 216.—Head of a butterfly seen from in front. The letters show the same parts as in previous figures.

Butterfly.—In this case the labrum, *lbr*, and the mandibles, *m m* (Fig. 216), are rudimentary and useless. The maxillæ, *mx mx*, are enormously elongated into muscular hollow semicylinders, which, when put together, form a long, flexible, hollow sucking tube. This is usually carried coiled up like a watch spring, but is uncoiled and straightened when used as a proboscis for sounding the nectar tubes of flowers.

Bees are a good example of *intermediate* form (Fig. 217). In these the labrum and mandibles are as usual, but the maxillæ and labium, with their appendages, are greatly elongated to form a sucking organ. This is especially true of that projection of the labium called the tongue, *t*, which is modified into an apparatus of marvelously complex structure. This is shown in Fig. 218, in which A shows the outer tube with the inner tube

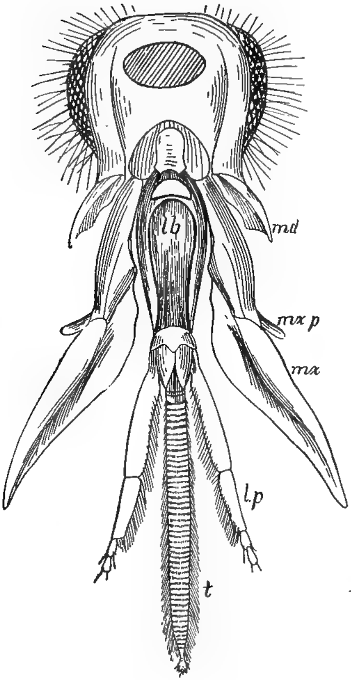

FIG. 217.—Head of a bee seen from behind. The labrum is not seen. The other parts are lettered as before; *t*, tongue.

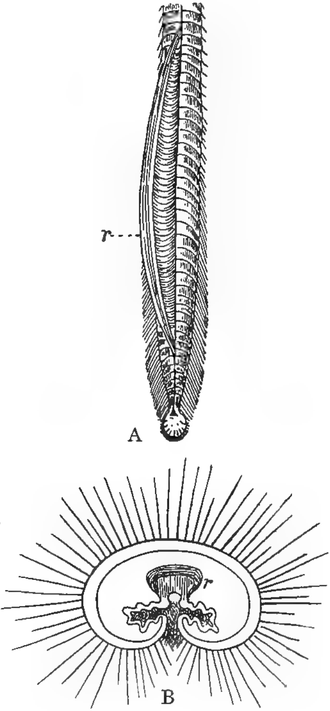

FIG. 218.—A, enlarged view of a bee's tongue; *r*, inner tube; B, section more enlarged, showing its structure.

pulled out; B, a section of the whole when the inner tube is in place. The bee, therefore, both bites and sucks. If the nectary tube of a flower is too long to reach the nectar with the sucker, he bites the nectary and reaches the honey more directly.

Digestive Apparatus.—Fig. 219 shows the whole digestive apparatus of a beetle. In Fig. 220 we give

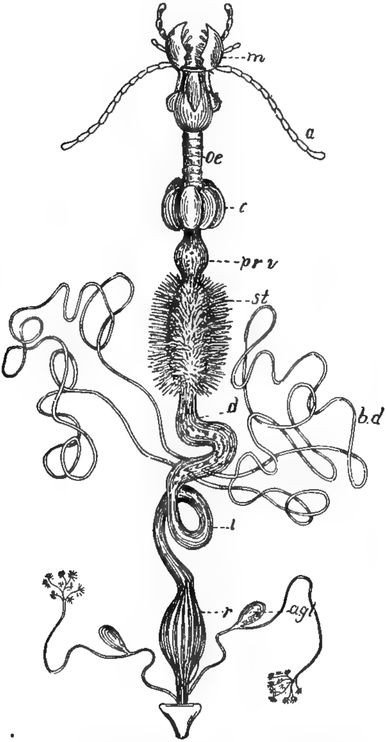

FIG. 219.—Digestive apparatus of a beetle: *m*, mandibles; *a*, antennæ; *æ*, œsophagus; *c*, crop; *prv*, proventriculus; *st*, stomach; *bd*, biliary ducts; *d*, duodenum; *i*, intestines; *r*, rectum; *agl*, anal gland.

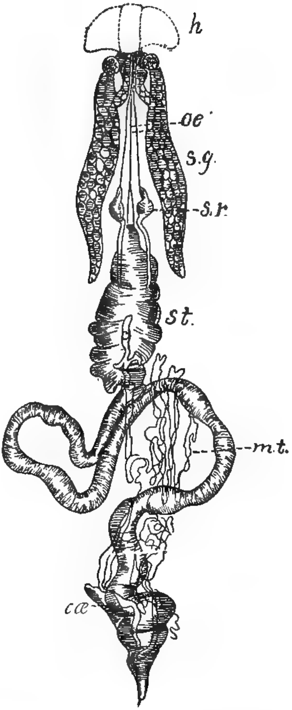

FIG. 220.—Digestive system of a Belostoma: *h*, head; *æ*, œsophagus; *sg*, salivary gland; *sr*, salivary receptacle; *st*, stomach; *mt*, Malpighian tubes; *cæ*, cæcum. (After Packard.)

also the same in another insect (*Belostoma*) to show the variations, and especially to show the salivary glands, not shown in the previous figure. The distinctive functions of these several parts are somewhat doubtful. The most probable view is given in the legends.

We have given the simplest case of a carnivorous beetle. In many insects, especially the herbivorous, like the grasshopper (orthopter), the digestive apparatus is much more complex and the intestines much longer and more convoluted.

It is well to remark that what we have called the biliary or Malpighian tubes are also, apparently, uriniferous tubes as well. These two functions are not yet well differentiated. The significance of this will appear hereafter.

Crustaceans: Mouth Organs.—We have already seen (page 268) that these are all modified appendages of the anterior somites. Four pairs, called maxillipeds, are food gatherers, and two pairs, maxillæ and mandibles, divide and chew the food (see Fig. 170).

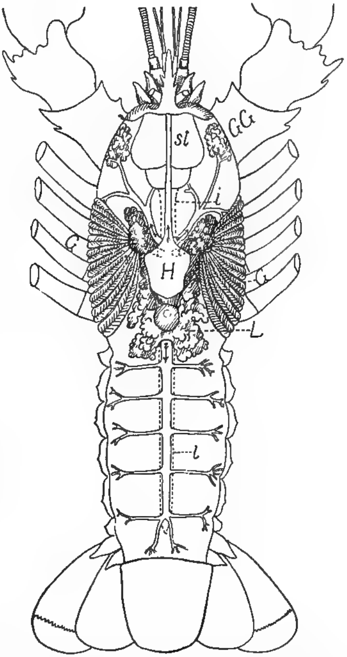

Fig. 221.—Lobster with the carapace taken off: *st*, stomach; dotted tube, *ii*, intestines; *L*, liver; *H*, heart.

Stomach.—The stomach is situated in the anterior part of the cephalothorax, immediately above the mouth and connected therewith by a short œsophagus. If we take off the carapace of a lobster by dividing the attachments with the sternum, Fig. 221 will represent what we see. Immediately beneath the carapace is the heart, *H*, with the blood vessels running fore and aft. We have nothing to do with these now. We will speak of them later. In front and beneath the heart is seen the large stomach, *st*, with the straight intestine, *i*, running backward beneath the great artery. Behind the stomach, on each side of the anterior part of the intestine, is seen the large liver, *L*, composed of many tubules opening into the intestine. The stomach is very muscular, and if opened is seen to contain what might be called *stomach teeth*—i. e., powerful triturating organs composed of chitin and armed with prickles of the same.

MOLLUSCA.

We take one example from each class.

Acephala.—Among these we take the *Mactra* (Fig. 222). In all acephala the food-taking is wholly *involuntary.* The clam buries itself in mud with the mouth downward and the siphon upward, just reaching the water. By ciliary action, currents are created which pass down one tube of the siphon, through the gills, contributing thus to respiration; then to the mouth, contributing thus to alimentation; then back again

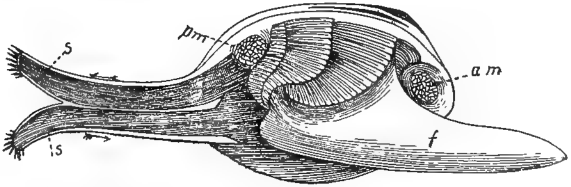

FIG. 222.—Mactra with one valve removed, showing the anterior (*am*) and the posterior (*pm*) shell muscles, and the foot (*f*). (From Gegenbaur.)

through the gills and out by the other tube of the siphon, carrying with it refuse or excretions of all kinds. The most remarkable thing about the digestive apparatus is the enormous liver (nearly the whole of the dark part of an oyster or a clam is liver), through which the long and convoluted intestine winds, receiving in its course the biliary secretion from many openings, and then, strange to say, passing through the heart on its way backward to the vent at the siphon. The stomach and the winding course of the intestine is shown in Fig. 223.

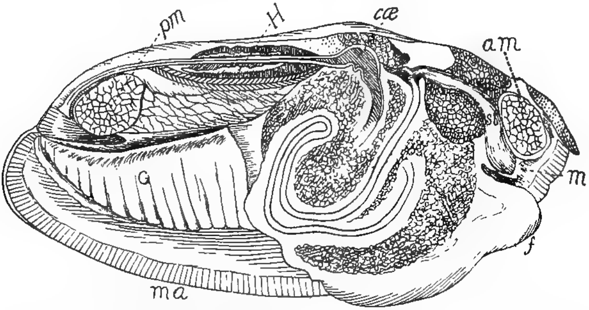

FIG. 223.—Vertical longitudinal section of Anodonta: *pm*, *am*, posterior-anterior adductor muscles; *m*, mouth; *st*, stomach; *cæ*, cæcum; *H*, heart; *f*, foot; *G*, gills; *ma*, mantle.

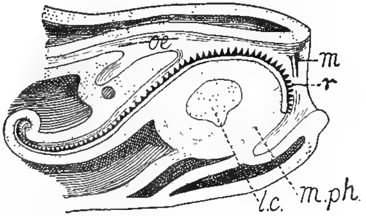

FIG. 224.—Section through snout of a carnivorous gastropod showing the radula, *r*, in place: *lc*, lingual cartilage; *mph*, muscle of pharynx; *m*, mouth; *œ*, œsophagus. (After Lang.)

Gastropoda.—For an example of these take a *snail.* Gastropods are much more highly organized than the acephala. They have a distinct head and their food-taking is voluntary. The mouth is armed with transversely ridged chitinous plates, which have been called jaws, and a ribbon of chitin, called *radula*, thickly set with sharp teeth, by which they rasp their vegetable food. In carnivorous conchs the radula is used for boring round holes through the shells of other species for the purpose of sucking their juices (Figs. 224 and 225). The intestine, as in acephala, winds through the liver, and in shelled forms turns forward to discharge at the opening of the shell. Here, in fact, in the snail we find four tubes opening: (1) Of course, the mouth; (2) the intestinal opening (anus); (3) the genital opening; and (4) the respiratory opening.

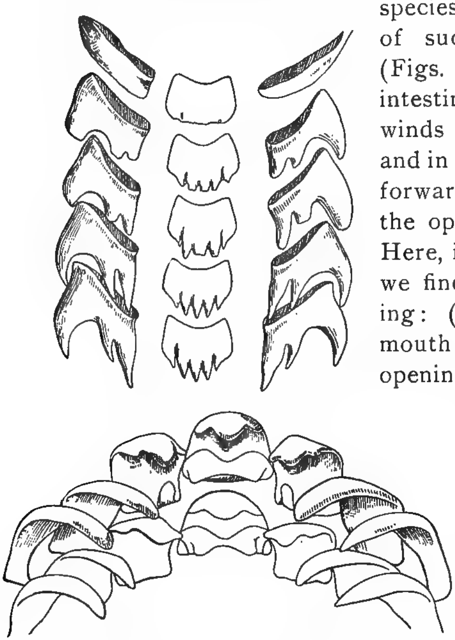

FIG. 225.—Different forms of the teeth of carnivorous gastropods.

Cephalopoda.—For this class we take the *squid* (*Sepia*). Squids take their food by means of the powerful muscular arms surrounding the mouth (Fig. 226) and divide it with their powerful parrotlike beak (Fig. 227), which moves up and down like the jaws of vertebrates, not laterally, like those of arthropods. The digestive tube is very simple, the long œsophagus passing into the large stomach and the intestines coming thenceforward to discharge in front, so that the *débris* is carried away by the water currents of respiration. These animals are the most highly organized among mollusca. All the organs contributive to digestion, such as salivary glands, liver, and perhaps pancreas, are found.

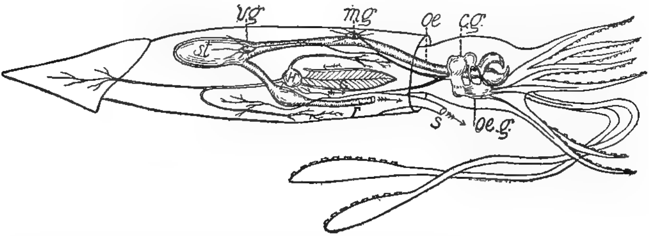

Fig. 226.—Diagram of digestive system of a squid: *cg*, cephalic ganglion; *œg*, œsophageal ganglion; *œ*, œsophagus; *st*, stomach siphon; *mg*, mantle ganglion; *vg*, visceral ganglion; *H*, heart; *G*, gills.

ECHINODERMS.

In the echinus, or sea chestnut, we have perhaps the most elaborate jaw structure to be found in the whole animal kingdom—viz., the so-called "lantern of Aristotle" (Fig. 228). This consists of five three-sided hollow prismatic pieces surrounding the œsophagus and fitted together so as to make a somewhat conical whole. Through each prismatic piece there runs, as through a

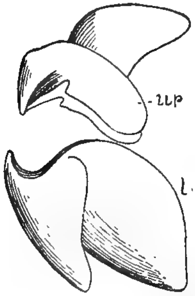

Fig. 227.—Jaws of a squid: *up*, upper jaw; *l*, lower jaw.

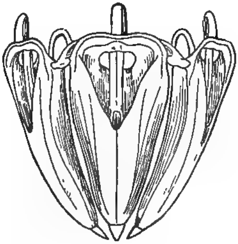

Fig. 228.—The masticating apparatus of an echinus.

sheath, a long, slender, slightly curved rod, sharp and enameled at the point. These prismatic pieces with their sharp teeth are worked by powerful muscles, so as to move radially to and from the center. The food is taken by curious nipping appendages (pedicellariæ) and handed on to the mouth and divided and chewed by the lantern apparatus. The stomach is immediately above the lantern; the intestine is much convoluted, and emerges by opening in the center of the radiated upper surface of the animal.

CŒLENTERATES.

Thus far we have found *intestinal* as well as stomachal digestion. The food preparation is carried to the condition of *chyle.* In all such cases there is a blood system distinct from the digestive system, and into which the chyle is absorbed, to become afterward changed into blood. In all animals spoken of thus far blood and digested food are distinct from one another. The digested food is absorbed and changed into blood (sanguified). But now we find a great change in this regard. In the cœlenterates, and below, there is no longer any intestine as distinct from the stomach. The digestion goes only as far as chyme-making. There is no longer any distinction between the digestive system and the blood system, nor between digested food and blood. The digested food *is* the only nutrient fluid. We take as an excellent example of cœlenterates the

Medusa, or Jellyfish, or Sea-Blubber.—These beautiful, almost transparent, saucerlike or bell-shaped animals (Fig. 229), with their long trailing tentacles and graceful movements, are the delight of the intelligent seashore visitor, and especially of the naturalist.

How do they take their food? The movement of their tentacles is far too slow for this purpose. They take it by means of what have been called nettle cells, or stinging cells, or thread cells (nematocysts), or, by Agassiz, most appropriately, *lasso cells.* They occur in clusters, especially on the tentacles. Their shape, like an electric lamp, is seen in Fig. 230, A. Examined with the microscope, they are seen to contain—like an electric lamp—a fine thread coiled within. If the animal be irritated the long thread flashes out like lightning (Fig. 230, B) and its extremity pierces, discharges a poison, and paralyzes its prey, which is then slowly brought to the mouth and swallowed. The effect of these stinging cells, with their invisible threads charged with poison, is so powerful that handling these animals will produce painful inflammation of the hands.

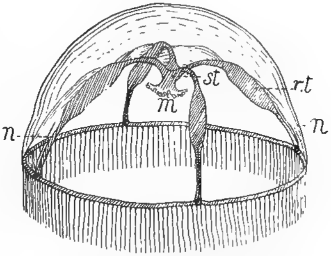

FIG. 229.—Diagram of a medusa: *n n*, nerve; *m*, mouth; *st*, stomach; *rt*, radiating tubes.

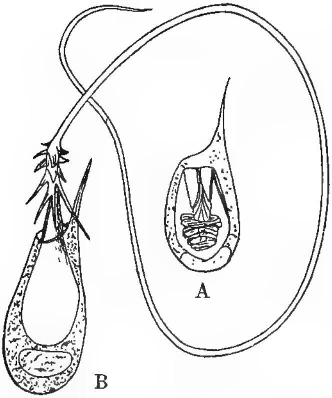

FIG. 230.—Lasso cell: A, in passive state; B, with the thread discharging.

The mouth is the opening at the end of the proboscis (Fig. 229), and the stomach—often called the œsophagus—the hollow proboscis itself. The food is taken by the mouth, and retained in the stomach until digested. Whatever is indigestible is rejected through the mouth, and the digested food is then circulated by ciliary currents through all the canals of the body (chymiferous canals), and thence directly absorbed into the tissues.

Polyp.—Another excellent example is the *polyp*, or *actinia*, or *sea anemone*. The well-known appearance of this animal is shown in Fig. 231, and the interior structure in Fig. 232. Imagine a short, hollow, fleshy cylinder (body cavity), with a disk below (the foot disk) and a disk above (the mouth disk). The upper disk is

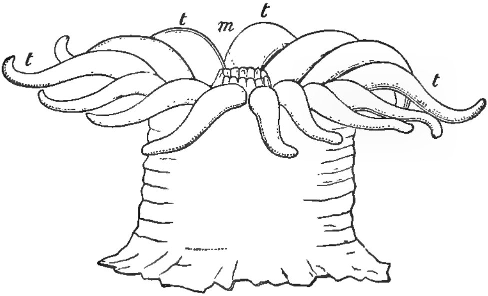

FIG. 231.—Simplified figure of an actinia.

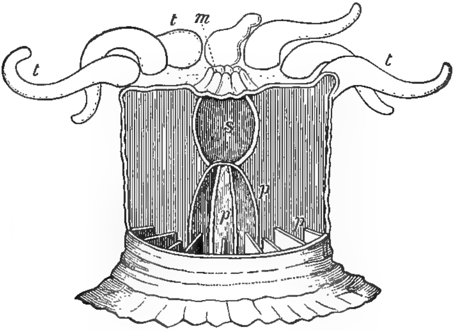

FIG. 232.—Ideal section, vertical and horizontal, showing structure : *t*, tentacles ; *s*, stomach ; *p p*, partitions.

surrounded with hollow tentacles opening into the body cavity, and in its center is the mouth, opening into the *stomach* or gullet, the lower end of which opens into the general cavity. The stomach does not hang free, but is held firmly in its place by partitions running from the outer wall to the stomach, and dividing the general cavity into many triangular apartments. Many partitions do not reach the stomach. Below the stomach the partitions end in free scythelike margins, so that all the triangular apartments are in communication with one another.

Process of Digestion.—The food is taken, as in medusæ, by thread cells, is put into the mouth and swallowed, and, partly at least, digested in the stomach. Whatever is indigestible is thrown back to the sea through the mouth. The partly digested food is then dropped into the general cavity, its digestion completed, and then circulated by ciliary currents throughout the whole interior cavity even to the extremity of the hollow tentacles, and directly absorbed and appropriated by the tissues.

PROTOZOA.

Here, again, we find a great step downward. Thus far we have found a circulating fluid, although in the cœlenterates it is not blood but digested food, and circulated not by the mechanical action of a heart, but by ciliary currents. But now we find no circulating fluid of any kind. The food is digested and at once appropriated by the living protoplasm. But even in protozoa we find *two grades*. In the *Infusoria* (Fig. 233) the mouth is surrounded by cilia, and particles of all kinds are brought there by ciliary currents. If any are suitable for food they are carried down into the stomach; if not, they are rejected and whirled away by the same current. In *Rhizopods* there is neither mouth nor stomach as a permanent organ. Food touching the *body anywhere* is ingulfed. The semifluid protoplasm flows around it, takes it in, and digests it. Whatever is indigestible is thrown out again, and the digested part at once appropriated and assimilated (Fig. 234); see also Fig. 156, page 240). These lowest animals have neither tissues nor organs of any kind, but extemporize these as wanted—whether locomotive organs, prehensile organs, mouth, or stomach.

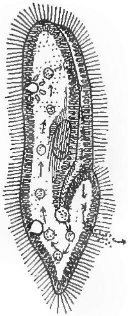

FIG. 233.—Paramœcum. The arrows show the course of the food until discharged.

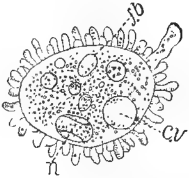

FIG. 234.—Amœba proteus: *fb*, food bodies; *cv*, contractile vesicle; *n*, nucleus. (After Leidy.)

It is from such low beginnings that, it is believed, all the types of animal structure have been gradually differentiated by a process of evolution through all geological times.

CHAPTER III.

BLOOD SYSTEM.

Returning again to man, we have now carried the food to the blood. We therefore take next the blood system. But first of all we must say something about the blood itself.

SECTION I.

The Blood.

Blood is an intensely red fluid, of a slightly viscid feel and a faintly nauseous smell and taste. To the naked eye it is quite homogeneous, but under the microscope it is easily seen to consist of a multitude of solid red particles or globules floating in an almost colorless liquid. The liquid part is called *plasma.* The color is wholly due to the globules. The quantity of this fluid in a healthy man is about one and a half gallon.

1. **The Globules.**—These are of two, possibly three kinds, viz.: (*a*) the *red* globules (Fig. 235); (*b*) the *white* or colorless globules; and, doubtfully, (*c*) the *blood plates.* Of these the red are far the most numerous and conspicuous, and are therefore taken first.

(*a*) *Red Globules.*—These in *size* are about $\frac{1}{3200}$ inch ($\frac{1}{125}$ millimetre) in diameter. In *shape* they are flattened circular disks, a little depressed in the middle, their thickness being about one quarter the diameter of the disk. Their immense number may be shown thus: From the size given above it is evident that it would take ten million to cover a square inch; but on account of their flatness it would take more than twelve thousand to make a pile an inch high. Thus a cubic inch of blood globules would contain one hundred and twenty thousand million globules. Now it has been estimated that the actual number in a cubic inch of blood is about seventy thousand millions. Therefore considerably more than half of the blood consists of these globules.

Behavior of Blood.—If we watch fresh-drawn blood with a microscope under a glass cover we observe that the disks run together and pile on one another like a pile of coins thrown down (Fig. 235). This is the result of coagulation. If a little water on the finger is touched to the side of the cover, so as to be drawn in and mingled with the blood, then the globules become round like marbles, and roll around freely in the current. They have imbibed the water and become swollen. If the fluid in which they float should dry away ever so little, they shrivel and become irregular in shape (Fig. 235 *r′*). The same change takes place if a strong solution of salt be added. The salt draws water out of the globules and shrivels them. But if a *weak* solution of salt be added it prevents coagulation, and at the same time does not alter the shape. The disklike shape may be thus examined at leisure.

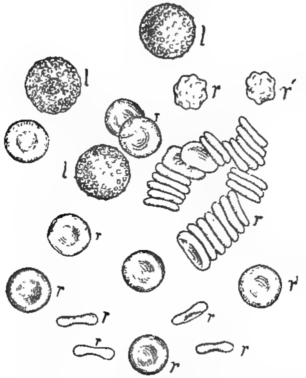

FIG. 235.—Blood globules: *r r r*, red globules; *l l*, white globules or leucocytes.

Structure.—The red globules are not cells, but solid masses, a little softer in the center.

(*b*) *White Globules* (*Leucocytes*).—These are much fewer in number, being on an average only about one in eight hundred. They differ from the red in *color*, being colorless; in *size*, being a little greater in diameter; in *shape*, being normally spherical instead of disk-shaped; in structure, being distinctly *nucleated;* and, last and most important of all, in being *living cells*, endowed with *amœboid movement*—in fact, in having all the properties and capacities of *living protozoa*, crawling about like living things. Some of the shapes which they take on are shown in Fig. 236.

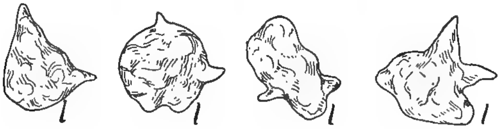

FIG. 236.—Different forms of leucocytes.

(*c*) *Blood Plates.*—These are very much smaller than either of the others. They are difficult of demonstration, and their function is doubtful. In fact, they are believed by some investigators to be not true blood elements at all, but only the disintegrated remains of wornout white corpuscles. This is still under discussion.

Chemical Composition.—The globules of blood seem to be composed of an albuminoid stroma, colored in the case of the red, with another peculiar albuminoid substance—*hæmoglobin.* This substance contains a notable quantity of *iron*, and has a remarkable relation to oxygen. It readily takes up oxygen, and as readily gives it up again, and in doing so changes color. In an oxidized condition (oxyhæmoglobin) it is intensely *scarlet red.* In the deoxidized condition it is *dark-purplish red.*

2. **Plasma.**—The liquid in which the globules swim (plasma) is a solution of *fibrin*, *albumen*, and *salts*, with often a trace of sugar and fats.

Coagulation of Blood.—If blood be drawn and allowed to stand it coagulates. This is produced by the solidification of the fibrin. All albuminoids pass more or less easily from the liquid to the solid state. Albumen, or white of egg, is solidified by heat at 160°, or by alcohol; casein of milk is solidified by acid and heat at 70° to 80° or less. Fibrin solidifies much more easily; exposed to air or touching any foreign body, it solidifies at once. The causes and conditions of the solidification of fibrin are still under discussion.

If blood be drawn and allowed to stand, as already said, it coagulates first into a tremulous jelly by the solidification of the fibrin. If it continues to stand, gradually the fibrin *contracts* more and more firmly, and a liquid is squeezed out. The whole mass thus separates into two parts, clot and serum. The clot consists of the solidified fibrin and the entangled globules. The serum consists of a solution of albumen and salts, with perhaps a trace of sugar. This is shown in the following schedule:

Blood

Fresh.		Coagulated.
Globules	Red.	Clot.
	White.	
Plasma, solution of.........	Fibrin.	
	Albumen.	Serum.
	Salts.	
	Sugar, a trace.	
	Fat, a trace.	

In fever blood coagulates more slowly. In coagulation the globules have time to settle a little before the solidification of the fibrin, leaving thus the characteristic *buff coat* of fevers on the top. If salt be added to fresh blood it prevents coagulation, and the globules will settle to the bottom. If freshly drawn blood be stirred or whipped with a bundle of twigs or wires, the whole of the fibrin coagulates on the wires or twigs as fleshy strings, and may be withdrawn. The defibrinated blood will no longer coagulate. This is important, because it is necessary sometimes to transfuse the blood of one person into the veins of another, or even the blood of an animal into the veins of a man. If so, then the blood so transfused must not be liable to coagulation.

Functions of the Blood.—1. *Plasma.*—The plasma may be regarded as essentially the finished result of albuminoid food, although it contains in small quantities many other substances for use or for elimination by excretory organs. It is essentially the peptones, sanguified, vitalized, and ready for use. Its fundamental function, then, is tissue building—i. e., repair and growth of tissue. Its peculiar property of easy change from liquid to solid form is eminently adapted for this purpose. Its liquid condition is necessary for circulation; its solid condition is necessary for making tissue. Further than this, however, the whole process of assimilation, or change from blood to tissue, is still enveloped in mystery.

2. *Red Globules.*—The function of these is better understood than any other part of the blood. They are undoubtedly carriers of oxygen from the air to the tissues for combustion of their waste. This it does by virtue of the property of hæmoglobin, already mentioned. This substance takes oxygen from the air in respiration, becomes oxidized as oxyhæmoglobin, is carried to the tissues, and there gives up its oxygen for the combustion of waste. It is easily seen, therefore, why an abundance of red globules is necessary for health and vigor.

3. *White Globules.*—The function of the white globules is much more obscure. In some way little understood they seem to vitalize the blood, for, as already seen, they are really living protozoa. It will be remembered (page 329) that as soon as these enter the chyle in the mesenteric glands this fluid becomes endowed with the property of coagulation. Again, it is believed that these globules act as scavengers of the blood, removing microbes and other offending substances by inclosing and devouring them after the manner of rhizopods (page 346). Again, as already seen, these corpuscles crawl about and change their shape like amœba. When the blood stagnates, as in inflammation, they actually squirm themselves through the thin walls of the capillaries, and wander about in the tissues; and, in case of breaking down of the tissues and the formation of pus, they probably become the characteristic pus corpuscles.

Origin and Life History of Blood.—1. *Plasma*, as already explained, is essentially the sanguified and vitalized peptones. Sugar is also taken up into the blood, and in so far as it remains there is a constituent of the plasma; but normally there is only a trace of sugar in the blood of the *general* circulation, because it is quickly burned up. We shall speak of this more fully in another place.

2. *White Globules, or Leucocytes.*—We have already seen that these are formed in the mesenteric glands; but these are only lymphatic glands situated in the mesentery. Leucocytes are formed in *all* lymphatic glands wherever situated and at all times, whether chyle be passing through them or not. They are also formed in the spleen, for the blood of the splenic vein before it enters the vena porta is ten to twenty times richer in leucocytes than that of the general circulation. It seems certain, then, that the leucocytes are formed in

the lymphatic glands and in the spleen, and that the blood receives them while passing through these organs. How they disappear is not certainly known. Possibly they break up into so-called blood plates.

3. *Red Globules.*—These are constantly changing; they have, like all living things, a definite life history; they are born, mature, decay, and die. If the body is depleted of blood it quickly recovers its supply. If the blood of another animal be transfused into the veins of a man, at first two kinds of globules may be seen in the blood, but as time goes on the animal globules decrease and the human increase until only the human remain. The red globules are therefore being renewed all the time. Where do they come from? At one time they were thought to be transformed leucocytes; but this is probably not true. It is now believed that they are formed in the *red marrow of the bones*, and perhaps also in the spleen, by the division of certain large cells observed there. This is their *birthplace.* Their active life is in the circulation, doing their work of oxygen carrying. Their death place is probably the liver and the spleen.

Briefly, then:

Leucocytes are born in the lymphatics and the spleen.

Red globules are born in the bones and the spleen.

Red globules die in the liver and the spleen.

It would seem, then, that the spleen has many and important functions, but that it shares all these with other organs. May not this explain the singular fact that, although so important, yet it has been extirpated in the dog without *immediate* serious injury to health.

Now the blood goes everywhere, touches every tissue and every cell. (1) It carries food, and thus becomes the *all-nourisher.* (2) It takes up all waste and carries it to the appropriate organ of elimination, and thus becomes the *all-purifier.* (3) It takes oxygen to every tissue to consume waste and food by combustion, and thus generates heat and force, and thus becomes the *all-warmer* and *energizer.* (4) It acts also as a reservoir, especially for food. The food taken to-day is not used to-day, but the blood is drawn upon for heat and force and tissue repair and again resupplied. The blood is like a lake in irrigation or a bank in currency. (5) To a much less extent it is also a reservoir for waste; to a less extent because the urgency of waste removal is much greater.

Comparative Morphology of Blood.—In all *vertebrates* we have two kinds of globules, the red and the white. The white, or leucocytes, are substantially similar in all; but the red differ in size, shape, and structure in the different classes.

1. *Mammalian Blood.*—The blood of all mammals (Fig. 237) is substantially similar to that of man, already described. The red corpuscles (globules) are all small *circular*, *non-nucleated* disks. The only exception in *shape* is in the camel, in which they are elliptic instead of circular, but otherwise they are as stated above. In *size* they bear no apparent relation to the size of the animal; those of a mouse, on the one hand, and of an elephant, on the other, not differing in any marked degree from that of man. Even expert microscopists are in doubt whether the blood of a dog can be certainly distinguished from that of a man.

All mammals (except monotremes) are viviparous or young-bearing. Therefore this style of blood may be called *viviparous vertebrate blood.*

2. *Birds, Reptiles, Amphibians, and Fishes.*—All other classes of vertebrates—viz., birds, reptiles, amphibians, and fishes—have blood globules differing in size, shape, and structure from those of mammals, but similar to one

another in *shape* and structure, though varying in ,*size*. In shape they are all elliptic; in *structure* they are *nucleated;* in size they vary from nearly the size found in mammals in certain fishes to very many times that size in some amphibians. The largest are found in some tailed amphibians, such as the *proteus*, in which they are ten times the diameter or one hundred times the surface area of those of man (Fig. 237).

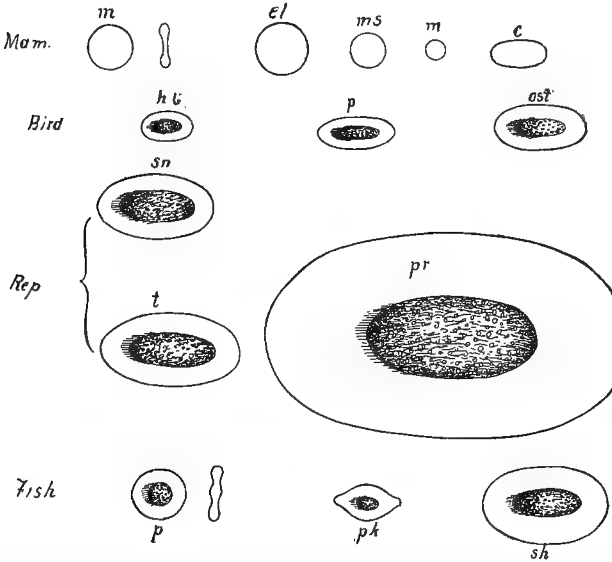

FIG. 237.—Blood of different classes of vertebrates, showing comparative sizes. All are equally magnified: *m*, man; *el*, elephant; *ms*, mouse; *m*, musk deer; *hb*, humming-bird; *p*, pigeon; *ost*, ostrich; *sn*, snake; *t*, toad; *pr*, proteus; *p*, perch; *pk*, pike; *sh*, shark.

All these classes of vertebrates are egg-laying. Therefore blood containing this style of red corpuscles may be called *oviparous vertebrate blood.*

All vertebrate blood (unless we except that of the *amphioxus*, which is very doubtfully a vertebrate) is *red.* Below this—i. e., in invertebrates—the blood is not red.*

3. *Higher Invertebrates.*—Among these we include arthropods, worms, mollusca, and echinoderms—i. e., all above cœlenterates; in other words, all that have a blood system and a true blood at all. In these the red corpuscles are wanting; only white corpuscles are found (Fig. 238). In these, therefore, the blood is colorless or nearly so. This kind we shall call *invertebrate blood.*

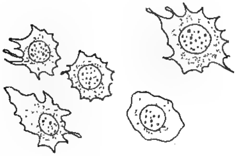

FIG. 238.—Blood corpuscles of a crustacean. (After Gegenbaur.)

4. *Cœlenterates.*—These include medusæ and polyps. In these, as already said (page 342), we have no true blood differentiated from digested food, nor blood system differentiated from the digestive system. The digested food carried by ciliary circulation is the nutrient fluid. This, therefore, may be called *food blood*, or cœlenterate blood.

5. *Protozoa.*—In these there is no circulating fluid of any kind.

The following schedule briefly expresses these facts:

Blood red.	1. Mammalian viviparous.	Blood — red, non-nucleated.
	2. Oviparous vertebrate blood — red, nucleated — birds, reptiles, amphibians, and fishes.	
Blood colorless.	3. Invertebrate blood — white, nucleated — arthropods, worms, mollusca, echinoderms.	
	4. Cœlenterate blood—white, no globules, food blood—medusæ, and polyps.	
	5. Protozoa — no circulating fluid.	

Embryonic Development of Blood.—Some of the above phases are found in the embryonic development

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* Some worms have a kind of red blood.

of mammals, and even of man. (1) In the earliest stages of egg development—i. e., before the organs are formed—there is, of course, no circulating fluid of any kind, no blood or blood system. This corresponds remotely to the lowest cell-aggregate animals in which there is yet no circulation. (2) The next thing observed is the *liberation* of *nucleated tissue-cells* along certain lines and the oscillatory movement of the liberated cells along these lines. This is the beginning of blood vessels and of a blood which has *colorless nucleated cells* like the *blood of invertebrates.* A heart is added later, by the development of a part of the vascular system. (3) The nucleated corpuscles become reddened, and we have now nucleated red corpuscles like the blood of the lower vertebrates. (4) The small non-nucleated round disks begin to appear among the others, which gradually disappear, and we have true mammalian blood.

It would seem now that in logical order we ought to take up the *circulatory system.* But the course of the blood is so wholly determined by its distribution through the *respiratory organs* that it would be impossible to understand that course, especially its comparative morphology, without a previous knowledge of the organs. These, therefore, must be first taken up. On the other hand, the *function* of respiration is wholly a *katabolic* process and the most important of all these processes, and must be treated along with these in the fourth chapter. Therefore, our plan will be to take up, first, the *morphology* of the respiratory organs in *vertebrates*, then the morphology of the circulatory system, also in *vertebrates;* then the morphology of circulation and respiration *together* in the invertebrates; and, finally, the physiology or *function* of respiration—which is the same in all animals. This, of course, will be treated with the *katabolic* processes, as the most important of all of them. All that is necessary now in regard to the respiratory function is only to remember that the *general object* of respiration is the aëration of the blood, and thereby the exchange of its CO_2 for oxygen of air.

SECTION II.

Respiratory Organs among Vertebrates.

Respiratory organs are of two general kinds, viz., *lungs* and *gills*. The one kind is adapted for *air breathing*, the other for *water breathing*. The general plan of the one is a complexly *in*-folded epithelial surface; of the other of a complexly *out*-folded epithelial surface (Fig. 239). In both cases alike the purpose is to expose as large a surface as possible to the oxygen of the air or the water. The two kinds are not homologous; the one is not transformed into, but, as already shown (page 242), *substituted* for the other. We take first lungs, and, of course, first of all the lungs of man.

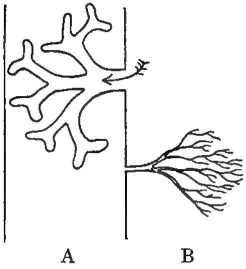

FIG. 239.—General plan of structure, A, of lungs; B, of gills.

I. LUNG RESPIRATION.

The Lungs of Man.—The lungs are by far the largest organ in the body, although in *weight* they are greatly exceeded by the liver. Their great volume is, of course, due to the contained *air*. Their grayish-purple color and soft, elastic feel is well known. They are a double organ, being divided into a right and left lung by the mediastinum.

Structure.—We have already said (page 204) that two tubes go down from the throat into the body cavity—the posterior one, the gullet, to the stomach, and the anterior one, the windpipe, or trachea, to the lungs. The one is soft and flaccid, but muscular; the other is a firm, open tube, being kept open by a series of cartilaginous rings. This is necessary in order that the air may come and go with the least resistance possible. The trachea is capped above by the larynx, as already explained (page 204). After a course of about five inches it divides into two great branches, one to each lung, called the *bronchi*. These are also ringed. The primary bronchi are subdivided into secondary bronchi, and these again into tertiary, and so on until the tubes become of capillary fineness and correspondingly numerous. This is shown diagrammatically in Fig. 240. They finally terminate in minute cells or cellulated cells (Fig. 241). The ringed structure continues, except in the smallest subdivisions and the terminal cells. The terminal cells are $\frac{1}{100}$ to $\frac{1}{200}$ of an inch ($\frac{1}{4}$ to $\frac{1}{8}$ millimetre) in diameter, and their number has been estimated as 600,000,000.[1] Now conceive this mass of finely divided tubes and terminal cells, *lined* through-

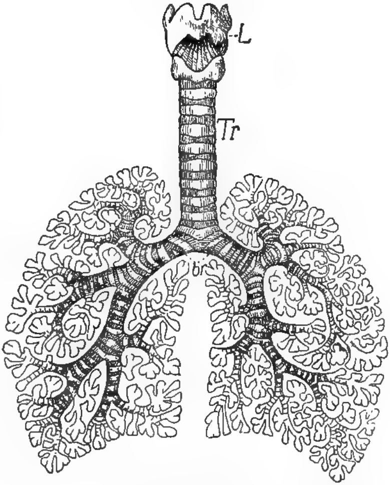

FIG. 240.—Diagram showing the general structure of the lungs of man: *L*, larynx; *Tr*, trachea; *br*, bronchi.

out with epithelial membrane—an extension of the mucous membrane of the mouth and throat—webbed together with loose connective tissue and invested with serous membrane, and we shall have a sufficiently clear idea of the general structure of the lungs.

The obvious purpose of all this is to expose as much surface as possible to the oxygen of the air. The minuter the ramification, the smaller the terminal cells; or the finer the sponge, the larger will be the surface. The area of the epithelial surface exposed in the lungs has been variously estimated from four hundred to fifteen hundred square feet. Now beneath this extensive epithelial surface the blood vessels ramify most minutely and exchange with the air CO_2 for oxygen (Fig. 242).

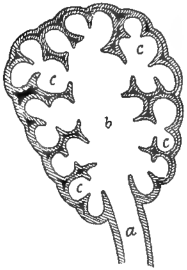

FIG. 241.—Termination of a capillary bronchus: *a*, bronchus; *b*, cell; *c*, cellule.

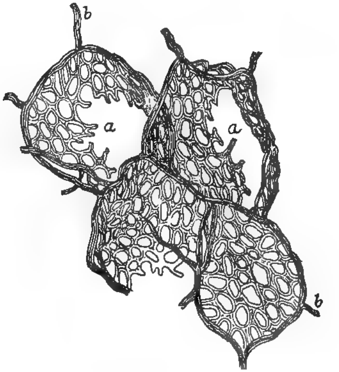

FIG. 242.—Showing the capillary blood vessels (*b*) ramifying on the surface of the cells (*a*).

But to make this exchange effective both the air and the blood must be in constant circulation. When the blood has discharged its CO_2 and taken in its supply of O it must get out of the way for other blood to do the same. Similarly, when the air has given up its O and taken in its supply of CO_2, it must move on and give place for other air. In the case of the blood the circulation is kept up by the mechanical action of the *heart;* in the case of the air, by the mechanical action of *breathing.*

Mechanics of Breathing.—The body cavity is divided by a thin transverse partition into an upper chamber, the *thorax*, and a lower chamber, the *abdomen.* In the one is found the lungs and heart, in the other the stomach, spleen, liver, intestines, kidneys, etc. The diaphragm is not a *plane*, or it could not be used for respiration. It is deeply concave below, or domelike. It is also a muscular partition, the fibers radiating from a clear membranous space in the middle—the skylight of this dome—in all directions and taking hold of the walls of the body cavity all around. Contraction of these fibers brings down the dome and flattens it. The arch of the dome is filled below by the stomach and spleen on the left and the liver on the right. These in their turn rest on the mass of convoluted intestines, and the whole is supported by the abdominal walls. Above the diaphragm the concave lower surface of the lungs rests directly on the upper convex surface of the dome. Although in *contact* with the viscera above and below, the diaphragm is not united with them.

Now, the thoracic, like the abdominal, cavity is lined with a smooth serous membrane. In the abdomen it is called the *peritonæum*, in the thorax the *pleura.* Like the abdominal, so the thoracic cavity is a *closed cavity*—i. e., the pleura lines the ribs, etc., and is then reflected to form the investing membrane of the lungs and heart. If it could be successfully dissected off it would form a continuous bag without a hole in it. The manner in which the pleura lines the thorax, is then reflected over the lungs as its investing membrane, and then between the two lungs as the mediastinum, is shown in Figs. 243

and 244. For greater clearness there is a space between the lungs and the walls. In reality they are in contact.

This description is necessary to make clear the mechanics of breathing, which we now proceed to explain.

Breathing consists in alternate expansion and contraction of the thoracic cavity by means of the respiratory muscles. The lungs are perfectly *passive* in the operation. To illustrate: Suppose we take a hand bellows and arrange a bladder within so as to connect with the nozzle, with no opening into the bellows, but only into the bladder, through the nozzle. Now, on expanding the bellows the air rushes in through the nozzle into the bladder and expands it, but no air enters the cavity of the bellows. On shutting up the bellows the air is again squeezed out from the bladder through the nozzle. In all these movements the exterior surface of the bladder and the interior surface of the bellows *never break contact.* But if there be an opening on the side of the bellows the air will rush in there and not fill the bladder.

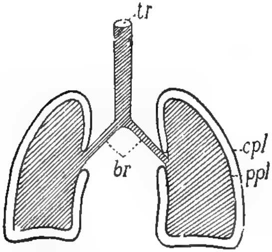

FIG. 243.—Vertical section through the lungs, showing the relation to the pleura: *tr*, trachea; *br*, bronchi; *cpl*, costal pleura; *ppl*, pulmonic pleura.

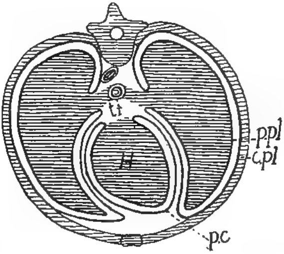

FIG. 244.—Horizontal section through the thorax: *tr*, trachea; *H*, heart; *pc*, pericardium; *ppl*, pulmonic pleura; *cpl*, costal pleura.

Application to Breathing.—So the lungs are placed in the thorax as the bladder in the bellows. If the thorax expands, air rushes in through the nostrils into the lungs, expanding them and keeping them in contact with the ribs. If the thorax contracts, it squeezes out the air through the nostrils. But if there be an opening into the thorax (by wound), then, on expanding the thorax, the air rushes in there, gets into the cavity instead of into the lungs, and the lungs do not fill.

Mode of expanding and contracting the Thorax.—This is done in two ways—viz., by the ribs and by the diaphragm. There are therefore two kinds of respiration—viz., costal or thoracic, and diaphragmatic or abdominal.

Costal Respiration.—The ribs do not run straight around the chest horizontally, but slope downward all the way. The simple lifting of the ribs, therefore, increases the whole transverse section of the chest. Now, between the ribs and connecting them there are two sheets of muscular fibers, external and internal. The fibers of the external sheet, *ex*, run obliquely downward and forward, those of the interior sheet, *int*, downward and backward (Fig. 245). The external sheet raises the ribs and expands the chest, the internal sheet pulls down the ribs and contracts the

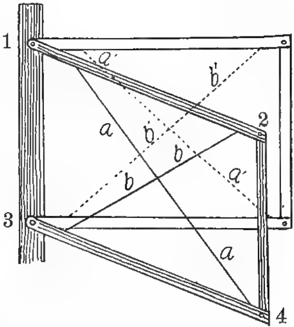

FIG. 246.—Diagram illustrating action of the intercostal muscles: *a a*, fiber of exterior sheet when passive; *a a′*, when contracted, *b′ b′* a fiber of interior sheet when stretched, and *b b* when contracted.

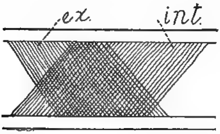

FIG. 245.—Showing two ribs and the intercostals between: *ex*, external, and *int*, internal sheet.

chest. Why this must be so is shown in diagram, Fig. 246. If 1, 2 and 3, 4 be two ribs connected with the backbone behind and the breastbone in front, and therefore compelled to *move together* and in the natural sloping position, and if *a a* represent one fiber of the external sheet, it is evident that if this fiber contracts it will elevate *both* ribs, because, although it pulls one up and the other down, yet the leverage on 3, 4, by which it pulls up, is greater than that on 1, 2, by which it pulls down; and since they must move together, the pair will move *up*. But upward movement *expands* the chest. Or, put it another way: Any position of the ribs will be assumed which *shortens the fiber* $a\ a$ to $a'\ a'$. For the same reason contraction of the fibers of the interior sheet ($b'\ b'$) will depress the ribs and contract the chest, because here the downward pulling acts with the greater leverage on 1, 2'. Therefore thoracic or costal respiration is accomplished by alternate contraction of the exterior and interior intercostal muscles. The one produces *in*spiration, the other *ex*piration.

Diaphragmatic or Abdominal Respiration.—This is accomplished by the alternate contraction of the diaphragm and the abdominal muscles. When the muscular fibers of the diaphragm contract, the high arch is brought down and the dome flattens. This increases the vertical diameter of the thorax as the intercostal contraction does the transverse diameter. But the descent of the diaphragm presses on the stomach and liver, and these again on the intestines on which they rest; and these in turn press outward on the abdominal wall, which therefore protrudes. This is *in*spiration. The stretched abdominal muscles reacting, by contraction, press on the intestines, and these upward on the stomach and liver, and these in turn lift the dome of the diaphragm and press on the lungs, squeezing out the air. This is *ex*piration.

These two kinds of respiration may be considered, and indeed may be used separately. Fig. 247, A, is a diagram representing pure thoracic, and Fig. 247, B, pure abdominal respiration. But the two are usually combined, and the whole body cavity enlarges and contracts as in Fig. 247, C. In labored respiration the thoracic predominates; in quiet respiration, and especially in sleep, the abdominal predominates. In men there is a slight predominance of the abdominal, in women of the thoracic.

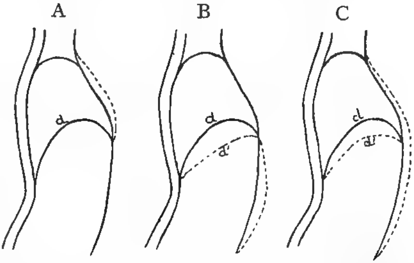

FIG. 247.—Diagrams showing the different kinds of respiration: A, pure thoracic; B, pure abdominal; C, mixed. The dotted lines represent the expanded condition.

Thus, then, the *in*spiratory muscles are the *ex*ternal intercostals and the diaphragm; the expiratory muscles are the internal intercostals and the abdominal muscles.

Coughing and *sneezing* are violent convulsive actions of the *ex*piratory muscles. It is a little singular that in popular literature, and even in many school text-books of physiology, these should be so often referred to convulsive action of the diaphragm. Of course, this is impossible since the diaphragm is an *in*spiratory muscle, and coughing and sneezing are *expulsive* efforts. Everybody knows that constant excessive coughing will produce soreness of the abdominal muscles. *Hiccough* is a spasmodic action of the diaphragm, and laughter a spasmodic alternate action of the inspiratory and expiratory muscles, with the latter predominating.

COMPARATIVE MORPHOLOGY OF VERTEBRATE RESPIRATION.

Mammals.—The respiratory organs and the mode of breathing among mammals do not differ from those of man. All mammals have a diaphragm, and therefore both kinds of respiration. On account of the horizontal position of the body, of course the body cavity is divided into an anterior and posterior instead of an upper and lower chamber.

Birds.—In birds we find large lungs of minutely spongy structure, and therefore a perfect aëration of the blood. They are, therefore, hot-blooded animals. Yet birds have no diaphragm. This, however, is of little disadvantage, as their thorax is large and abdomen small, and their thoracic respiration very perfect. It is interesting to note, however, that some birds, such as the ostrich, seem to have the beginnings of a diaphragm. In these, certain muscular fibers arise from the backbone and lowest ribs behind and take hold on the lung and pull it downward, and undoubtedly assist in breathing.

Reptiles.—Reptiles have no diaphragm; but since their ribs surround the whole body cavity to the hips, there seems to be no use for a diaphragm in them (Fig. 248). Probably the shortening of the rib series, in order to give greater freedom to the loin created the necessity

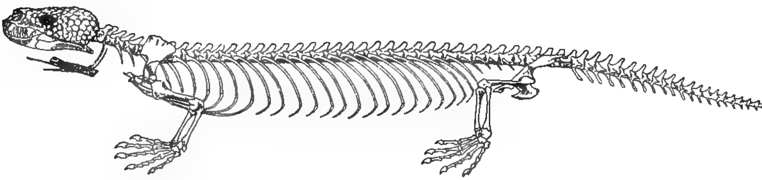

FIG. 248.—Skeleton of a lizard (*Heloderma*), showing how the ribs surround the whole body cavity.

of a diaphragm in mammals. The aëration of the bloo of reptiles, however, is very imperfect, for reptiles ar cold-blooded. This, however, is due not so much t imperfect respiration as to the coarseness of the spong structure of the lungs, and therefore the smaller surfac of contact of blood with air. It is due, also—as we sha see hereafter—to the fact that *only a part* of the bloo is exposed to the air.

Tortoise.—There is one order of reptile the mechanics of whose respiration is entirely peculiar—viz., th tortoise. Like other reptiles, they have no diaphragn and therefore can not have this kind of breathing, bu neither can they have costal breathing, for their ribs ar immovably consolidated with the shell. The problen then, is how to expand the body cavity. As might b expected, therefore, the breathing of tortoises and turtle is exceptional. It is effected partly by muscular sheet which arise from the shell and pass over the viscera including the lungs, and by contraction compress ther and force out the air; and partly (especially in lan tortoises) by movements of the shoulder and hip girdle In most vertebrates the shoulder girdle is movable, bu the hip girdle is fixed; but in tortoises *both girdles ar movable.* In inspiration the shoulder girdle is draw forward and the hip girdle backward, and the bod cavity is thus enlarged. In expiration there are contrary movements—i. e., backward of the shoulder girdl and forward of the hip girdle, and the body cavity i contracted.*

Amphibians.—The respiration of these, e. g., th frog, is far inferior to even that of reptiles. (1) Th lung is no sponge at all, but only a sac. There is n trachea and very short bronchi. The glottis opens fror

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* Charbonnel-Salle, An. des. Sci. Nat., vol. xv, art. 6, 1883.

the throat almost directly into two large sacs; only each sac is *sacculated* on the interior, so as to increase its surface (Fig. 249). The aëration of the blood, therefore, is still more imperfect than in reptiles. (2) Again amphibians not only have no diaphragm, but they have *no ribs.* The mechanics of their breathing is entirely different from all previously mentioned. It is not diaphragmatic nor yet costal. It is a *throat respiration.* The submaxillary space, or space between the branches of the lower jaw, is large. This space is pressed down by the hyoid or tongue bone, and thus draws air through the nostrils and fills the throat. The nostrils are then closed, the throat is brought up, and the air is forced down into the lung sacs. This, of course, swells the walls of the abdomen, which, reacting by contraction, drive out the air again through the nostrils.

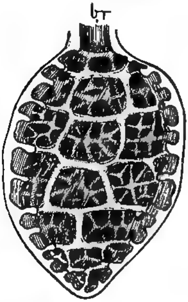

FIG. 249.—One lung of a frog: *br*, bronchus.

This is the lowest form of lung respiration and grades into gill respiration. In fact, all amphibians in their early larval life breathe by gills, and only afterward by lungs. This, therefore, leads us naturally to gill respiration.

2. GILL RESPIRATION.

The most perfect form of gills, or *branchiæ*, is found in the ordinary typical fishes (teleosts). We take this as a type.

Take any typical fish, such as a perch or a salmon (Fig. 250). We observe on each side of the head an opening extending downward and forward to beneath the chin. It is covered with a movable flap, the operculum or gill cover. Lift this and look in; we see se eral rows of *red gill fringes*, between which there a openings into the throat—*gill slits.* Look next into th throat; we see several cartilaginous arches, *gill arche* with gill slits between. On these arches are fixed th gill fringes, extending backward and outward unde

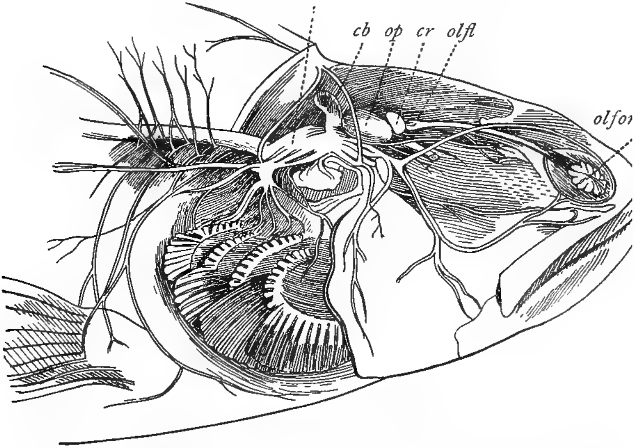

FIG. 250.—Head of a fish with parts cut away so as to show the brain, spin cord, and the gills: *cb*, cerebellum; *op*, optic lobes; *cr*, cerebrum; *ol* olfactory lobes; *olforg*, olfactory organ. The opercle is removed ar the gill fringes partly removed, so as to show the four gill arches.

the opercle. The fringes are thin, flat plates fixed t the gill arches, like the teeth of a fine comb to its sten They are very thin, very numerous, and arranged in tw rows (Fig. 251). The purpose is to make as much su face as possible. They are intensely red, because th blood is profusely distributed in them. The blood passe along each arch, and is thence distributed on the fringe

Mechanics of Breathing.—The mouth is opene and the throat enlarged and filled with water. By shu ting the mouth and contracting the throat the water forced through the gill slits. The current, quickened by bringing down the opercles, runs between all the teeth of the fringes and aërates the blood there. This series of movements is y have nly repeated.

anics of ëration of the blood in gill different fro y means of the *free* oxy-tioned. It i in the water. If water be boostal. , as to drive out all the dissolved gases, it will no longer support life. If the gills of fishes be kept moist and the fringes separated, life out of water may be maintained for some time. Some fishes have the means of keeping their gills moist. Such fishes often leave the water and crawl about on land for hours.

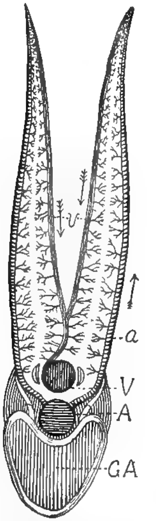

FIG. 251.—Transverse section of a gill arch *GA*, showing a pair of fringe plates; *A*, artery; *V*, vein; *a*, arteriole; *v*, veinlet.

Variation of Gills among Fishes.—We have taken teleosts as a type. Gills of other fishes may be regarded as modifications of this type. In *sharks* (Fig. 252) there are *five* gill slits in the throat and five corresponding separate gill openings on the sides of the head, but *not covered by an opercle.* There are cartilaginous *plates* between the gill openings and the throat slits, and on these are fixed the gill fringes. The breathing is similar to that already described in teleosts, except in regard to the movements of the opercle.

In the lamprey (petromyzont, Fig. 253) we have seven holes in the throat and corresponding holes on the side of the neck, connected each by a *pouch.* In this pouch are arranged the fringes. The breathing is the same (Fig. 254).

In the lowest of all fishes, if fish it may be callec viz., the lancelet (amphioxus), the enormously larg

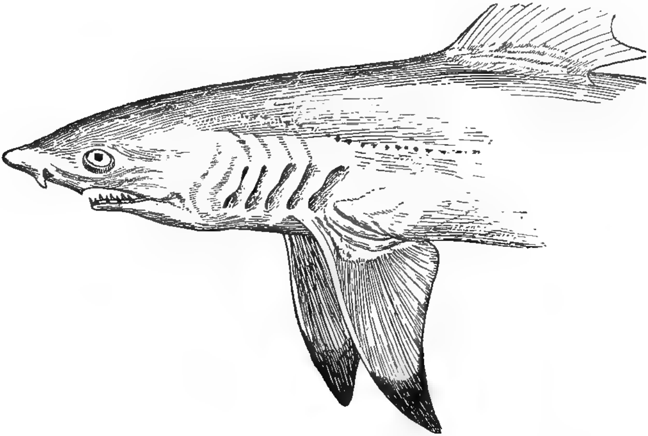

FIG. 252.—Anterior portion of a shark (*Carcharias*), showing the five gil openings.

throat has many—twenty or more—slits, edged with imperfect fringes (Fig. 255).

Going up now the other way, in *ganoids*, such as th garfish or bony pike (*Lepidosteus*) of our American fres waters, and in the *Polypterus* of the Nile, we have a opercle and gills like the teleosts, but gill breathing i

FIG. 253.—Petromyzon marius, showing the seven branchial openings. (After Cuvier.)

supplemented by a little air breathing by means of ai taken into a vascular air bladder (Fig. 256).

Finally, in the most reptilian of all fishes, such as th protopterus of Africa, the lepidosiren of South America

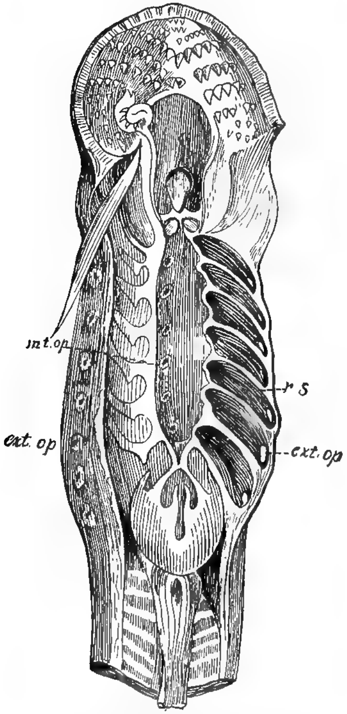

FIG. 254.—Anterior portion of a lamprey with parts cut away so as to show the structure of the gill pouches : *int op*, interior opening ; *ext op*, exterior opening ; *r s*, respiratory sac.

and the ceratodus of Australia, besides their gill breathing by organs of the pattern of the teleosts, we have nostrils opening into the throat and very good lungs, almost as good as some amphibians, and therefore both lung breathing and gill breathing in about equal proportions. These are therefore called *lung fishes.*

Classification of Fishes by Respiratory Organs. — The form of the respiratory organs is so characteristic of the various orders of fishes that Huxley has made it the basis of classification. According to Huxley, fishes may be divided into six orders—viz., (1) *Dipnoi*, or nostril breathers, represented by the protopterus, lepidosiren, etc. These breathe equally by lungs and gills. (2) *Ganoids*, so called

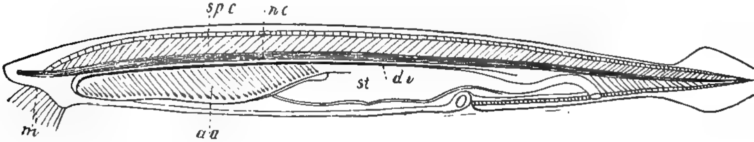

FIG. 255.—Amphioxus : *spc*, spinal cord ; *nc*, notochord ; *dv*, dorsal vessel ; *st*, stomach ; *aa*, aortic arches or gill arches.

from their bony, enameled scales, which form a complete external armor. They supplement their gill breathing by a little air breathing. They were abundant in early geological times, but are now represented by the *Lepidosteus*, *Polypterus*, etc. (3) *Teleosts* (perfect bone), or ordinary bony fishes. They breathe wholly by gills, but in some the air bladder opens into the throat. (4) *Elasmobranchs* (plate gills), represented by sharks, skates, rays, etc. (5) *Marsipobranchs* (pouch gills), represented by the lampreys or conger eels. And (6) the *pharyngobranchs* (throat gills), represented only by that strange creature the amphioxu or lancelet. The schedule will express this classification in brief space:

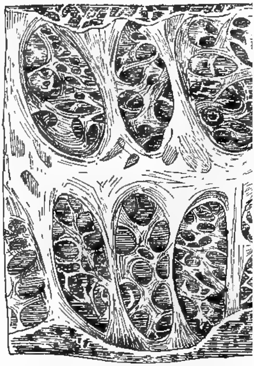

FIG. 256.—A portion of the interior of the air bladder of Lepidosteus (enlarged), showing its cellular structure.

1. Dipnoi—lung fishes.
2. Ganoids—armored fishes.
3. Teleosts—typical fishes.
4. Elasmobranchs—sharks, skates, etc.
5. Marsipobranchs—lampreys.
6. Pharyngobranchs—lancelet.

TRANSITION FROM GILL BREATHING TO LUNG BREATHING.

We have seen pure gill breathing in teleosts an lower fishes. We saw pure lung breathing attained i the higher amphibians, as frogs, etc. Now, in the highe fishes and the lower amphibians we find every gradatio between—not, indeed, by *transformation* of the one *int* the other, but by *substitution* of the one *for* the other. Some steps we have already seen in the higher fishes, the others we find in the lower amphibians. In *Ganoids* we saw a little supplementing of gill breathing by the taking of air into a vascular air bladder. This is the beginning of lung breathing. In *Dipnoi* we saw an equal gill breathing and lung breathing. Now, in the lowest amphibians, such as the siren and others, we find but little advance on the *Dipnoi*. These breathe both by gills and by lungs all their lives. They do not lose their gills. They are called *perennibranchs*. The necturus and the siren are examples of these (Fig. 257). In the next higher amphibians the gill breathing is confined to their early life. They drop their gills in maturity. These are called *caducibranchs*. The salamanders and water dogs are of this kind. In the highest amphibians, such as frogs and toads, the changes are greater. These lose their gills somewhat earlier, and also lose their tails, and are therefore called *anura*, or tailless. Therefore amphibians may be classified thus:

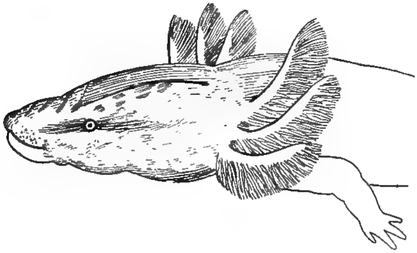

FIG. 257.—Head and gills of Necturus.

Anura—tailless, such as frogs and toads.

Urodela—tailed, { *Caducibranchs*.
{ *Perennibranchs*.

Here there is one great distinction between amphibians and reptiles. Amphibians all breathe by gills during some period of their lives, and some always; reptiles never.

Again, fishes are all *throat* breathers. They must be, for they must force the water outward through their gills. Now, amphibians also have gills, at least in early life, and therefore must be throat breathers, at least in early life. When they become lung breathers they retain the throat method, and now force air *down* to the lungs, instead of water out through the gills. Reptiles never have this mode of breathing.

Amphibians were once regarded as an order of reptiles, but now they are recognized as not only a different class, but as more nearly related to fishes than to reptiles.

SECTION III.

Blood Circulation—Vertebrates.

Having given the general morphology of respiratory organs among vertebrates, we are now prepared to give the course of circulation, and show how it is controlled by the necessity of aëration. We take first mammals, and, as usual, man as the type.

Circulation in Man.—Circulation means a going round in a *circle* and a coming back to the starting-point. A machine for circulation implies (1) a pumping organ and a system of pipes. In the animal body the pumping organ is the heart and the pipes are the blood vessels. It implies (2) two kinds of pipes, one carrying away, efferent; the other bringing back, afferent. In the animal body these are called *arteries* and *veins*. There is, however, a third kind, connecting these with one another, called the *capillaries*. The arteries carry *to* the tissues, the capillaries *among* the tissues, and the veins back again *from* the tissues. The arteries carry blood to the work, the veins bring it back after the work, but the work itself is done in the capillaries. (3) In a good machine the pump must have two chambers—a receiving chamber and a pumping chamber. This latter chamber must be strong, for it urges the whole circulation. In the animal body the receiving chamber is called the *auricle* and the pumping chamber the *ventricle.*

(4) But there are two distinct objects to be subserved in animal circulation—viz., the nutrition of the tissues and carrying away of waste, on the one hand, and *aëration* of the blood on the other. In the highest animals these two are wholly differentiated and jealously kept separate. There are, therefore, two complete circulations and two hearts, each with its two chambers (auricle and ventricle) and its three kinds of blood vessels (arteries, veins, and capillaries). But for convenience the two hearts are put together and form a *four*-chambered heart, but separated by a dead wall between. The blood starts out from the heart on its journey in one circulation and comes back; then starts again on the other circulation and comes back, and so on continuously. The first is called the greater or *systemic* circulation, and its function is to nourish the tissues and carry away their waste. The second is the lesser or *pulmonic* circulation, and its function is to aërate the blood or exchange the CO_2 of the blood for O of the air. Of the two hearts, that on the left side is the systemic and that on the right the pulmonic. Through each of these circulations the whole blood passes, and so jealously are they kept separate that although the whole of the blood passes through the lungs in the pulmonic circulation, yet none of it is used for the nutrition of the lungs, but this work is done by a small branch from the systemic circulation.

General Course of the Circulation.—Fig. 258 gives a very generalized idea of this course. The arrows show the course of the current. Commencing at the left ventricle, the blood is thrown into the great arterial trunk, called the *aorta.* This forms an arch—the aortic arch—from the top of which go branches to the upper part of the trunk, arms, and head, while the main part turns downward, running along the backbone, branching and rebranching to supply the viscera and lower trunk and limbs. It left the heart bright blood; in the tissues it gives up O and takes CO_2 and becomes dark blood, and in this condition is brought back—that from above by the vena cava descendens, that from below by the vena cava ascendens—to the right auricle. The right auricle contracts and throws it into the right ventricle, which in turn throws it through the pulmonic artery, to be distributed through the capillaries of the lungs, where it discharges its CO_2 and retakes O, and becomes again bright blood. Thence it goes to the left auricle and to the left ventricle, to commence again another round.

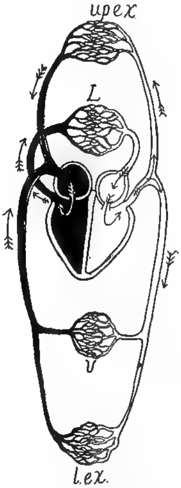

FIG. 258.—Diagram showing general course of the circulation: *upex*, upper extremities and head; *lex*, lower extremities; black = dark blood.

Such is a most generalized formula. Fig. 259 shows it still very diagrammatically, but yet a little more in detail, especially as to the great branches supplying the liver, spleen, the intestines, and the kidneys, and the corresponding veins to make up the vena cava ascendens. Mark here the *portal vein* already spoken of (page 328) and its singularity.

In both these diagrams the arterial trunks are on one side and the venous trunks on the other. This is merely for convenience of diagrammatic representation. Really they lie close together along the backbone, as if the diagram were folded along the middle backward. Again, of course, the aorta in its lower part divides into two branches to supply the legs, and similarly the great branches going upward divide to supply the arms and head. These are not represented.

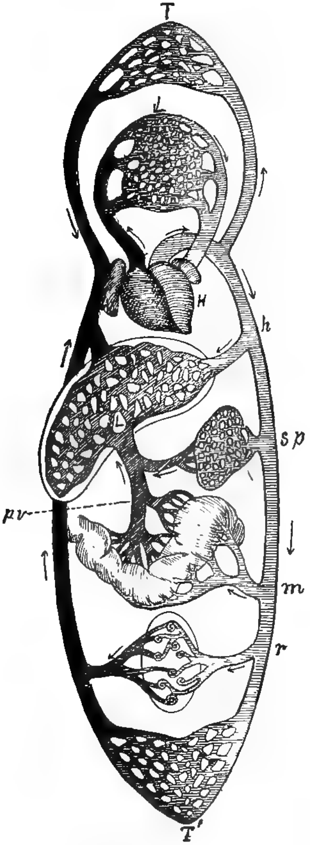

FIG. 259.—Diagram showing course of circulation, more in detail: *T* and *T'*, tissues; *h*, hepatic artery; *sp*, splenic artery; *m*, mesenteric artery; *pv*, portal vein; *r*, renal artery; *H*, heart; *L*, lungs. The arrows show the course of the circulation. (After Dalton.)

For pure purposes of *physiology* the formula expressed in these diagrams is sufficient. But there is so peculiar a significance in relation to evolution in the great *outgoing* (not incoming) vessels of the heart that a more particular account of these is necessary. The aorta coming out of the *left* ventricle (Fig. 260), as already seen, makes an arch to the left and goes down to form the abdominal aorta. From the top of the arch it sends off upward three branches. The first is on the right side of the arch (left in the diagram). This again divides into two branches, one (carotid) going to the right side of the head and brain, the other (right subclavian) going to the right arm. The next in order coming from the arch is the left carotid. It goes to the left side of the head and brain, while the third and last bends to the left as the left subclavian and goes to the left arm. In the *right* heart all that is necessary to point out is the great outgoing vessel. The pulmonary artery arches to the left to go to the left lung, but sends back a branch of equal size to supply the right lung. The significance of all of these special arrangements will be seen later.

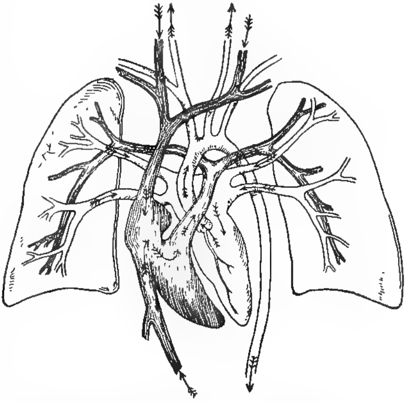

FIG. 260.—The heart and the great vessels, incoming and outgoing. The right heart and its vessels are shaded.

The change from the bright blood to the dark blood takes place in the capillaries of the tissues; the change back again to bright blood in the capillaries of the lungs. Therefore in the *systemic* circulation the *arteries* carry bright blood and the veins dark blood, while in the pulmonic circulation the *reverse* is the case. All the blood going from the lungs to the heart and from the heart to the tissues is bright blood, and all the blood from the tissues to the heart and from the heart to the lungs is dark blood. Or, all the blood that ever visits the left heart is bright and all the blood that ever visits the right heart is dark. It is common to speak of the bright blood as *arterial* and the dark blood as *venous.* This is true only of the systemic circulation. The very reverse is true of the pulmonic circulation.

Structure of the Heart: The Valves.—We have given the *course* of the circulation; but the question arises, How is it maintained continuously in the same direction? This is done in the same way as it is done in machinery—viz., by a system of *valves* which prevents its going in the other direction.

The *valves* of the heart are of two kinds, which may be called *curtain* valves and *pocket* valves (semilunar valves). The former are between the two chambers of one heart, to prevent the blood from going back to the auricle; the latter are placed at the outlet of the ventricles into the great outgoing arteries, i. e., at the base of the aorta and the pulmonary artery to prevent the blood discharged into these arteries from falling back into the heart when the ventricle expands again. The *curtain* valves I so call because they are thin membranous curtains between the two chambers of the heart and opening always into the ventricle. From the interior of the wall of the ventricle there go *cords* (heart strings), which are attached to the edges of the curtain, so that while these open easily into the ventricle, allowing blood to pass (Fig. 261, A), yet if blood attempts to pass back

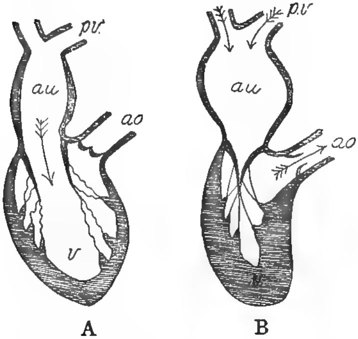

FIG. 261.—Left heart. A, auricle contracted, ventricle expanded. B, ventricle contracted, auricle expanded: *pv*, pulmonary vein; *au*, auricle; *v*, ventricle; *ao*, aorta.

into the auricle they flap back, pressing against one another, closing the way, and are held in place by the cords * (Fig. 261, B). The valve between the *right* auricle and ventricle is called the *tricuspid*, because it has three cusps. That in the left heart is called the *bicuspid*, as having only two cusps.

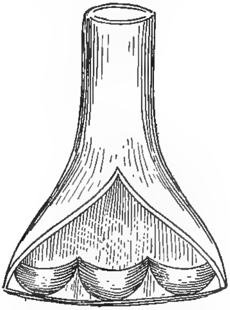

FIG. 262.—Aorta cut open and spread out to show the semilunar valves.

The *semilunar*, or *pocket* valves are at the base of the aorta and of the pulmonary artery, three in each, of crescentic shape like shallow pockets, which, when filled, press against each other from three sides and completely close the artery. When the ventricle contracts, the blood rushes into the artery, the valves pressing close against the wall; but as soon as the ventricle relaxes, the pockets fill, press against each other, and close the gate (Fig. 262).

We now follow again the course of the blood, showing how the valves work. Blood, dark from the tissues, enters the right auricle. The auricle contracts, the curtains flap wide open into the ventricle, and the blood enters freely. The ventricle contracts, the blood shuts the curtains, they are held in place by the cords, and the blood is forced into the pulmonic artery. When the ventricle relaxes, in order to fill itself again, the pocket valves fill and close the way. The action on the other side of the heart is the same. The blood coming from the lungs into the auricle is thrown into the ventricle and the door closed behind. It is therefore forced upward into the aorta and again the door closed behind. It is

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* To appreciate the action of these they must be examined on a heart or a good model.

the flapping and closing of these valves, both curtain and pocket, that make the characteristic sounds of the beating heart, and it is the inflammation and thickening of them that constitute the commonest and gravest disease of the heart.

Blood Vessels.—[illegible]d cont.—In the dissection of a body the arteries can [illegible] in [illegible]ce distinguished from the veins by the fact that t[illegible]em o[illegible]ain their form as pipes, while the thinner veins colla[illegible].

Structure.—They consist of three coats: an *outer* thin, very tough fibrous coat; a middle elastic, muscular, or proper coat; and an inner lining epithelial coat. The outer coat gives toughness, the middle gives elasticity and firmness, the inner is in some way necessary to the life and integrity of the blood. In tying an artery the surgeon draws the thread until he feels the cutting of the middle and interior coats, and then secures the knot. In aneurism the inner and middle coats are broken and the tough outer coat is extended into a pulsating tumor. The firmness of the middle coat is necessary to maintain an open passage for the blood under powerful action of the heart, and by its elasticity it yields to the impulse of the heart, and then, contracting, it carries forward the blood in its course. It is this propagated wave of swelling and contraction that constitutes the *pulse.* From the great aortic trunk, of course, the arteries branch and rebranch until they become of capillary fineness in all the tissues, and finally grade into the capillaries proper. The blood does not ooze through the arterial walls; these pipes do not leak. The nutrition of the tissues is the function of the capillaries alone.

2. *Veins.*—The veins are much larger than the arteries, and yet far less conspicuous, because they collapse when empty. *In structure* they are similar to the arteries. They, too, have three coats, but the middle coat is much

thinner. The veins are found in two positions: (1) deep-seated and accompanying the arteries, and (2) superficial or subcutaneous. It is the subcutaneous which show bluish through the skin, especially in blondes. The greater size and number of the veins is necessary because the blood current is sluggish in them as compared with the arteries.

Valves.—The comparative sluggishness of the current is also the reason for the existence of semilunar valves in veins. These are not in triplets, as at the opening of the great arterial trunks into the heart. They are scattered along their course irregularly and singly. They can not, therefore, arrest, but only *retard* the backward flow of the blood. The knotted appearance of the subcutaneous veins when gorged with blood (as when the arm is corded) is due to the filling of these valves (Fig. 263).

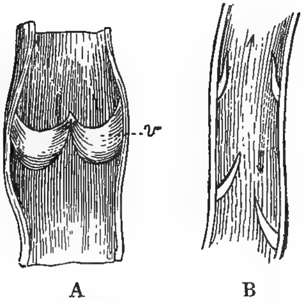

FIG. 263.—Vein: A, cut open so as to show the valves, *v*; B, section through the valves.

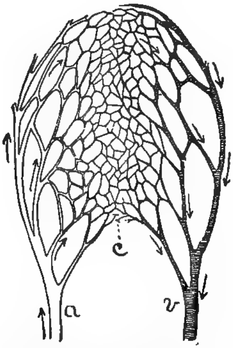

FIG. 264.—*a*, arteriole; *v*, veinlet; *c*, capillary network. The arrows show the course.

3. *Capillaries.*—The blood system is a *closed system* of pipes. There is no discharge of the blood from the arteries into the tissues and taking up of it from the

tissues by the veins; on the contrary, the arterial pipes are continuous through the capillaries with the veins. Yet the capillaries are quite distinct from both in several respects: 1. *In the mode of branching.* The arteries branch and rebranch *tissueward*, growing ever smaller and more numerous; the veins run together *heartward*, growing ever larger and fewer; the capillaries branch and run together again, without change of size and without definite direction, forming a fine *network* (Fig. 264). 2. *In the course of the current.* The course of the current in arteries and in veins are alike *fixed.* In capillaries it may go in *any direction*, although it works deviously toward the veins. 3. *In structure.* The walls of the capillaries are of extreme thinness, and therefore permeable to the *blood plasm*, and in case of engorgement even to the leucocytes. 4. *In function.* The function of the arteries is to carry the blood, *without loss by leakage*, to the tissues; the function of the veins is to bring it back without loss to the heart; the function of the capillaries is to allow the blood to exude into the tissues. In any good system of irrigation the pipes carrying the water to the soil and bringing it back from the soil must be *impervious*, but those running among the soil must be permeable. The blood system is such a system of pipes. So jealously is this function of nutrition restricted to the capillaries that even the arteries and veins themselves are not nourished by the blood that flows through them, but must have their own arterioles, veinlets, and capillaries (vasa vasorum) for that purpose. In the capillaries, then, the nutritive matters of the plasma and the oxygen of the red globules exude into the tissues (exosmose), and the waste matters of the tissues and the CO_2 transude into the blood (endosmose). But the exact nature of this process is yet obscure.

COMPARATIVE MORPHOLOGY OF THE BLOOD SYSTEM IN VERTEBRATES.

Mammals.—In all essential features the blood system of mammals is exactly the same as that of man, already described. All mammals have a four-chambered heart—i. e., a double heart with no communication between except through the capillaries. They all, therefore, have a complete double circulation, with the whole blood passing through both.

Birds.—Birds have also a double heart and complete double circulation. There is only one thing worthy of note, and that only on account of its significance in the evolution of birds. It is that the aortic arch turns to the *right* instead of to the left, as in mammals.

Reptiles and Amphibians.—The first important variation from the model already given is found in these. The heart of the reptile and the amphibian is *three*-chambered instead of four-chambered. If the heart of mammals and birds may be compared to two tenements, each with two chambers, joined together, but with dead wall between, then the heart of reptiles and amphibians may be compared to one tenement with a suite of three rooms. With such a structure it is impossible to have a complete double circulation. The pulmonic circulation is only a branch of the systemic, and therefore only a *part* of the blood passes through the lungs to be aërated, and therefore also not pure oxygenated, but more or less *mixed blood goes to the tissues.*

Course of Circulation.—Fig. 265 is a schematic diagram showing the course of circulation in reptiles. The heart, as is seen, consists of two auricles and one ventricle. The blood is thrown out of the ventricle into the aorta, which makes an arch, but there divides and sends a large branch to the lungs, while the main branch goes to the tissues above and below. That which goes to the tissues comes back to the right auricle as dark, and that which goes to the lungs to the left auricle as bright blood. The auricles contract and empty their contents into the common ventricle as *mixed* blood, which is again thrown into the aorta, to be again divided between the tissues and the lungs.

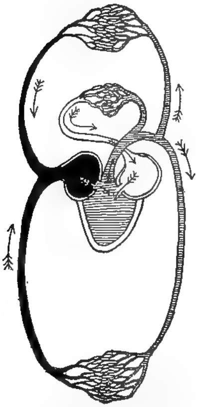

FIG. 265.—Diagram showing the structure of the heart and the general course of the circulation in reptiles and amphibians.

There is a double reason why these animals are *cold-blooded:* (1) We have already seen that the lungs in them are a *coarse* sponge, and therefore the surface of exposure of the blood to the air is small; (2) and now we see that not the whole but only a part of the blood is oxidized in each round of the circulation. *Mixed blood* goes to the tissues. The metabolic process—i. e., waste and supply—is less active, and therefore the *heat is less.*

We have given in Fig. 265 a schematic diagram illustrating the general principle. This is sufficient for physiology but not for morphology, and especially not for evolution. The actual course is far more complex, and it differs also a little in different reptiles. We can not take all the cases. We take the typical case of the *lizard.*

The lizard (Fig. 266) has three aortic arches on each side—six in all. What conceivable use can there be for six aortic aches? The blood from two of these—the lower one on each side—goes to the lungs to be aërated, while that of the other four, after sending a branch to the head, unite to form the abdominal aorta which goes to supply the viscera and lower portion of the trunk and limbs.

I have taken the lizard as a type both of the three-chambered heart and of the structure of the aortic arches. But there is considerable variation among reptiles in both of these, and these variations show transitions such as one would expect on the theory of derivative origin of organic forms. For example, the perfect three-chambered heart is general among reptiles, as in lizards and tortoises, and also in all amphibians —e. g., in frogs, toads, etc.; but in serpents there is an imperfect four-chambered heart. The ventricle has been partly but not completely divided. In the crocodile there is a *complete four-chambered heart*, but still the blood is mixed in the course of the circulation, though not in the heart. Also the arches are more or less modified from the type given above.

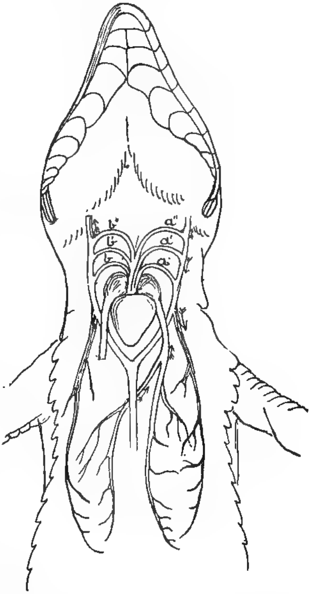

FIG. 266.—Showing heart and outgoing blood vessels of a lizard. The arrows show the course of the blood. (After Owen.)

Fishes.—Fishes have a still simpler, viz., a *two-chambered heart*, and yet the whole of the blood passes through the gills to be aërated, and therefore pure blood only goes to the tissues. Fig. 267 is a schematic diagram showing the general course of the circulation in a teleost fish. The blood from the single ventricle, *v* (dark blood), is thrown into the aorta, which then divides into three or four arches on each side, in order to pass through the gill *arches*, to be distributed in the gill fringes and aërated there. From the gill fringes it is gathered as bright blood, and passes on to unite into the abdominal aorta *without going back to the heart*, and is then distributed to the tissues. Its course is shown by the arrows.

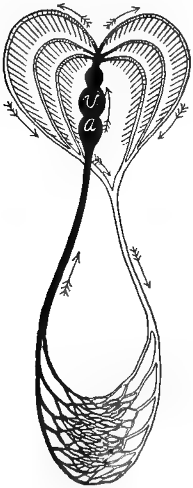

FIG. 267.—Diagram showing structure of the heart and course of circulation in fishes.

This is schematic. The actual course is shown in Fig. 268, which shows also the change in the blood in passing through the gill fringes. As to variation from this type, it is sufficient to say that in sharks there are five arches, in lampreys seven, and in lancelets twenty or more on each side. On the other hand, the *Dipnoi* or lung fishes, lepidosiren, and protopterus, like the reptiles, have only three on each side.

Several interesting questions occur here. (1) We have seen that fishes have a *single* heart. Which is it? Physiologically it is a *pulmonic heart*, for nothing but dark blood visits it. But morphologically it doubtless corresponds to the whole double heart of mammals. (2) Is the circulation of reptiles or that of fishes the better? Physiologically, in some respects the one, in some respects the other is the better. The reptile has the advantage of air breathing, which aërates the blood more efficiently than water breathing, but, on the other hand, the fish has the advantage of aërating the whole of the blood, and therefore sending only aërated blood to the tissues, while in reptiles only a part of the blood is aërated, and therefore mixed blood goes to the tissues. *Per contra*, however, the fish has again the disadvantage of the blood not coming back from the gills to the heart to receive fresh impulse, so that the heart has to do the double duty of sending the blood by one impulse through two capillary circulations. In a morphological point of view the reptile is undoubtedly the higher form of circulation, for it is a transition to the still higher forms. The three-chambered heart is a transition from the two-chambered heart of the fish to the four-chambered heart of birds and mammals, and what might be called the one-and-one-half circulation of reptiles a transition from the *single* circulation of the fish to the *double* circulation of the bird and mammal.

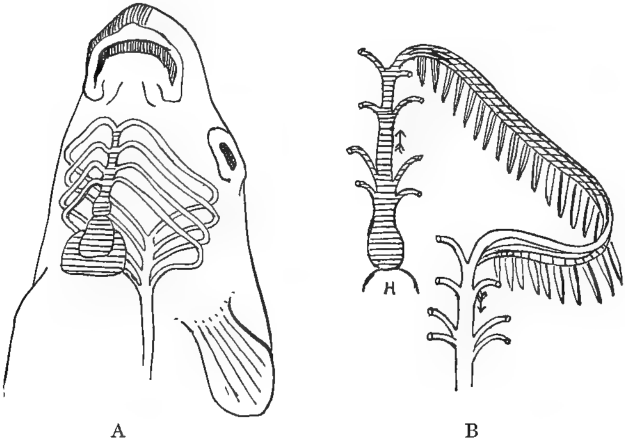

FIG. 268.—A, heart and gill arches of a fish; B, one arch with fringe (after Owen); *H*, the heart. Dark blood is shaded.

BEARING OF SOME OF THESE FACTS ON EVOLUTION.

1. **Heart Structure.**—There is abundant evidence, both in the taxonomic series (animal scale) and the embryonic series, that the heart has been gradually formed by a process of evolution, for nearly all the stages may be traced from the simplest pulsating organ to the complex four-chambered valvulated structure of the higher animals. The steps are briefly as follows:

(1) First there is a simple pulsating *dorsal vessel*. This stage is found in many invertebrates, and even among vertebrates in the amphioxus.

(2) Then comes a one-chambered heart. This is found in many invertebrates.

(3) Then comes the two-chambered heart of many invertebrates, and of fishes among vertebrates.

(4) Then the three-chambered heart of the typical reptile and amphibian.

(5) Then the imperfect four-chambered heart of serpents, the two sides of the heart still connected.

(6) Then the perfect four-chambered heart of crocodilians; but even yet a connection (ductus arteriosus) by which the blood to the tissues is mixed, and therefore the circulation is not completely double.

(7) The final step is the perfect four-chambered heart and complete double circulation of birds and mammals.

Nearly all these steps are found also in the embryonic development of mammals and even of man.

2. **Origin of Aortic Arches.**—But by far the most interesting question in this regard is the origin and meaning of *aortic arches*.

We have already drawn attention to the fact that the aortic arch in the bird turns to the *right*, and not to the left, as in mammals. This shows that mammals did not come from birds by modification, for the intermediate stages from a right-turning to a left-turning arch would be unsuitable. We will show that they both came from reptiles, but by different routes.

Again we have drawn attention to the strange fact that in reptiles (e. g., the lizard) there are three arches on each side—six in all. Why six arches? Surely, one arch is enough: for birds and mammals have but one, and they have the most perfect circulation of all. The key to the mystery is found in the circulation of fishes. Fishes have three or four or five arches on each side, but the reason in their case is obvious. They are the *gill arches.* They are absolutely necessary for the aëration of the blood. If the reptiles came by modification from fishes, then the explanation of their numerous arches is plain. They are *the remnants of ancestral gill arches.* Some of the highest of fishes, the *Dipnoi*, have only three arches on each side like the lizard. These fishes also breathe by lungs as well as by gills. Now, suppose in successive generations the lungs of *Dipnoi* to increase in efficiency, and the gills to dwindle and dry up, it is evident that exactly the structure found in the lizard would remain.

That exactly this did take place in the history of the evolution of vertebrates is proved by the fact that every step is found now among fishes, amphibians, and reptiles, and furthermore that the same change takes place now in the *individual* history of every one of the higher amphibians, as, for example, the frog. We have already traced the successive steps, through teleosts, ganoids, *Dipnoi*, perennibranchiate amphibians, caducibranchiate amphibians, to reptiles. We wish now to trace the same change in the individual development of a frog.

The frog, as we all know, is at first a tadpole; without feet, swimming only by the tail; without lungs or air breathing—in fact, breathing only water by gills. In this state it is essentially a fish. Now this fishlike gill-breathing animal changes into a lung-breathing land animal,

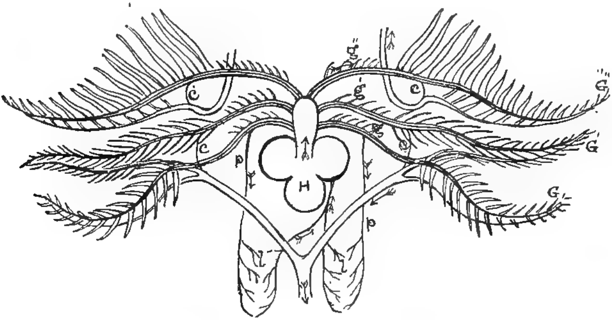

FIG. 269.

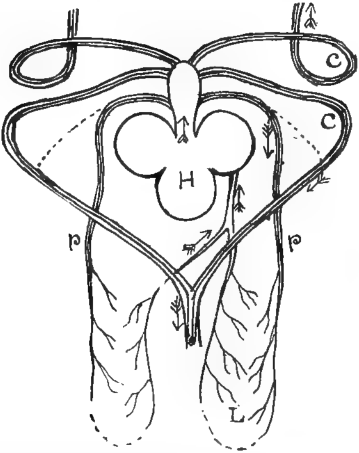

FIG. 270.

FIGS. 269, 270.—Diagrams showing the change of the course of blood in the development of a frog. Fig. 269, the tadpole stage. Fig. 270, the mature condition: *H*, heart; *G G' G''*, external gills; *g g' g''*, internal gills; *c c*, connecting branches in the tadpole; *p p*, pulmonary branches.

and in doing so the gill arches are changed into aortic arches before our eyes. The process is a little more complex than I have represented, because the amphibian has *external* as well as internal gills. But the same was doubtless true in the evolution of reptiles. How, then, does the change take place? Fig. 269 represents the circulation of the embryo or tadpole, and Fig. 270 the adult. In the embryo (Fig. 269), although all the blood goes through the gills, yet note rudimentary vessels to the rudimentary lungs, not yet used, and also rudimentary vessels connecting gill arch to gill arch. Again note in the adult (Fig. 270) remnants of dried-up gill vessels. The letters are the same in the two figures, and the arrows show the direction of the current.

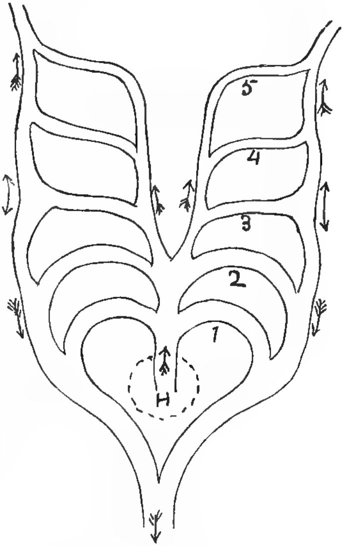

FIG. 271.—Ideal diagram representing the primitive aortic arches. (After Rathke.)

We have thus proved the origin of the aortic arches of the lizard. Now, *the same is true of all aortic arches*, even those of man himself.

Birds and Mammals.—In birds and mammals the modification has become so great as to obscure the homology. The proposition to be proved is that the great *outgoing* vessels of the heart are the modified remnants of gill arches. Indeed, this is obvious enough if we take the early embryonic condition of a bird or mammal. The early mammalian, and even human, embryo has gill slits, several of them on each side of the neck, and gill arches through which the blood passes, forming, in fact, several aortic arches on each side. But afterward these are modified into the outgoing vessels of the heart, and their original arch form is retained only by *one*. The manner in which the change takes place is shown in Figs. 271, 272, and 273. Fig. 271 shows in a schematic way the primitive aortic or gill arches (almost exactly represented now by sharks), and Figs. 272 and 273 the same as it is modified for a bird and mammal respectively. Finally, Fig. 274 is the mammalian heart slightly modified to suggest the homology of the several parts.

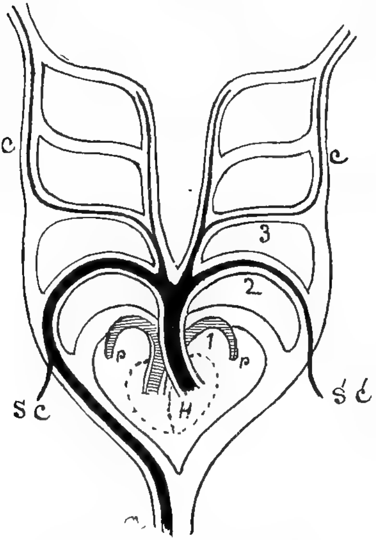

FIG. 272.—Modified for bird.

To explain: The gill arches are five in number on each side, as in a shark (Fig. 271). The two upper pairs are soon aborted, even before leaving the class of fishes, and only three on each side remain to be accounted for. These are the three found in the lizard, and inherited with modifications in birds and mammals. These are therefore the only ones we have to deal with. Fig. 272 shows the modification of this formula in birds. It is seen that the first arch on each side becomes the two pulmonic arteries, one going to each lung, precisely as in the lizard and in the frog. Of the next pair of arches, that on the right (left of the figure) becomes the aorta, and that on the left the subclavian on that side. The subclavian on the other side is a branch of the aorta. The next pair became the carotids. They are already so in the lizard and in the frog (see Fig. 270).

In the mammals the modification is a little different. It is seen (Fig. 273) that of the *first* pair of arches, that on the left is the pulmonary artery, which in this case supplies both lungs, while that on the right is aborted. Of the *second* pair, that on the *left* (right of the figure) becomes the aorta, while that on the right the subclavian on that side. The *third* pair, as in birds, and as already in reptiles and amphibians, becomes the carotids. In Fig. 274 we give a figure of the heart, with its outgoing vessels a little modified, to suggest their homology, and numbered so as to show the corresponding parts.

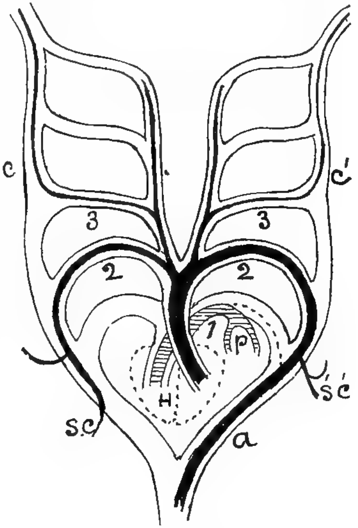

FIG. 273.—Modified for mammal.

We see now that the only difference between bird and mammal in the aorta and other outgoing vessels of the heart is that among the various arches different ones have been selected to be retained in the arch form as aorta and for pulmonary artery and for subclavian. In both cases—i. e., in both birds and mammals—the steps of the change may be traced in the embryo.

Illustration of a Fundamental Law of Evolution.—It is a fundamental law of evolution that the *phylogenic* or evolution series is repeated more or less perfectly in the *taxo-ontogenic* or embryonic series, and often also in the *taxonomic* or classification series. An admirable illustration of this is found in the life history of amphibians.

We have already seen that the frog in its embryonic development is at first a legless, gill-breathing animal.

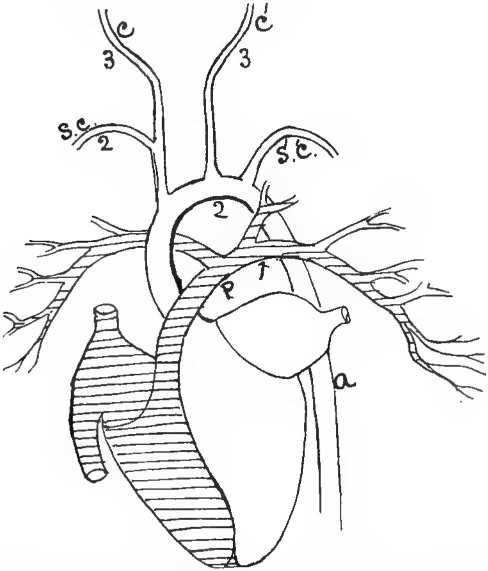

FIG. 274.—Diagram of mammalian heart: *a*, aorta; *p*, pulmonary artery; *sc*, *s'c'*, subclavium on each side; *c*, *c'*, carotids on each side. The numerals give the ordinal numbers of the arches as in the previous figures.

If it stopped there it would be classed as a *fish;* but it goes on. It next gets itself legs and an imperfect lung, and breathes now both air and water. If it stopped here it would be classed as a *perennibranch;* but it goes on. It next loses its gills and improves its lungs and breathes air only, but retains the tail. If it stopped now it would be classed as a *caducibranch;* but it still presses on. Finally, it loses its tail and reaches the highest order of amphibia—the *Anura.* Of course the caducibranchs and perennibranchs pass through similar stages, but stop earlier. So much for the similarity of the ontogenic and taxonomic series.

Now, there can be no doubt that the phylogenic series is also similar, that the amphibians were evolved from the dipnoan fishes, and that in the course of geologic times they passed through the same stages—i. e., perennibranch, caducibranch, and became anurous only in Tertiary times. Thus the three series are similar. All these facts are expressed in the following diagram:

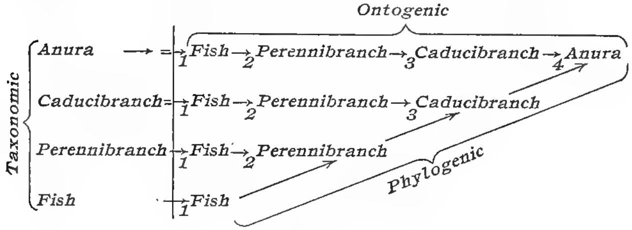

FIG. 275.

SECTION IV.

Morphology of Respiratory and Circulatory System in Invertebrates.

Some General Introductory Remarks.—(1) In the case of *vertebrates* we gave first the morphology of the respiratory organs and then of the circulatory organs separately, but in the case of the invertebrates we shall take these together in each class treated.

(2) In the vertebrates the blood system is a system of closed pipes, continuous and without either discharge or intake, except by exosmose and endosmose. In nearly

all invertebrates there are blood-sinuses or reservoirs in various parts of the body, into which the blood is discharged, and from which it is again taken up.

(3) In vertebrates the oxidized blood is bright red and the deoxidized blood dark purple-red, and this, therefore, is the conventional mode of representing these two kinds of blood in colored diagram. In default of color we have used unshaded and shaded spaces to represent the same. We continue to use the same purely conventionally, although in the case of invertebrates there is no such marked change in color or shade.

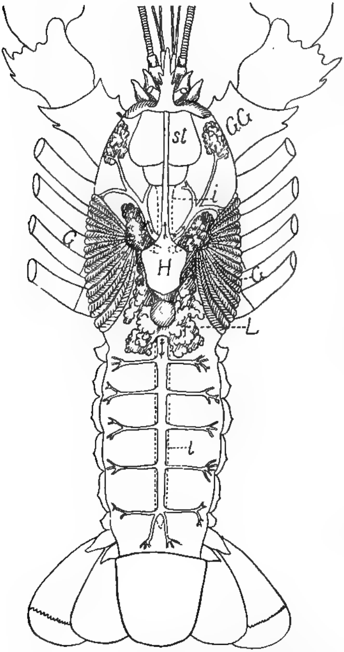

FIG. 276.—Lobster with the carapace taken off: *st*, stomach; dotted tube, *ii*, intestines; *L*, liver; *H*, heart; *G*, gills; *GG*, green gland.

(4) The diversity among invertebrates is so extreme that it is impossible to do more than select a few striking examples from each department.

(5) In this selection we pass over insects for the present to come back to them. The reason is the same which induced us to do so in giving the comparative morphology of the eye (page 162)—viz., that in respiration and circulation insects are entirely peculiar, and are outside of the direct line of evolution, or of increasing complication as we go up.

Arthropods: Crustacea.—As an example of the department of arthropods, therefore, we select *crustaceans.*

Respiratory Organs.—Take a crab, lobster, or crawfish, and remove the carapace or dorsal shell. Directly exposed on each side and occupying a large part of the upper surface are seen a great number of tapering, finely lamellated or tufted organs, Fig. 276, *G G.* These are the gills. They are not *within* the body cavity, but wholly *outside*, in special respiratory chambers, opening by a large cleft on each side of the shell (Fig. 277). The gills are, some of them, connected each with a limb or a maxilliped, and are indeed appendages of these, and some with the thoracic walls. The fine mosslike structure is a device for producing as large a surface as possible of exposure of the blood to the aërated water.

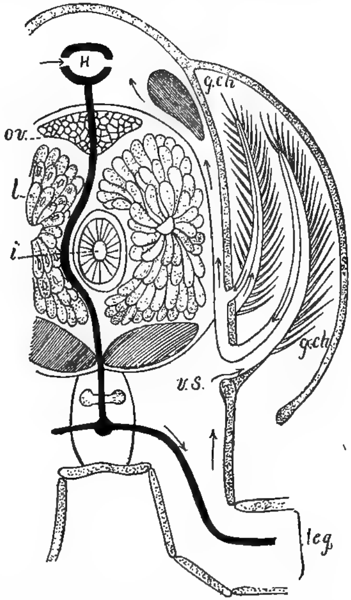

FIG. 277.—Transverse section through a crawfish, showing the gills: *gch*, gill chamber; *H*, heart; *l*, liver; *i*, intestine; *vs*, blood sinus. The arrows show the course of the blood.

Breathing.—The exchange of water is effected partly involuntarily by *ciliary currents*, partly in some by the action of the maxillipeds, and partly—i. e., when in active locomotion—by the movements of the limbs, and therefore of their appendages, the gills.

In all animals violent motion causes increased respiration, but the mechanism may be different. In vertebrates increased motion causes, of course, increased waste in the blood. This in time stimulates the respiratory centers (medulla), and determines through the pneumogastric nerve increased action of the respiratory muscles. In crustaceans the increased motion produces increased respiration not only through the mediation of the nervous system, but also directly by the motion of the gills themselves.

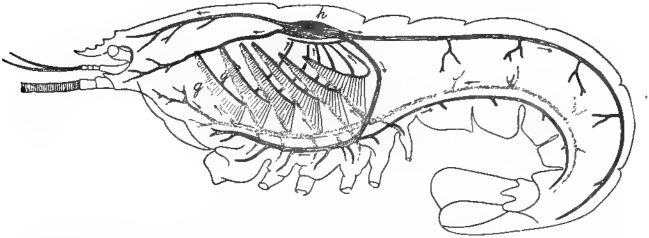

FIG. 278.—Side view of the circulatory and respiratory system of a crawfish: *h*, heart; *g g*, the gills. The arrows show the course of the blood.

Circulation.—In the dorsal region behind the middle, immediately beneath the carapace and between the points of the gills, is seen the heart (*H*, Fig. 276), a large organ whose pulsations throw the blood fore and aft through the large dorsal arteries (*a a*) to the tissues. Another artery goes from the heart downward to form the sternal artery, and thence to the limbs and lower part of the body (Fig. 277). From the tissues the

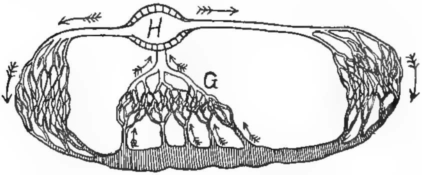

FIG. 279.—Diagram showing the general course of the circulation in crustaceans: *G*, gills; *H*, heart.

blood is gathered into large reservoirs (blood sinuses), one on each side, running along near the base of the limbs. From these sinuses the blood is again taken up by the veins, to be distributed to the gills (Fig. 278) and oxidized, and thence to the heart, to be again distributed to the tissues. Fig. 279 is a schematic diagram showing the general course.

It is plain that the heart in this case is physiologically a *systemic* heart, since it contains only oxidized blood, and throws it to the tissues.

MOLLUSCA.

Acephala, or Bivalves.—Take as an example the river clam (*Anodonta*). Fig. 280 is a longitudinal, and Fig. 281 is a transverse section. The gills, two on each side, are cellulated sacs, very much divided, to produce large surface of contact with the aërated water.

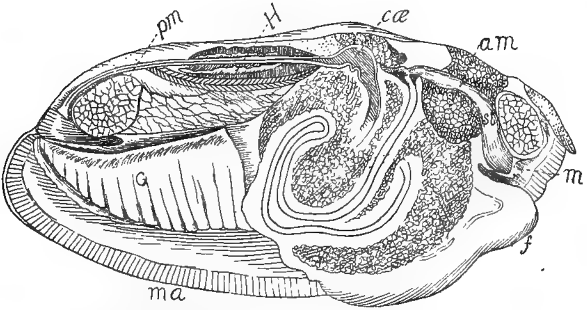

FIG. 280.—Vertical longitudinal section of Anodonta: *pm*, *am*, posterior-anterior adductor muscles; *m*, mouth; *st*, stomach; *cæ*, cæcum; *H*, heart; *f*, foot; *G*, gills; *ma*, mantle.

Breathing.—Ciliary currents pass from behind forward through the gills, determining oxidation of the blood, and thenceforward to the mouth for alimentation, as already explained (page 338), and then backward to carry away excretions. In siphonated bivalves, as already seen, the currents pass down one siphon and out the other.

Circulation: Heart.—In the longitudinal section (Fig. 280) *H* is the heart, through which runs the intestine, *i*, on its way to the vent. The heart consists of one ventricle, and usually of two auricles. The relation of the heart to the gills is seen in Fig. 282. The blood from the ventricle is thrown fore and aft to the tissues, thence gathered from capillaries by veinlets and emptied into several sinuses scattered in different parts of the body. From these it is taken up by the branchial vessels, which distribute it to the gills, where it is aërated, and thence by branchial veins to the auricles on each side and to the ventricle, which again throws it in the tissues. A schematic diagram which represents this would be similar to that used for crustaceans (Fig. 279), except for the addition here of the auricle, but the details of the circulation are, of

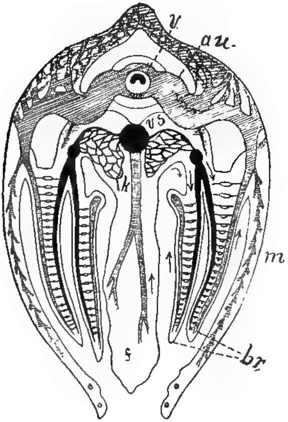

FIG. 281.—Transverse section of Anodonta: *v*, ventricle; *au*, auricle; *vs*, venous sinus; *m*, mantle; *br*, branchiæ or gills; *f*, foot; *k*, kidneys. The arrows show the course of the circulation.

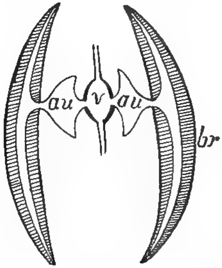

FIG. 282.—Diagram of heart and branchiæ of a bivalve, viewed from above: *v*, ventricle; *au*, auricle; *br*, branchiæ.

course, quite different. Like the crustacean, also, the heart is a systemic heart—i. e., aërated blood fills the heart and is distributed to the tissues.

Gastropods, Univalves.—Take, for example, a snail. These are air breathers. As already said (page 340), there are four openings of the body in front. These are (1) the mouth, (2) the genital opening in the immediate vicinity, (3) the vent, and (4) the pulmonic opening beneath the shell on the right side. We are concerned now only with this last. It opens into a sac immediately beneath the anterior upper portion of the shell (pulmonic sac), on the interior of which are profusely distributed capillary blood vessels.

Breathing.—The change of air seems to be effected by a *muscular arched* membrane just beneath the lung sac, which may be compared to a diaphragm. The contraction of this membrane lowers the arch, expands the lung sac, and draws in the air. This contraction, of course, compresses the viscera, on which it rests. On the relaxation of the membrane the natural elasticity of the compressed viscera lifts the arch and expels the air.

Circulation. — The heart has three chambers, two auricles and a ventricle. Contraction of the ventricle throws the blood to the tissues, whence it is gathered into the sinuses, and thence it is again taken up and distributed over the inner surface of the lung sac, where it is aërated and then returned to the heart, to be distributed again to the tissues as *aërated* blood.

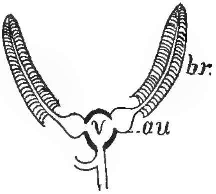

FIG. 283.—Diagram of heart and branchiæ of a Gastropod : *v*, ventricle ; *au*, auricle ; *br*, branchiæ.

We have taken the higher air-breathing forms of snails and slugs, but in water breathers, of course, we have gills instead of lung sacs and water breathing instead of air breathing. In Fig. 283 we show in diagram the relation of heart and gills in these.

In many lower forms (*Nudibranchiata*) the gills consist of external tufted projections from the skin, waving in the water.

Cephalopoda.—These are the highest of mollusca. They are always water breathers, but their gills are quite complex and efficient. The gills of these animals lie on each side, in the dorsal region, and the breathing is by the contraction of the hollow *water-filled* muscular mantle, which throws out the water through the siphon (see Fig. 226, page 341), and its own elasticity restores again its form and draws in the fresh water.

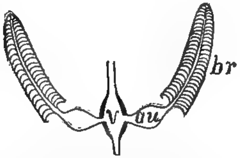

FIG. 284.—Diagram of heart and gills of dibranch Cephalopod: *v*, ventricle; *au*, auricle; *br*, branchiæ.

Circulation. — In dibranchs (two-gilled) or naked cephalopods, such as the squid and cuttlefish, there are two auricles, one to each gill; in tetrabranchs (four-gilled) or shelled cephalopods, such as the nautilus, there are four auricles. In all there is but one ventricle. The relation of the heart to the gills is seen in Fig. 284.

ECHINODERMS.

As an example of these we take the starfish (*Asterias*).

Respiration.—The respiration of these is performed in two ways: 1. The whole body is hollow and the body cavity is only partially filled with the viscera, leaving a large perivisceral space filled with water. Contraction of the whole body presses out the water through a multitude of pores (Fig. 285, *a a*), while fresh water is drawn in by the restoration of the body form. The contained water is stirred about by ciliary currents and the blood in all the viscera aërated. 2. The second method is by

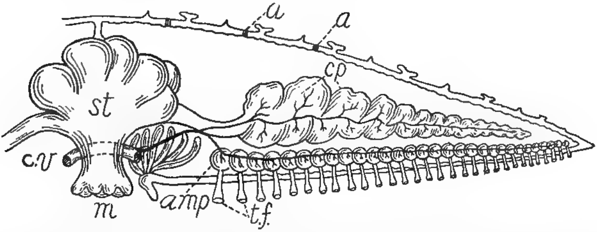

FIG. 285.—Section through one arm of a starfish: *st*, stomach; *m*, mouth; *cp*, cæcal pouches; *amp*, ampullæ; *tf*, tube feet; *cv*, circular vessel or heart from which go the blood vessels; *a a*, openings into the perivisceral cavity.

the vesicles of the *ambulacra.* On the underside of each of the five arms there is a longitudinal space perforated with rows of holes (ambulacra), through which project hollow tentacles, which are used for walking (tube feet). Each hollow tentacle is connected with a vesicle within (ambulacral vesicle, or ampulla), so that corresponding with the rows of ambulacral tentacles on the outside there are rows of ambulacral vesicles within (Fig. 285 and Fig. 286). These vesicles are connected with the aquiferous system, characteristic of echinoderms, in such wise that they can be filled with water and again partially emptied and the water changed.

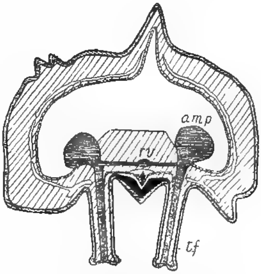

FIG. 286.—Transverse section of an arm of a starfish: *amp*, ampulla; *tf*, tube feet. (After Parker.)

Circulation and Aëration.—The heart in these is a pulsating organ, extending from a vascular ring under the dorsal skin above to another vascular ring surrounding the mouth below (*cv*, Fig. 285). From these rings go vessels to the end of each arm, which distribute blood to all the viscera. This blood is aërated on the spot by the water in the perivisceral cavity. Moreover, a portion of the blood is specially aërated by distribution on the ambulacral vesicles.

In addition to these two methods the highest echinoderms, such as the *Echinus*, have tufted external gills attached around the mouth.

CŒLENTERATA.

Thus far we have a distinct blood system. The three systems—food system, blood system, and respiratory system—are well differentiated. But in the cœlenterates these three are not yet completely separated. The digested food serves as blood, and the digestive system as blood system. Neither is there any respiratory system distinct from either, for the aëration of the tissues takes place through the contact of water on the outside and ciliary circulation of the food mixed with water on the interior surface.

Taking the polyp (actinia) as example, as already shown (Fig. 232, page 344), food taken into the stomach, *s*, is retained by pyloric contraction until digested, then dropped into the general cavity, and mixed with fresh sea water. The mixture is stirred about by ciliary currents and directly aërates the tissues. Also the tissues are similarly aërated by contact with sea water on the whole exterior surface.

PROTOZOA.

Finally, in the protozoa there is no circulation of any kind, nor is there any interior aëration, but the living protoplasm is directly aërated only by contact of water with the external surface.

This kind of aëration is sufficient for animals so low in the scale of life, and especially of so *small size*, for in these small animals the surface is large in proportion to the bulk. But with increasing size, since bulk increases as the cube while surface only as the square of diameter, it is evident that the same degree of aëration can not be effected without some device to increase the surface of contact—i. e., a respiratory organ; and this must be still further increased when the organization is higher as well as the bulk greater. And then, last of all, for greater efficiency the whole is relegated to an *internal* surface.

The same is true of the nutritive system proper—i. e., food system and blood system. In a small body sufficient food may be taken directly by a simple surface, external or internal; but in a large body the absorbing surface is not great enough, and many parts are too far away from the absorbing surface. There must be a system of vessels to carry nutriment to distant parts. This is the blood system. To illustrate: In a small island no elaborate system of internal carrying trade is necessary, for all parts are near the coast where products are delivered. But as the island becomes larger, and especially as the commercial life becomes higher, the internal carrying trade becomes more elaborate.

INSECTS.

It will be remembered that we passed over these because the whole plan of their circulation and respiration is entirely different and wholly out of the line of gradual simplification which we otherwise find. In all other classes the respiration controls the course of the blood, and was taken up first; but in insects the blood system controls the character of the air system, and therefore the blood system must be taken up first.

Blood System.—Insects are very highly organized animals, and yet their blood system is very simple and incomplete, far more so than in mollusca or even echinoderms.

Along the dorsal aspect of the body, immediately beneath the chitinous shell, there is a long, valvulated, pulsating vessel—dorsal vessel (Fig. 287). This may be called the heart. The valvules are so arranged as to direct the course of the blood continually *forward.* This dorsal vessel divides into several arterial branches at its anterior end, and receives several venous branches at its posterior end. The anterior branches discharge into the tissues forward, while the posterior branches suck in from the tissues behind. This is apparently all that there is of true vessels. In vertebrates the blood system is a closed system of pipes. In the higher invertebrates there are indeed a number of reservoirs scattered about the body; but still the blood system is essentially a vascular system. But in insects there are no vessels at all except the large vessels of the heart, but the tissues are everywhere full of minute intratissue spaces (*lacunæ*) connected with one another in *all directions.* Now, by the continuous discharge of blood in front and the sucking up of blood behind, it is evident that the blood must work round among the tissues without definite channels, but in a general way backward, to be taken in again into the heart and forced forward. This, therefore, is called *lacunary circulation.* There are also probably valvular open-

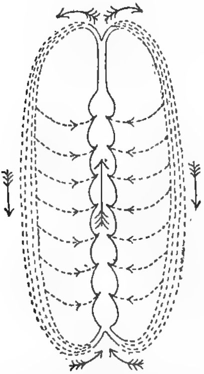

FIG. 287.—Diagram showing the heart and general course of the circulation in insects.

ings on the sides of the heart by which blood may be taken in. The diagram (Fig. 287) is an attempt to represent schematically the general course of the circulation. The dotted lines represent the lacunary circulation without definite vessels.

The difference between this lacunary circulation and a true vascular circulation may be illustrated by an irrigation system. The circulation of vertebrates may be compared to a pump and a system of pipes closed throughout and impermeable until the soil to be irrigated is reached and there permeable. After use the overplus of liquid is again gathered into impermeable pipes and returned to the pump to be again used. The circulatory system of an insect, on the contrary, is like a pump with short pipes discharging on the soil in front and sucking up from the soil behind. But the soil, instead of being penetrated in all directions by pipes which confine and guide the currents, is covered with *little pools* connected by *channels.* Under these conditions the water would work around in an indefinite way, and be sucked up behind, to be used again.

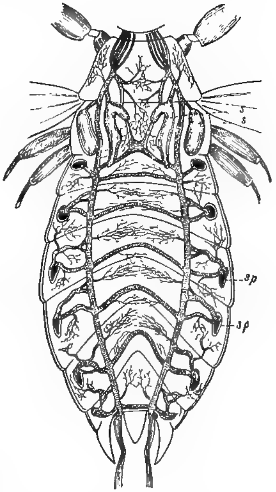

FIG. 288.—Tracheal system of an insect: *sp sp*, spiracles; *s s*, air sacs.

Respiratory System.—Now, it is this peculiar mode of circulation that compels the very exceptional kind of respiratory apparatus. Insects are active, and somewhat warm-blooded animals, and therefore require a perfect aëration of the blood; but with a lacunary circulation this is impossible in any *localized* organ. In a pipe system the whole of the blood may be made to go through an organ *localized in* some part, but in a lacunary system a local organ can receive only its small share of the blood. Evidently, then, if the blood can not go to the air, there is nothing left but that the *air must go to the blood.* This is exactly what it does. The air, by means of ramifying tubes, is carried to every part of the body and aërates the blood on the spot everywhere.

Air Tubes; Tracheæ.—On the margins of the dorsal part of the chitinous shell are openings, one on each side of each movable joint. These openings (spiracles) connect by a short tube with a long *lateral tube* extending on each side the whole length of the body (Fig. 288). The lateral tubes connect across the body with one another by several transverse tubes; and from the lateral tubes and their transverse connections go branches and sub-branches until the minute capillary branches touch every cell of every tissue. All these tubes are kept open by a spiral thread in their interior (Fig. 289).

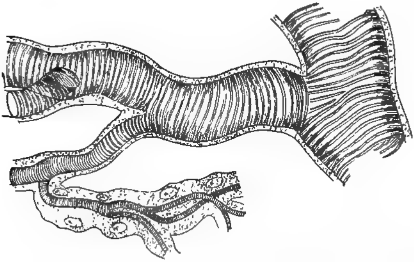

FIG. 289.—Tracheæ enlarged to show the spiral structure.

Now, as in vertebrates, in proportion to the vitality of a part is the minuteness of the distribution of the capillary blood vessels, so in insects, in proportion to the vitality of any part is the minuteness of the distribution of the air tubes. We have given the most common arrangement, but there is some variation in this regard.

Breathing.—If we watch a hornet or wasp at rest, we will observe a back-and-forth movement, an alternate lengthening and shortening, of the abdomen. This enlargement and contraction of the body cavity draws in and expels air. We at once, therefore, see why *oil is so fatal to insects.* It covers the spiracles with a film and thus suffocates the insect.

SECTION V.

Lymphatic or Absorbent System.

Besides the blood system, there is another system of vessels penetrating the tissues everywhere, which may be regarded as supplementary to the blood system. It carries not blood, but a clear liquid called *lymph*, and is therefore called the *lymphatic system.* It is not a circulatory system, but purely an *absorbent* or *drainage* system. We have already seen those of the intestines—viz., the *lacteals* (page 326); but they are not confined to the intestines, but occur everywhere. Nor is their function even in the intestines confined to the absorption of food; they absorb many other things. They are far less understood, both as to their distribution and as to function, than the blood system, for they are difficult to see, as they carry colorless liquid; and they are difficult to inject on account of their valvular structure. We treat them, therefore, very briefly.

General Description.—They begin by blind extremities in all the tissues, but especially in the abdominal viscera, forming a capillary network (Fig. 290), and therefore increasing but little in size until they reach the larger trunks. The great emptying trunks are (1) the thoracic duct on the left side of the backbone, This we have already seen as the trunk of the lacteals, but it is also the trunk of much else. This is the largest. (2) Another smaller duct similarly situated on the *right* side. These two empty into the circulation similarly—the one, as already explained, into the angle of junction of the left subclavian and left jugular veins, the other at

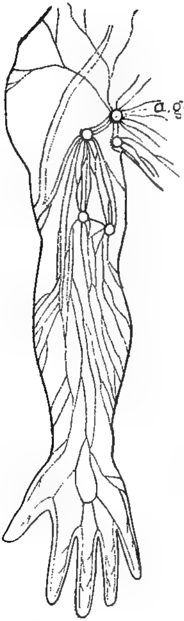

FIG. 290.—Lymphatics of the arm : *agl*, axillary glands.

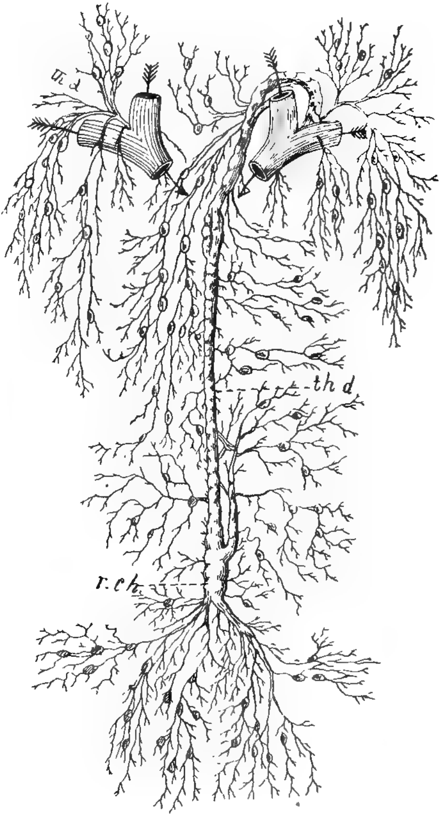

FIG. 291.—Diagram of the lymphatic system : *rch*, receptacle of chyle ; *thd*, thoracic duct ; *th'd'*, right thoracic duct. The arrows show the course of the blood in the jugular and subclavian veins.

the junction of the right subclavian and right jugular veins. The former (left thoracic duct) drains the whole of the viscera, the whole of the lower limbs and the left side of the trunk, the left arm, and the left side of the head, while the latter (right thoracic) drains only the right side of the trunk, the right arm, and right side of the head. Fig. 291 is a diagram showing this.

Structure.—The valvular structure is everywhere conspicuous, and gives a beaded appearance to these vessels. The valves open toward the main trunks, and therefore toward the heart, and tend to prevent backward movement. This is the more necessary as there is no impelling heart, the force of motion being only a suction force at the extremities. Doubtless movements of the body and pressure of the muscles tend to force on the contained fluid (Fig. 292).

FIG. 292.—Enlarged section of a lymphatic vessel, showing valves, *v*.

Function.—Their function seems to be: 1. The *absorption of waste.* 2. The absorption of excess of plasma exuded from the capillaries into the tissues. These two are going on everywhere and at all times. 3. In the case of those of the intestines (lacteals), in addition to these two and at particular times, also the *absorption of the digested food.* In all these functions they are assisted by the capillary blood vessels.

Lymphatic Glands.—In the course of the lymphatic vessels everywhere, but especially the *bend of the joints*, as in the bend of the elbow and knee, in armpit and groin, and in the spaces between the swelling muscles, as on the side of the neck, and still more especially in the visceral cavities, are found glands. We have already spoken of those of the mesentery in connection with the lacteals.

Function of the Glands.—The functions of these glands are (1) *to furnish leucocytes to the blood.* We have already spoken of this function in connection with the mesenteric glands, but now add that all the lymphatic glands have this important function. (2) They also, as already seen in the case of the mesenteric glands, seem to confer upon the lymph, and upon the blood, perhaps through the presence of the leucocytes, the property of coagulation. (3) They seem also to have the power to arrest poisons on their way to the blood. The lymphatic vessels seem to absorb everything. They absorb also poisons. Such absorbed poisons are arrested in the glands, producing inflammation and suppuration especially in the armpit and groin. The poison is thus eliminated, and the patient saved. They suffer vicariously to save the body.

Comparative Morphology of the Lymphatic System.—This system is found *only in vertebrates.* The distinctive functions of the two systems—blood system and lymph system—have not yet been differentiated in invertebrates. The blood system performs the functions of both.

In lower vertebrates the lymphatic vessels become much more distinct than in man; and in amphibians—e. g., in frogs—we find even propelling organs, lymphatic hearts. Two of these are found in the sacral region and two in the scapular region. They are also found in some birds, especially in the embryo of birds. These vessels empty into the blood system in various places.

The lymphatic *glands* seem to appear first in birds, or perhaps in *Crocodilia.*

Mammals in this regard are in all respects like man.

CHAPTER IV.

KATABOLISM.

SECTION I.

Introductory.

THUS far we have treated of *food preparation* and *distribution.* Now we take up tissue *decomposition* and waste *elimination.* Thus far the processes are ascensive and distributive; those now to be discussed are descensive and eliminative. In a word, thus far we have had to do with *anabolism.* Now we take up *katabolism.*

Introductory.—Exchange of matter with the external world can take place only through an external surface or an *infolding* of an external surface. Foreign commerce can take place only through a *coast line* or an infolded coast line or *bay.* Many of the so-called interior surfaces, such as the stomach, the intestines, the lungs, the bladder, etc., are examples of such infoldings of the exterior surfaces. Real interior surfaces—i. e., surfaces which have no connection with the external world—are found in the cavities of the blood system and of the nervous system (brain), and also in the pleural and peritoneal cavities. We repeat, then, that exchange with the external world can take place only through an external surface or an infolding of the same.

In *plants* it takes place on a directly external surface —on an exposed coast line. Air containing food bathes the surface of the leaves, and water containing food the surface of the roots. But in *all animals* a part at least of the exchange is through an infolded surface, or a bay or harbor. In the lowest animals (*Protozoa*), absorption or imports are through an infolded surface or bay, the *stomach ;* but elimination or exports are still through a directly external surface, an exposed coast line. In the highest animals all exchange, both imports and exports, are through an infolded surface.

In going up the scale of life there are three progressive changes in this regard. 1. The relegation of more and more of exchange to an infolded surface or bay until *all* is thus relegated. 2. The gradual differentiation of the several kinds of functions, both absorptive and eliminative (which in the lowest animals are performed in every part alike), and their localization, each in its own separate place. 3. The increasing complexity of the infolding until it becomes almost inconceivably great. If the simple infolding may be compared to a bay or harbor, then the infolding of this again may be compared to the slips and docks of the harbor.

Now, every such surface through which exchange takes place, as already said (page 20), no matter how complex, is covered with a pavement of living nucleated epithelial cells, through the agency of which the exchange takes place. Such a complexly infolded surface, covered with epithelial cells webbed together by connective tissue and invested and isolated by fibrous or serous membrane, constitutes an organ absorptive or eliminative. The extreme complexity is especially characteristic of *eliminative* organs, and among these the most complex of all is the lungs.

Secretion versus Excretion.—Now, elimination and eliminative organs are of two kinds—viz., secretions and excretions, secretory organs and excretory organs. In the former the products do not *pre-exist* in the blood, but are *manufactured* out of blood and used in the economy of the animal mainly in the preparation of food. In the latter the products *pre-exist* in the blood, are poisonous to the blood, and must be removed. In the former there is first manufacture and then elimination of a *useful* product. In the latter there is simple elimination of a *hurtful* product. Salivary glands, peptic glands, pancreas, and mammary glands are examples of secretory organs. The lungs and the kidneys are the best examples of excretory organs. The liver is peculiar and of a mixed character. The pure secretory organs connected with the process of food preparation we have already discussed. They are concerned with anabolic processes. We are now concerned with the purely eliminative or excretory organs, for these belong to katabolism. The liver, being mixed in its functions, will be taken up later. By far the most important of all the katabolic processes is that of *respiration.*

SECTION II.

Function of Respiration.

We have already given the *morphology* of the *respiratory organs*, because this could not be separated from an account of the circulation. But the physiology of respiration—i e., its function in animal economy, its relation to katabolism—is the same in all animals and must be taken now.

We have already seen (page 358) that the general purpose of respiration is the aëration of the blood, or, more specifically, the exchange of CO_2 of the blood for oxygen of the air. Thus much it was necessary to assume in order to understand the course of the circulation and the changes in the blood in that course. We must now explain the essential nature of the function and its necessity. For greater clearness we throw the explanation into the form of several propositions.

1. **The Chemistry of Respiration.**—The essential chemical nature of respiration is an *oxidation of food and waste* in the blood. Now, oxidation is a process of combustion. Respiration is, therefore, a burning of food and waste; more specifically, it is a process of union of O of the air with C and H of the blood, and the formation of CO_2 and H_2O, which are returned to the air. The fouling of the air by respiration is due mainly to the accumulation of the eliminated CO_2.

Proof.—The proof that oxygen is consumed and CO_2 eliminated in respiration is so familiar that it is unnecessary to give it except in bare outline. (*a*) Thrust a lighted taper into a gallon jar, and it burns freely; but blow into the jar through a tube reaching to the bottom until the jar is filled with the expired air only, and again introduce the taper; it is immediately extinguished. (*b*) Fill a test tube with clear limewater and blow through the water with a glass tube for some time. The limewater becomes milky with precipitated lime, *carbonate.* (*c*) Take an equal bulk of pure air and of expired air and compare their composition by analysis. It will be found that in the expired air a certain volume of oxygen has disappeared and been replaced by an equal or nearly equal volume of CO_2. So much for the CO_2. Now for the H_2O. (*d*) Breathe on cold glass. Immediately the clear glass is clouded with deposited water.

Now, the union of oxygen with carbon and hydrogen —i. e., the combustion of carbon and hydrogen, always produces *heat.* This, then, is *the source of animal heat*, and the difference between warm-blooded and cold-blooded animals is simply a difference in rate of combustion. In warm-blooded animals, as birds and mammals, the whole of the blood is oxidized, the surface of exposure is larger, the internal fires burn fiercely, and therefore the temperature of the blood is high and independent of the temperature of the exterior medium. In cold-blooded animals, such as reptiles, amphibians, and fishes among vertebrates, and in nearly all invertebrates, the fires burn so low that the temperature of the blood follows somewhat closely that of the exterior medium. Every stage of gradation, however, may be traced between them.

2. **The Purpose of the Combustion.**—The purpose of the combustion is *threefold:* (*a*) To remove waste. The waste of tissues is highly poisonous and must be quickly removed; most of it is removed in respiration by burning it up and changing it into gaseous CO_2 and H_2O vapor, which are readily exhaled from the lungs. (*b*) A still more fundamental and necessary purpose of combustion is the *generation of force.* This, indeed, is the origin of the *vital* force, as it is that of the force of the steam engine. (*c*) A third purpose is the *generation of heat*—i. e., animal heat. This, however, is of secondary importance. In the animal machine, as in the steam engine, the real purpose is force, and the heat is a necessary concomitant. In the animal body the heat is sometimes a comfortable (in cold weather), sometimes an indifferent, and sometimes a distressing (in hot weather) concomitant. But we *can not get the force without the heat.* It is worthy of note, however, that from this point of view the animal body is a far more efficient machine than any engine ever constructed—i. e., of the heat of combustion, a *far greater proportion is converted into force.*

3. **The Fuel.**—Again, the *fuel* used in combustion is of three general kinds—viz., the *amyloids and fats*, the *albuminoid excess*, and the *waste.* (*a*) The amyloids and fats consist only of C, H, and O, and therefore these

burn into CO_2 and H_2O *without residue*, and are eliminated by the lungs alone. They do not form tissue. They are used for fuel only. (*b*) Albuminoid excess—i. e., albuminoid over and above what is necessary for tissue building, both repair and growth. (*c*) *Waste tissue.* These last two—i. e., albuminoid food excess and waste—consist of C, H, O, and N, and often a small quantity of sulphur and phosphorus. They are not wholly combustible into CO_2 and H_2O, and wholly eliminable by the lungs. In burning they leave an incombustible residue to be eliminated by the kidneys. They are, as it were, *split* into two parts, a combustible and an incombustible. The combustible, consisting of the larger portion of the C, H, and O, is eliminated by the lungs, but a portion of the C, H, and O, together with the whole of the N, is eliminated as urea by the kidneys. This is diagrammatically represented by the formula (Fig. 293), in which the line *a b* represents the line of *splitting*. Therefore these two organs, the lungs and the kidneys, are complementary to one another. They divide the albuminoid food excess and the waste between them. But the amyloids and fats are disposed of only by the lungs.

FIG. 293.—Diagram showing the splitting of albuminoids in a combustible and incombustible portion.

We have seen that the three kinds of fuel used are (1) amyloids and fats; (2) albuminoid excess; and (3) waste. Now, since in the mature body the repair just balances the *waste*, it is evident the fuel burned is exactly equivalent to the *whole of the food.*

4. But the question occurs: (1) How is force created by combustion? and especially (2) How can force enough be generated not only to do the work of repair and main-

tenance, but also for growth and activities of all kinds? These are obviously *the* questions most fundamental in physiology.

In answer to the first question we may say that in the passing of matter from a more complex to a simpler condition, from a more unstable to a stabler condition, as in combustion or in organic decomposition, force or energy is liberated which is converted partly into heat and partly also into other forms of energy, mechanical or vital. To illustrate: Matter on a high plane (organic matter) running down (katabolism) to a lower plane (CO_2 and H_2O) generates force to raise (anabolism) other matter (food) from a lower to a higher plane (tissue). Thus while a *large part* of the force of *plant* life (viz., the creation of organic matter) is derived from the sun in the form of light, the *whole* of the force of *animal* life is generated by the katabolic process going on in the body.

But it will be objected that a certain amount of matter running down can do no more than raise the *same* amount of matter the same height. The whole force of *waste* is consumed in *repair* and nothing is left over for the other activities of the body. This objection is embodied in the second question. The answer to it is (1) that in case of waste tissue, the running down is to a much lower plane (CO_2 and H_2O) than that from which the lifting took place (food). Therefore the running down of say one pound of tissue to CO_2 and H_2O will easily lift one pound of albuminoid food to the plane of living tissue and leave much force over for activities of all kinds. (2) There is also much food—viz., all the amyloids and fats and all the albuminoids in excess of that necessary for repair—that runs down and generates force without expending its force in lifting at all.

I have constructed the following diagram to illustrate this process (Fig. 294):

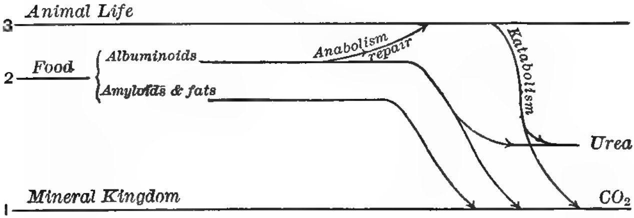

FIG. 294.—Diagram illustrating the generation of animal heat and animal force.

We have represented here three planes raised one above the other, viz., (1) the plane of the mineral kingdom, (2) the plane of food, and (3) the plane of living tissue. The plane of food is subdivided into a lower and a higher. The lower form of food—viz., the amyloids and fats—is at once burned without residue; the whole of it runs down to the mineral kingdom CO_2 and H_2O * and generates a corresponding amount of force. The higher form of food, albuminoids, if in excess of the necessities of repair and growth, also runs down, but in its downward course is split (see Fig. 293 on page 420) into (*a*) a combustible portion which is burned to CO_2 and H_2O, and eliminated by the lungs, and (*b*) an incombustible portion which is eliminated on a little higher plane as urea by the kidneys. Another portion of albuminoid food is raised to the plane of living tissue for repair and growth, and after remaining on that plane and playing its part there for a time, also runs down as

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* In the diagram we have used only CO_2, because this really gives the amount of force, the H and the O being already in the food in proportions forming H_2O, and therefore supplying no heat or force.

waste to be disposed of in a similar way—i. e., partly by the lungs and partly by the kidneys. The whole process may be likened to a current in a siphon: the shorter arm is anabolism, the longer arm and the one which *determines the whole current* is katabolism.

5. We have said that respiration is a process of combustion in which oxygen of the air unites with C and H of the blood and produces CO_2 and H_2O. Now exactly the same takes place in the burning of oil. The material is the same (C and H); the process is the same (union with oxygen of the air); and the product, chemical and physical, is the same—viz., CO_2 and H_2O and heat. Moreover, it is certain that, estimating the whole force produced in terms of heat, the amount of heat is the same in the two cases. But in the case of the animal body the heat is spread over a larger space and over a longer time, and is therefore less intense.

6. Another important question is, *Where* does the combustion take place? The old view was that it takes place in the lungs, and that this organ is the furnace of the animal machine, that circulation brings the fuel and respiration brings the air, and that the fuel is burned at once then and there. It is now known that this is not the fact. The blood brings the products of combustion (CO_2) to the lungs to be eliminated. Respiration brings a fresh supply of oxygen to be taken by the blood to the place of combustion. This place of combustion is in the capillaries in contact with the tissues. Yet neither are the decomposing tissues burned *at once*, but circulate in the blood and undergo changes *there* before they are finally consumed into CO_2. These changes are very obscure and little understood. Some of them are spoken of later.

Thus the blood is a reservoir for many things. It is a reservoir for *oxygen*, which circulates in it until used.

It is a reservoir for CO_2 until eliminated by the lungs. It is a reservoir for *food*, which is drawn upon and resupplied by digestion and absorption. It is a reservoir for *waste* tissue until it is finally prepared for combustion. In a word, it is a reservoir both for material and for force. It acts like a fly wheel in the animal machine.

7. **The Relation of Plants to Animals in regard to the Creation of Animal Force.**—It is seen from the diagram (Fig. 294) that the anabolic *lift*, determined by the katabolic descent, *begins more than half-way up the scale of existence.* Otherwise there could be generated only force enough to make the lift and maintain the tissues, and none would be left over for activities of all kinds. The question then occurs, How does matter attain this half-way plane? The answer is: It is raised to that plane by sunlight acting on the green leaves of plants. Animals must feed on organic matter, but they have no power to make it. It is prepared ready for them by plants. The reason is, animals are wholly dependent on katabolic processes *within themselves* for the generation

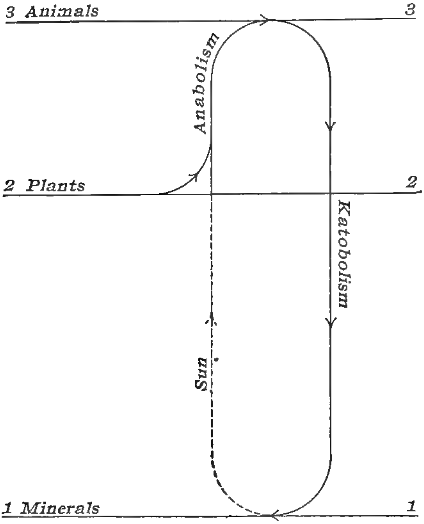

FIG. 295.—Diagram to show the forces of circulation of organic matter.

of vital energy, and therefore the katabolic descent must go far below the plane from which material is drawn by anabolism. Plants, on the contrary, take much energy, viz., that expended in making organic matter, directly from the sun; an energy generated by a katabolic process, true—viz., decomposition of CO_2—but determined by an *external* force, sunlight. So that in the eternal circulation of matter from the plane of minerals to that of animal life and back again to the plane of minerals the anabolic ascent begins in plants and completes itself in animals; but the katabolic descent completes itself at once in animal katabolism. So that the whole circulation may be represented by an endless chain, as in the adjoining figure (295). This circulation must be driven in part by a force *external* to the chain. That force is the sun. It is evident that animal force in activity, in excess of maintenance of tissues, is the equivalent of the excess of katabolism over anabolism—of the excess (*2*, *1*) of the katabolic branch of the siphon. But this is exactly equal to the lift by the sun (*1*, *2*). Therefore animal force or activity is equivalent to sun force in making organic matter.

SECTION III.

The Kidneys: The Organ and its Function.

The Organ.—We have already said that the lungs and kidneys are the two great organs for elimination of the products of katabolism. They are also correlative, since they divide between them the final disposal of the albuminoid food and the waste. The kidneys, therefore, must be our next subject.

Place and Form.—The kidneys are in the abdominal cavity, in the hollow on each side of the lumbar vertebræ, and just below the roots of the diaphragm. The shape is very like a kidney bean, and they lie with their concave sides toward each other. The blood supply is large in proportion to the size of the organ, because, as in the case of the lungs, the supply is not mainly for nutrition of the organ, but for purification of the blood (Fig. 296). The blood brought back from the kidneys by the renal vein is the purest blood in the body, for it is brought to the kidneys as bright blood purified of CO_2 in the lungs, but still containing urea; but now it is purified of its urea in the kidneys and returned to the vena cava ascendens. There, however, it is, of course, again mixed with impure blood from other tissues.

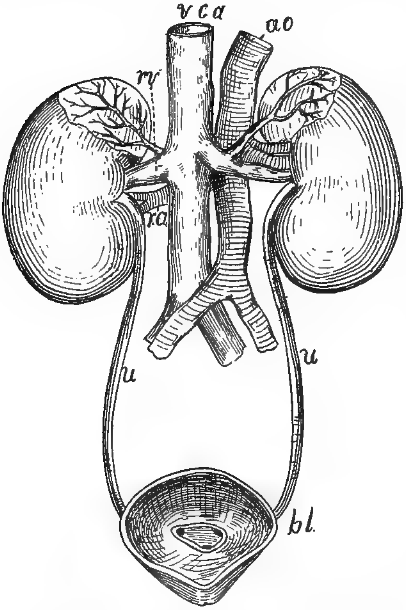

FIG. 296.—Showing form and position of the kidneys: *ao*, aorta; *vca*, vena cava ascendens; *ra*, renal artery; *rv*, renal vein; *u*, ureters; *bl*, bladder.

Excretory Duct.—The excretory ducts (the ureters) are peculiar. By a trumpet-shaped mouth each ureter grasps the deeply concave part (the pelvis) of the kidney so as to receive the excretions; then passes down on each side as a tube about the size of a crow quill and about fifteen inches long and enters the bladder on each side below by a valvular opening, which effectually prevents regurgitation. The secretion of the kidneys drips, little by little, continually. It accumulates in the bladder, and is thence from time to time voided through the *urethra*.

Pelvis of the Kidney.—If the ureter be cut away, we expose a deep concavity called the pelvis. Its whole interior is covered with mammillary protuberances, like the ends of the fingers put together. These are the ends of the *cones*. In the living animal (chloroformed) we may see liquid oozing from innumerable pores on this surface, collect into drops, and run down. These pores are the openings of the uriniferous tubules.

Section.—By longitudinal section through the pelvis (Fig. 297) it is at once seen that there are two parts of the kidney, differing in color and structure—an inner portion, of lighter color and radiated structure, and an outer portion, darker and nonradiated. The former is the *medullary* and the latter the *cortical* portion. The excretion takes place mainly in the cortical portion; the medullary mainly transmits it to the pelvis.

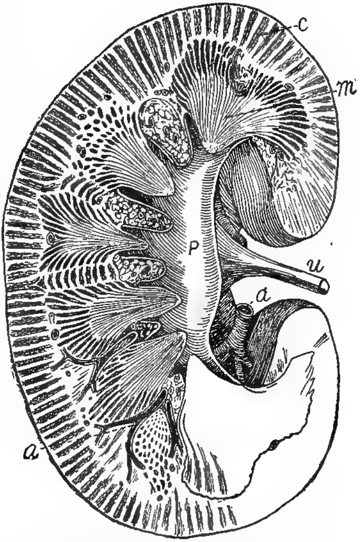

FIG. 297.—Section of the kidney showing structure: *P*, pelvis; *u*, ureter; *m*, medullary, and *c*, cortical portion; *a a*, arteries.

Minute Structure.—Examined with a microscope, the medullary portion is seen to consist of straight tubes, branching and becoming more numerous, but the branches lie parallel, and give rise to a radiating arrangement. In the cortical portion, on the contrary, the tubes are much *convoluted*, and finally terminate each in a vesicle, which is filled with a tuft of capillary blood vessels, looping round and connecting with an arteriole *on the one hand* and with a veinlet *on the other* (Fig. 298). Blood vessels are also abundantly distributed among the tubules. These terminal vesicles are the *Malpighian* corpuscles, and the contained vascular tufts *glomerules.*

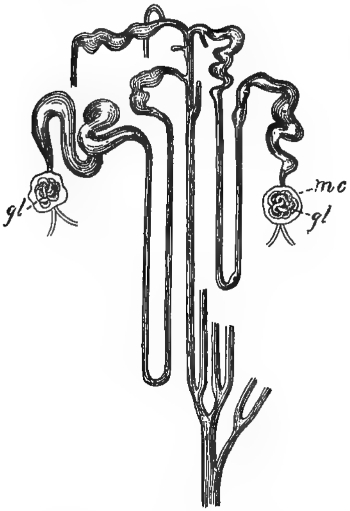

FIG. 298.—Uriniferous tubules: *m*, Malpighian corpuscles; *gl*, glomerules.

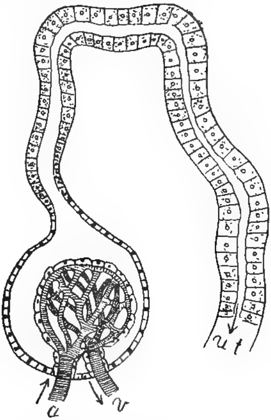

FIG. 299.—Uriniferous tubule: *ut*, with its Malpighian corpuscle and glomerule; *a*, arteriole; *v*, veinlet.

Now, as in all eliminative organs, so here the whole is lined throughout with epithelial cells (Fig. 299). The epithelial membrane passes from the surface up the urethra into and lines the bladder; from the bladder it passes up the ureters and covers the pelvis. It then passes up and lines the tubules and their terminal vesicles. In fact, the kidney is little else than a mass of such tubes, lined with epithelium, webbed together with connective tissue, and invested with peritoneal membrane, and then the whole liberally supplied with nerves and blood vessels. The epithelial surface thus produced is enormously great.

Function.—The function of the kidneys is apparently twofold—the one *physical*, the other *vital*. The one is a purely physical and therefore *nonselective filtration*, the other is a selective *excretion* of a particular product of katabolism—viz., *urea*. The one is probably through the capillary tufts of the terminal vesicles, and apparently *not* by the agency of the ordinary epithelial cells (cells here are squamous epithelium); the other, as in the case of all the secretions and excretions, is by the agency of the living nucleated cells lining the tubes. These are glandular epithelium. By the former are eliminated from the blood superabundant water and salts of all kinds, normal or accidental. By the latter is removed a characteristic product of katabolism—*urea*. This is the special characteristic function of the kidneys.

Composition of Urine.—The secretion of the kidneys is a solution of urea (sometimes partly replaced by uric acid) and of various salts—viz., sulphates, phosphates, chlorides and carbonates of potash, soda, and lime. The most important parts are the *urea* (or its equivalent, uric acid), together with the *sulphur* and *phosphorus* of the sulphates and phosphates. The chlorides and carbonates are constantly present in the blood, and their excess eliminated by the kidneys. *Urea* and to some extent also the sulphates and phosphates are products of katabolism. The essential function is the elimination of N and a little S and P. Of the elements of albuminoids—viz., C, H, O, N, and S and P, as already explained—the larger part of the C, H, and O are removed through the lungs as CO_2 and H_2O; but the whole of the N, P, and S, together with enough C, H, and O to form with the N the substance urea, are removed by the kidneys. The composition of urea is CH_4N_2O.

$$\text{Urine} = \text{Solution of} \begin{cases} \text{Urea} \\ \text{and} \\ \text{Salts} = \left\{ \begin{array}{l} \text{Chlor.} \\ \text{Carb.} \\ \text{Sulph.} \\ \text{Phos.} \end{array} \right\} \text{of} \begin{cases} \text{Na} \\ \text{K} \\ \text{Ca} \end{cases} \end{cases}$$

The manner in which albuminoids, both food excess and waste, are divided between lungs and kidneys is shown in Fig. 300, already given, but repeated here slightly modified. The amyloids and fats are not eliminated by the kidneys, but only the lungs.

FIG. 300.—Diagram showing the division of albuminoids between the lungs and the kidneys.

It is evident, then, that the quantity of urea eliminated is in proportion to the *quantity of albuminoid food*, and is therefore greater in carnivores than in herbivores, and also in proportion to the *waste*, and therefore to the work done or degree of activity. The estimation of the urea excreted is therefore the most convenient mode of *measuring waste*, and is constantly used for this purpose.

When urea decomposes in the presence of water it is wholly converted into ammonium carbonate.

$$\begin{array}{ccccc} CH_4N_2O & + & 2H_2O & = & (H_4N)_2CO_3 \\ \text{urea} & + & \text{water} & = & \text{am. carb.} \end{array}$$

Comparison of Lungs and Kidneys.—The comparison between these two complementary organs is interesting in many respects.

1. We have alluded (page 419) to the importance of the quick removal of the products of katabolism. Stop respiration, and death by blood poisoning takes place in five to ten minutes. If the function of the kidneys stops, death by blood poisoning (uræmia) occurs in twenty-four to forty-eight hours. See, then, the much greater importance of the lungs.

2. It is on account of this supreme importance that in the higher animals the whole of the blood passes through the lungs, that there is complete double circulation, and that blood completely purified of CO_2 goes to the tissues. On the contrary, only a portion of the blood passes through the kidneys; the *renal* circulation is only a branch of the systemic circulation, and therefore only mixed blood, so far as urea purification is concerned, goes to the tissues. But it will be remembered that the same is true of the *pulmonic* circulation in reptiles and amphibians.

3. Of foods, amyloids and fats are wholly removed by the lungs, while the albuminoids are divided between the lungs and the kidneys in the manner already explained. Of the *elements* of organic matter, the larger part of the C, H, and O is removed by the lungs, but the whole of the N, S, and P by the kidneys.

4. The lungs not only *eliminate* CO_2 and H_2O, but *take in* O for combustion. The function of the kidneys, on the contrary, is *purely eliminative.* The eliminated product in case of the lungs is the result of *oxidation;* in the case of the kidneys, of *decomposition.*

5. The circulation of the elements of organic matter back to the atmosphere is through both of these organs. The return of C in the form of CO_2 is through the lungs; the return of N in the form of ammonia is through the kidneys as urea, which, as we have seen, is quickly changed into carbonate of ammonia. Thus all the ele-

ments of living organisms taken from the atmosphere and embodied for a brief time are again returned, and the same matter is worked over and over again by an eternal circulation. The circulation of C and O through the atmosphere, plants, and animals back to the atmosphere is represented in diagram (Fig. 301, repeated from page 5). It is seen that C is taken in the form of CO_2 from the atmosphere by plants, is decomposed, the C fixed in organic matter, and oxygen returned to the air. The C is taken from plants by animals as *food*, is then combined with O from air taken in respiration, and returned to the air in its original form as CO_2, and so on continually.

The circulation of all the elements of organic matter between the organic kingdom and the atmosphere is represented by the diagram (Fig. 302). The food of plants consists of CO_2, H_2O, and NH_3. These are taken from the atmosphere and embodied in organic form of both plants and animals. In their death these are again returned to the atmosphere as CO_2, H_2O, and NH_3, to be again taken as before. Thus the same small quan-

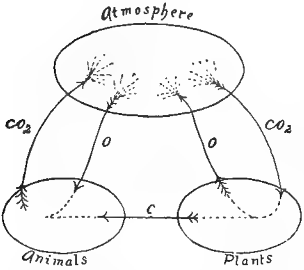

FIG. 301. Diagram illustrating the circulation of carbon and oxygen.

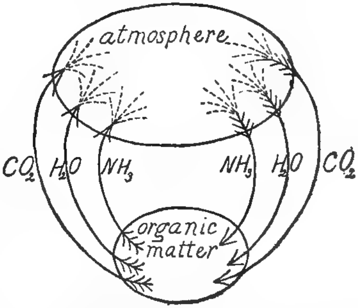

FIG. 302.—Diagram showing the circulation of the elements of organic matter.

tity of CO_2 and NH_3 are embodied and disembodied many times in the history of the organic kingdom.

COMPARATIVE MORPHOLOGY OF THE KIDNEYS.

Vertebrates: Mammals.—Little need be said on the mammalian kidney. The organ has a similar position in all mammals, and in most a similar shape and structure to that of man. In the ox the surface is mammillated as if there were a commencing separation of the cones. This separation is realized in some living water mammals, such as the otter and the porpoise (Fig. 303). But in these cases the difference is not significant. Each cone consists of a medullary and a cortical portion, and they all discharge into one pelvis and ureter.

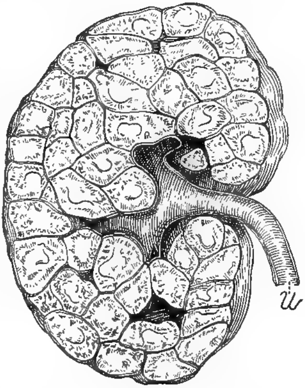

FIG. 303.—Section of the kidney of a porpoise, showing its structure: *u*, ureter. (From Owen.)

Birds.—The first important change in this, as in so many other characters, is found in birds. In these (1) the kidneys are not yet clearly differentiated into two parts, a cortical and a medullary, having different functions. (2) In these there is *no bladder*, but the ureters empty into a *cloaca* or enlargement of the rectum just within the vent.

Reptiles and Amphibians (i. e., all cold-blooded land vertebrates) have a *cloaca*; but some—e. g., snakes and lizards—like birds, have no bladder, the ureters emptying directly into the cloaca; while others—e. g., tortoises and frogs—have a bladder. In these cases the ureters empty into the bladder and the *urethra* into the cloaca.

The diversity in structure in the different orders of fishes is so great that their description would carry us beyond the scope of this work.

Invertebrates: Insects.—The essential character of the kidneys—i. e., its significance in katabolism—is the excretion of *urea*. This is therefore the true test of an organ corresponding functionally to the kidneys. Now, there is an extremely delicate chemical test of *urea*—viz., the splendid *purple* produced by certain reagents. It is wholly by this test that we are able to determine the renal organ in invertebrates. In this way it is determined that the so-called biliary tubes of insects (Fig. 219, *bd*, page 336) are also their kidney—i. e., they excrete *urea*.

In **crustaceans** the so-called *green glands* (Fig. 221, *gg*, page 337), which are large glands near the base of the antennæ and very liberally supplied with blood, are the kidneys. But it is very noteworthy that in addition to a peculiar form of uric acid (carcinuric acid) there is secreted also *leucomaines*,* which is the first product of albuminoid waste in higher animals, and which in them is split into a combustible portion, for use as fuel, and an incombustible portion excreted as urea (pages 420 and 430). In crustaceans some of these substances is excreted unutilized, and thus wasted. This is evidence of low organization.

Mollusca.—By similar tests renal organs have been detected in different classes of mollusca—viz., the "*spongy bodies*" of cephalopods, the organ of Bojanus of acephala situated at the base of the gills (Fig. 281, page 402), and the lamellar gland near the pulmonic sac, or the branchiæ of gastropods.

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* Marchal, Rev. Sci., li, 178, 1893.

Below these the renal organ has not been detected. Probably this function has not yet been differentiated from others.

Observe, then: (1) Only a little way down the vertebrate scale (*birds*) the distinction of cortex and medulla is lost. (2) Only a little farther down the animal scale (*insects*) the functions of liver and kidneys are merged, although they are found separate even lower down. (3) A little lower down (*crustacea*) the function of the kidneys is incompletely performed—i. e., a part of the waste escapes decomposition and is thus wasted by not being utilized as fuel. (4) A little lower down—i. e., below mollusks—this organ has not been certainly found. Probably the function is not yet differentiated.

SECTION IV.

The Skin and its Function.

We have spoken of the lungs and kidneys as the two great organs which share the elimination of katabolic products between them. But there is still a third, the *skin*, which, though less important, must not be neglected.

Function.—All organs and functions are sympathetically related to one another, so that the importance of healthy action of an organ is not to be measured by that of its more obvious and distinctive function. The distinctive function of the skin is *the moderation of the blood heat* produced by continual combustion, by the elimination of excess of water, and its *evaporation on an exposed surface.* The elimination of water it shares with the kidneys and is complementary with it, but it is peculiar in the elimination of water in such wise as thereby to *cool the blood.*

But elimination of water by the skin, as also by the kidneys, is of two kinds—physical and vital. The former is *exhalation*, the latter *excretion*. The one is always insensible, the other is sensible—sweat.

Exhalation.—Water in a porous earthenware jar or in a canvas bag, if hung up in the air in a hot, dry climate, keeps cool, and even grows cooler. The water soaks through and evaporates on the surface, but never drips. So the tissues of the body are all permeable and filled with water. Evaporation *from* the surface calls the water *to* the surface as fast as it is evaporated. It can not drip as sweat, because it is called there only by drying. It is for this reason that in very arid regions the suffering from heat is not very great, and sunstrokes are unknown, although the thermometer in the shade may run up to 110° to 120° F. Of course the water which comes out and evaporates in this physical way is nearly pure water.

Excretion.—But besides this physical exhalation, which would go on even if there were no special organs, there is also the excretion of *sweat*. This is the product of the sweat glands. It is not called out by evaporation, but as if it were *pushed* by the specific activity of the glands, and may exude in such quantity as to roll down and drip from the skin. This also spreads and evaporates, and thus cools the surface. This is not pure water like the other, but water containing many salts with a little oil and a little CO_2 and a trace of urea.

Structure of the Skin.—The skin, as already explained, is composed of two parts—viz., the dermis or *true skin* and the epidermis. The dermis is a mass of felted interlacing fibers. It is very strong, highly organized, and full of blood vessels and nerves. The epidermis, which alone concerns us here, is continuous with the epithelium, and, as to its truly living parts, similarly constituted. There is, however, this difference: The epithelium consists of only a few layers of living cells, which are constantly dying, shedding, dissolving, and forming the slimy mucus which covers the interior surface and again renewing; while in the epidermis the lower layer in contact with the dermis consists also of living nucleated cells, which are also constantly dying and renewing; but the dying cells, instead of dissolving and forming slime and leaving the surface still composed of living cells, gradually dry up, mummify, flatten more and more, and finally pass off as scales of the scarf skin. Thus, besides the lower layer (*Malpighian* layer) of living cells, there are many layers in various stages of dying and mummification. This mummified part is the cuticle. The color of the skin is in the lower living layer. A blister is a lifting of the epiderm from the derm and an accumulation of lymph beneath.

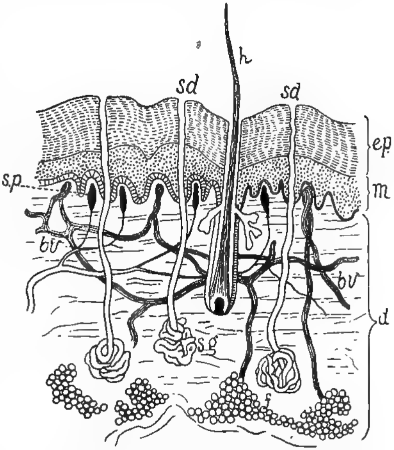

FIG. 304.—Section through the skin, showing its structure: *ep*, epidermis, and *m*, its Malpighian layer; *d*, dermis; *sg*, sweat gland; *sd*, sweat duct; *sp*, sense papillæ; *h*, hair; *bv*, blood vessels.

Sudorific Glands.—Scattered in great numbers over the surface of the skin are found pores formed by the infolding of the living or Malpighian layer of the epiderm, forming *tubes* (*sd*, Fig. 304) opening on the surface. They pass through the dermis into the subcutaneous connective tissue, and are there convoluted into a pellet, *sg*. These are the sudorific glands. The number of the pores has been variously estimated at from five hundred to twenty-eight hundred to the square inch, and from one and a half million to seven millions on the whole surface of the body. The aggregate length of the tubes has been estimated at twenty-eight miles.* Like all infolded surfaces, the tubes are lined throughout with living epithelial cells, which preside directly over the excretion. Blood vessels furnishing the materials are distributed over the exterior surface of the tubes.

It is quite possible that the number and aggregate length of the uriniferous tubes may be as great as that of the sudoriferous, but in the one case these are compacted into an organ (the kidney), and the excretion gathered into a reservoir (the bladder), while in the other they are spread over the wide surface of the skin. The reason is obvious. The purpose of cooling the blood by evaporation could only be subserved by a large surface of direct exposure.

Lungs, Kidneys, and Skin compared.—All three of these eliminate CO_2, H_2O, and urea. But the distinctive duty of the lungs is the elimination of CO_2, that of the kidneys *urea*, and that of the skin *water in such wise as to cool the blood.* In each case the elimination of the other two products is subsidiary and, as it were, accidental. Nevertheless, we ought not to be surprised to find a mingling of these functions more and more as we go down the scale.

COMPARATIVE MORPHOLOGY AND PHYSIOLOGY OF THE SKIN.

Genera Remarks.—1. If the skin be dry, harsh, and without glands, it is a sign either that cooling of the blood is not necessary, as in cold-blooded animals,

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* Nature, l, 257, 1894.

or else that this function is performed in some other way. On the other hand, if the skin be soft, moist, and mucous, it is a sign that it is very active, and performs many functions which have yet been but partially differentiated and relegated to an infolded surface.

2. The function of cooling the blood by evaporation can only exist in air-breathing and land-inhabiting animals.

Mammals.—The structure and function of the skin in mammals are similar to the same in man; yet there are many mammals that are nonsweating. Such, in many cases at least, are *panting* animals. The most familiar illustration of this is the *dog*. The dog is a *very hot-blooded* animal, and yet in it there is no visible sweat, although there is, of course, exhalation. The cooling of the blood is largely *through the lungs* by *panting*. A dog pants not because he is tired and wants more oxygen, but because he *is hot*. By panting he fans his lungs.

Birds are also very hot-blooded, and in hot weather they also supplement the cooling of the blood through the skin by panting.

Reptiles have dry, scaly, inactive skin. But little or no cooling of the blood is required in them, because the internal fires burn low; they are cold-blooded.

Amphibians have the extreme opposite condition. They have soft, moist, mucous, and very active skins, not, however, because they require cooling of the blood, for they are cold-blooded and live mostly in the water, but because many other functions are to some extent performed by the skin—for example, respiration and even the absorption of food.

Fishes live in water, and there can be no evaporation from the skin; also, like amphibians, the skin is soft and slimy and active.

Insects are more or less warm-blooded and require blood cooling, yet they are covered with a dry, hard, skeletal coat, which cuts off entirely any evaporation. The function of blood cooling is undoubtedly performed by the tracheæ, which are admirably adapted for this purpose.

Crustaceans are similarly covered and have no air tubes, for they live in water, but they are again cold-blooded.

Mollusca, again, go to the other extreme. The skin of these is soft, mucous, and very active, and doubtless performs many functions and supplements many other organs.

In **Echinoderms,** again, we find the hard shell and inactive surface.

In **Cœlenterates** we return again to the soft and active condition, which is found also in most *Protozoa.*

SECTION V.

The Liver and its Function.

We have now treated of the eliminative organs connected with *anabolism* (secretory) and those connected with *katabolism* (excretory); but there are still some whose functions are of a *mixed* character, and therefore put off to the last. Chief among these is the *liver.*

1. **The Organ: Position and Structure.**—The liver, together with the stomach and the spleen, fill up the concavity of the diaphragm, the liver being chiefly on the right and the stomach and spleen on the left. Its color, shape, and size are well known, and need not detain us, as they have no special relation to function. In *structure* it differs from other glands in not being entirely or chiefly an aggregate of excretory tubes. On

the contrary, it consists mainly of certain peculiar, very solid, nucleated cells called *liver cells* (Fig. 305).

Four Systems of Tubes.—An eliminating organ or gland has usually *three* systems of tubes or vessels: (1) The artery and its branches, carrying blood to the work. (2) The vein and its branches, carrying back the blood when the work is done; these two connect through the capillaries. (3) A system of excretory or secretory tubes, carrying away the product of manufacture. But the liver has *four* systems of tubes ramifying through its mass of liver cells: (1) The hepatic artery, (2) the hepatic vein, (3) the *portal vein*, and (4) the biliary ducts. The one which is peculiar is the *portal vein*. We have already (page 328) drawn attention to the peculiarity of this vein. It is the vein corresponding to the mesenteric and splenic arteries. But, instead of emptying its blood, like all normal veins, into the vena cava, close at hand, it goes to the liver, to be ramified by capillaries through its substance, and only after doing so carries its blood to the hepatic vein and thence to the vena cava and the general circulation. So that instead of two systems of vascular pipes, arteries, and veins, connecting with one another through the capillaries, we have three systems of such pipes—viz., hepatic artery, portal vein, and hepatic vein—all connected continuously by capillary circulation, so that water injected into any one of these trunks will flow out of the other

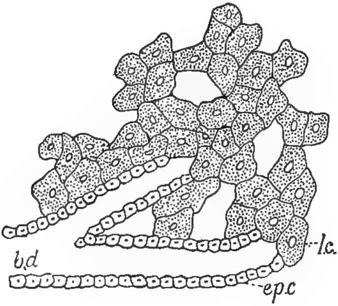

FIG. 305.—Microscopic structure of the liver: *lc*, liver cells; *epc*, epithelial cells; *bd*, biliary duct.

two. Besides these tubes, of course, there are the bile ducts (Fig. 306); but these, like all excretory tubes, end in blind extremities (Fig. 305). As we shall see presently, the products of the liver are *bile* and *sugar*. Of these, the bile is carried away by the *biliary ducts* into

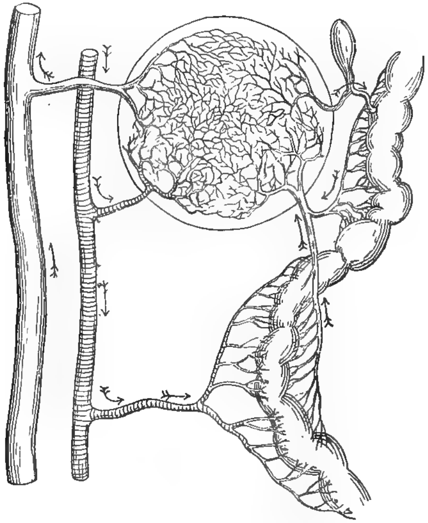

FIG. 306.—Diagram showing the distribution of the blood through the liver. The arrows show the direction of the current.

the intestines, while the sugar is delivered to the blood and carried into the general circulation by the *hepatic vein*.

2. **Function: Two General Kinds of Glands.**—Glands are of two general kinds—*ducted* and *ductless*. The one delivers its products by a duct to the surface, the other delivers its product directly to the blood without a duct. We have already seen two examples of these in the *lymphatic glands* and the *spleen*, and have stated (page 324) that the pancreas is also partly so.

But there are several others—viz., the thymus, the thyroid, the suprarenal, etc. Their functions are very obscure, but very important. Only recently has attention been strongly drawn to them. Their products have been called *internal secretions.*

Again, the *ducted* glands, as already explained, are of two kinds—secretory and excretory. The one manufactures useful products out of the blood, the other eliminates hurtful products of katabolism *from* the blood.

Now, the liver belongs to all three kinds. It manufactures two things—viz., bile and sugar. As a ducted gland it delivers its bile by a duct into the intestines. As a ductless gland it delivers its sugar directly to the blood. Again, the bile is both a secretion used in the digestive process and an excretion, purifying the blood of the hurtful katabolic products.

Therefore the function of the liver is threefold: (1) The manufacture of sugar, (2) the manufacture of bile as a *secretion,* and (3) the elimination of bile as an *excretion.* This last is probably connected with the destruction of the red blood-globules in the liver. We have already discussed the bile as a digestive secretion. We have also already spoken of the liver as the cemetery of red globules, and said all that was necessary in the very imperfect state of knowledge on this subject. All that remains is the discussion of the liver as a manufactory of sugar. This introduces the very important subject of glycogeny.

Glycogeny and its Relation to Vital Force and Vital Heat.—If we examine the blood of the hepatic vein we always find a notable quantity of sugar. Whence comes it? It is at first natural to suppose that it comes from the digested food, the sugar of which, we have already seen, is taken up by the capillaries of the portal vein and carried to the liver. But, no. It may be shown to be formed in the liver itself. The following experiments show it:

1. An animal may be fed on flesh alone (which we know contains no sugar-making substance) for weeks continuously, and yet sugar will be found in the hepatic vein. Or else an animal may be starved for weeks, and still sugar will be found in the hepatic vein. Evidently it must be made in the liver.

2. Let the liver be taken from a recently dead animal and laid on the table. If now water be injected into any one of the trunk vessels, the liquid running out of the other two, if tested, will, of course, show sugar; continue the current until only pure water runs out, pure both of blood and of sugar. Let the liver stand a while —say an hour. If now the current be started again, the issuing water will again show sugar. This may be repeated many times with similar result until finally no sugar comes out. The material out of which sugar is made is exhausted. The sugar, therefore, is evidently made from some insoluble or nearly insoluble substance, which is continually being changed into soluble sugar and washed out.

3. If a liver be kept a considerable time the sugar accumulates until the liver becomes perceptibly sweetish to the taste, even when cooked.

Now, the substance from which sugar is formed has been isolated and its properties and composition determined. It is a colorless, tasteless, odorless, nearly insoluble substance, having the composition of *starch*— $C_6H_{10}O_5$. It is indeed a kind of animal starch. It exists in the liver in large quantities—two per cent, seven per cent, and even fifteen per cent of the whole weight. Like starch or dextrine, but more readily than either, it is changed into sugar by enzymes. There is an enzyme for this purpose in the liver cells. The process of change is, of course, a *hydration*, exactly like that which saccharizes starch—viz., $C_6H_{10}O_5 + H_2O = C_6H_{12}O_6$. This substance is called *glycogen*, or the sugar-maker. It has the same equivalent composition as starch and dextrine, but almost certainly a different *molecular structure*, and therefore slightly different properties. For example, it is more easily changed into sugar, and it gives a different reaction with iodine. The sugar formed from it, though it has the same equivalent composition as glucose or intestinal sugar, has also probably a different molecular structure, and therefore also slightly different properties. It is apparently more easily oxidized into CO_2 and H_2O. It is better, therefore, to call it liver sugar or *hepatose*.

The formation of this sugar is a pure *chemical* not a *vital* process, for it takes place in the dead as well as in the living liver. The true vital process is the formation of the glycogen, not the sugar.

Such are the undoubted facts. But the question occurs, Whence comes the glycogen and what is its purpose? There are certain other facts which throw light on this question.

1. The amount of amyloid food—say, potatoes and rice—which is consumed by a man in a day, or even at a single meal, may be two pounds. The whole of this is changed into sugar, and, if carried *at once* into the blood, would make that liquid as sweet as sirup. But, on the contrary, the quantity of sugar in the general circulation is very small—only a trace. What becomes of it?

2. It will be remembered that the whole of the sugar is taken up by the capillaries of the portal vein, and carried to be distributed through the liver before reaching the general circulation.

Now, putting these facts together, it is evident that the large quantity of sugar carried by the portal vein to the liver *is detained there by dehydration* into the insoluble form of glycogen, and then slowly and continuously rehydrated into the soluble form of liver sugar, and delivered little by little to the blood as the necessities of combustion require.

Observe the double change. The sugar from the intestines is *de*hydrated only to be *re*hydrated. The reason is twofold: (1) It must be *stored* and delivered little by little, because sugar in the blood in large quantity is hurtful. Among other hurtful effects, see the cataract and blindness of diabetic patients.

(2) Liver sugar is a more easily oxidizable sugar, a more combustible fuel, than glucose. Glucose will circulate in the blood for a long time until it is finally excreted through the kidneys in diabetic patients. But liver sugar seems to burn up almost as soon as it touches the oxidized blood.

We have, then, *one source* of glycogen—viz., the glucose taken up from the intestines and dehydrated in the liver; but this can not be the only source, for flesh-fed animals also make liver sugar. Therefore glycogen must be made from albuminoids also. How it is made is more uncertain. I believe it is made as follows:* Remember that albuminoid food excess is split into a combustible carbohydrate part and a nitrogenous incombustible part; the one eliminated by the lungs, the other by the kidneys. Now I believe that the *place* of this splitting is the liver, the combustible carbohydrate formed is *glycogen*, and the incombustible part is urea.†

But this is not yet enough. There must be still a

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* See writer's views, Am. Jour., xv, 99, 1878, and xix, 25, 1880.

† Urea is proved to be formed in the liver (Nature, lvii, 395, 1898).

third source, for *starving* animals still continue to make liver sugar. Glycogen must also be made from *waste* tissue. Remember, again, that waste also is split somewhere into a combustible and an incombustible part, the one eliminated by the lungs as CO_2 and H_2O, the other by the kidneys as *urea.* Now, again, is it not probable that the *place* of splitting is the liver, and the combustible portion is *glycogen?* The splitting has long been known. My view is that the *place is the liver*, the combustible product *glycogen*, and the incombustible *urea.*

Therefore, according to my view, there are three sources of glycogen: (1) The whole of the amyloids dehydrated and detained in the liver, (2) the combustible part of the albuminoid food excess, and (3) the combustible part of the waste tissue. But since in adults waste is equal to repair, this is equivalent to the whole of the amyloids and the whole of the combustible part of the albuminoid food, or the whole combustible food.

But there are also exactly the *same three sources of vital force.* Therefore the whole purpose of this function of the liver is *the preparation of fuel, and the only fuel used in the animal body is glycogen.* The liver prepares the fuel, the lung burns it, the kidney removes the incombustible residue, or *ash.* The only food not taken into account here is the fats. How this is burned, whether directly, or whether it also, as is most probable,* is changed into glycogen, is not certainly known.†

Strong confirmation of this view, so far as waste is concerned, is brought out by some experiments of Schiff.‡ If the trunk vessels of the liver of a dog (Fig. 306, page 442) be ligated so that the blood can not trav-

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* Chittenden, Nature, lv, 303, 1897.

† Berthelot, Rev. Sci., viii, 129, 1897. Chittenden, Sci., v, 517, 1897.

‡ Arch. des Sci., lviii, 293, March, 1877.

erse that organ, the animal speedily falls into deep coma and dies in a half hour. Frogs bear well the ligation of the liver, because katabolic processes are very slow in these cold-blooded animals; but if a few drops of the blood of a dog dead of ligated liver be injected into a frog's veins it speedily dies if *its liver be ligated; but if its liver be not ligated it is not harmed at all.* Evidently, therefore, there is formed by katabolism a virulently poisonous substance, *which is decomposed and rendered innocuous in the liver.* This is certain. Now, my view is that the manner in which this substance is decomposed is by splitting into glycogen and urea.

The exact process of change of waste and of albuminoids generally in katabolism is very obscure and imperfectly known. Probably it is complex and contains many steps. But the poisonous results of albuminoid descensive change are called in a general way *leucomaines.* Now, the proposition is that leucomaines are decomposed in the liver in the manner already explained. After this explanation we now repeat the diagram on page 422, with some additions, and are prepared to explain it more fully (Fig. 307).

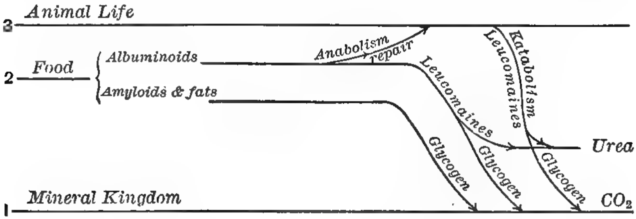

FIG. 307.—Diagram illustrating the generation of animal heat and animal force, and the products formed in the process.

This figure, in addition to the general process by which vital force is generated, gives also some details: (1) that amyloids, and probably fats also, are changed into glycogen before turning into CO_2; (2) that albuminoid excess and waste are changed into leucomaines before splitting, and, when split, glycogen is the combustible result.

If this view be true, then glycogeny is indeed a most fundamental function, and its failure must sap the vitality of the body in a marked degree. I believe that this is shown in glycosuria or diabetes.

Cause of Diabetes.—This very grave and obscure disease, in which sugar in large quantities is excreted by the kidneys, is marked by extreme failure of vitality. At first it was supposed that the kidney was at fault, but, on the contrary, it does all it can to help the patient. Sugar in large quantity in the blood is hurtful. The kidneys remove it. Then it was supposed that the lungs were at fault. The lungs, it was said, failed to take in oxygen enough to burn up the sugar, and therefore it must be excreted by the kidney. But not so, for in these cases the blood seems to be sufficiently oxidized. Then it was supposed that the fault lay in the liver, which was thought to make too much sugar, more than the lungs could burn. According to my view, the liver is indeed in fault, but not in that way. Not by *too much* sugar-making, but by *too little glycogen-making*. The sugar from the intestines is not arrested and dehydrated in the liver, but passes right through and floods the general circulation, and therefore must be removed by the kidneys. Probably also the leucomaines are not split as promptly as they ought to be, and remain to poison the blood. There is therefore an inadequate supply of liver sugar, which is the necessary fuel of the body. It is easily seen, then, why this disease is characterized by low vitality.

Recently another cause has been assigned for this disease—a cause very important in relation to the whole subject of glycogeny—by Chavaux and Lepine.* According to these authors, the *pancreas*, like the liver, is both a ducted and a ductless gland. As a ducted gland it pours its digestive secretion into the intestines; as a ductless gland it pours into the blood a peculiar ferment, which has the property of changing liver sugar in such wise that it is more readily combustible, and which is therefore called glycolytic ferment. With the failure of this function of the pancreas the sugar is not burned, and must therefore be excreted by the kidneys.

It seems almost certain, then, that the cause of diabetes is either the failure of the liver to form glycogen (by dehydration and arrestation of sugar in the case of amyloids, and by splitting in the case of albuminoids), or else it is the failure of the pancreas to secrete a glycolytic ferment necessary for combustion of sugar in the blood.

COMPARATIVE MORPHOLOGY AND PHYSIOLOGY OF THE LIVER.

We have already spoken briefly of the liver in connection with the digestive organs and functions of different animals, and little more need be said here. Its position, shape, and even color is similar in all vertebrates, and its function is doubtless the same in all. It remains a very large and important organ in invertebrates even down very low in the scale. It is nearly always distinguishable by its dark color.

As to glycogeny, this function is still performed by the liver, yet glycogen is found somewhat widely diffused in the tissues of many invertebrates, especially mollusks. It is significant that the same is true of the embryos of higher animals. This is exactly in accord-

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* Rev. Sci., li, 376, 1893.

ance with the law of differentiation, specialization, and localization of functions as we rise in the scale. Both in the embryonic series and in the taxonomic series functions are at first performed everywhere and by all the tissues; and as we rise in the scale they are more and more separated, localized, and perfected. This one has been gradually more and more localized in the liver.

CHAPTER V.

TEGUMENTARY ORGANS—SKIN STRUCTURES.

SECTION I.

Vertebrates.

It will be remembered that the whole surface, both external and internal (by infolding of the external), is covered with a pavement of living nucleated cells, and that all exchange by absorption or elimination is by the agency of these cells. When these are very active the surface is soft and covered with a slimy mucus by the continual decay and solution of dead cells, and is called *epithelium.* When less active the old cells accumulate in many layers and dry up, mummify, and flatten, and finally pass away as scales. This is called the epidermis.

The epiderm, therefore, is said to consist of two layers—viz., a layer of living nucleated cells in direct contact with the dermis and called the *mucous or Malpighian layer*, and a layer of accumulated cells in all stages of dying and flattening and mummification, and called the *cuticular layer.* The color of the skin, whether blond or brunette, or brown or black, is determined by the amount of pigment in the mucous layer. The cuticular layer, in the act of drying up, may harden in *various degrees.*

For example, if the epithelial cells only *mummify* they form the ordinary cuticle. If they simply harden, they form horn, as in hair, nails, claws, hoofs, horns, feathers, scales, whalebone, etc. If they calcify or ossify by deposit of lime carbonate or phosphate, then they form bony scales, scutes, shell, etc.

Importance in Classification. — As the skin comes directly in contact with and is modified by the environment, these structures are very characteristic of the various classes, orders, and families of animals, and are therefore very important in classification. We have already shown that teeth are skin structures, and their importance in classification is universally acknowledged. The structures about to be described are hardly less so. We give only the most important.

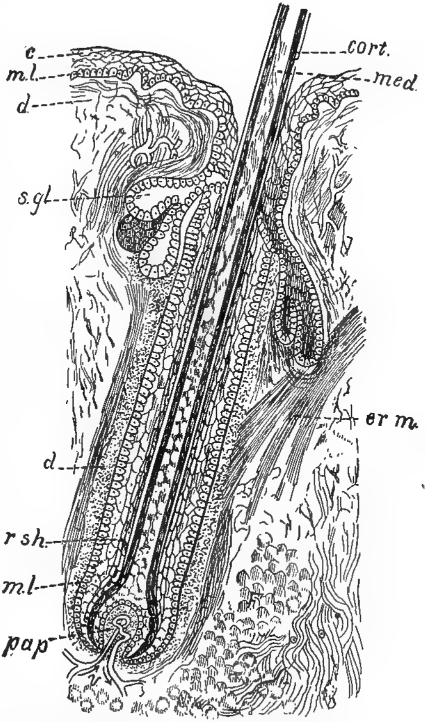

FIG. 308.—Section of skin showing hair follicle: *pap*, papilla; *ml*, Malpighian layer; *rsh*, root sheath; *d*, dermis; *sgl*, sebaceous gland; *c*, cuticle; *cort*, cortical, and *med*, medullary part of the hair.

Hair.—True hair is entirely *characteristic of mammals.* It is always formed in a follicle or infolded socket, in which the epithelial cells multiply more rapidly than elsewhere and at the same time harden to the condition of *horn* (Fig. 308). Hairs, therefore, grow by successive additions to the bottom, pushing outward, not by additions to the top like a tree. The follicle in which it is formed acts as a mold, determining its shape. The *quills of the porcupine* are only *large hairs*.

Nails.—If we tear off a finger nail, we find beneath an exquisitely tender surface of dermis covered with a layer of very active epithelium. At the base of the nail is a pocketlike infolding, where the epithelium is especially active. Over the whole surface the epithelial cells harden into horn, but this process is especially active in the pocket (Fig. 309). Therefore the nail, by its more rapid formation in the pocket at its base, is pushed forward continuously, and, if not worn away or pared away, will grow indefinitely. In some countries, as in Japan, they are sometimes protected and become enormously long, as a badge of a leisure class.

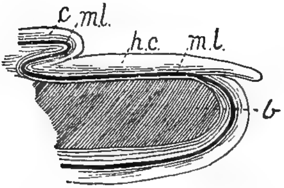

FIG. 309.—Section of the end of the finger, showing how the nail is formed: *c*, cuticle; *ml*, Malpighian layer; *hc*, the horny cuticle; *b*, the bone.

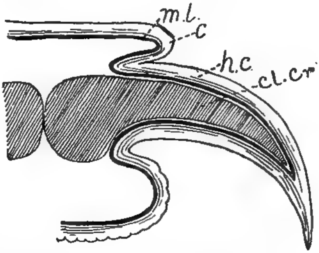

FIG. 310.—Section through terminal joint: *clcr*, claw core; *hc*, horny cuticle; *ml*, Malpighian layer; *c*, unhardened cuticle.

Claws.—These differ from nails only in the fact that they grow on *all* sides instead of one side of a peculiarly shaped terminal joint of a finger or toe. The bone of the terminal joint is the claw core and determines the shape of the claw. The core is covered with dermis and with an active layer of epithelium, which hardens into horn. At the base there is an infolded pocket in which growth is more active, so that the claw is pushed forward in proportion as it is worn off by use (Fig. 310).

Hoofs.—These, again, differ from claws only by the size and shape of the terminal joint on which they are molded. This terminal joint is the hoof core or *coffin bone*. We have here the same pocketlike infolding, and the forward-pushing growth in proportion to wear (Fig. 311). If wearing is prevented by shoeing they must be trimmed from time to time.

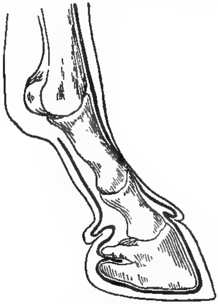

FIG. 311.—The joints of the toe of a horse. The parts are similar to the last two figures.

The horny armature of the terminal joints of the toes is characteristic of *land vertebrates*—i. e., reptiles, birds, and mammals. They are absent even in amphibians on account of their greater alliance to fishes. Furthermore, mammals, by the character of this armature, are divided into *ungulates* (hoofed) and *unguiculates* (clawed).

The original generalized form of this armature was apparently of flattened shape on the dorsal side of the toe somewhat like that of man. This was the case in some of the earliest mammals, as, for example, the *Phenacodus*, and has been retained by apes and by man. From this generalized form have been differentiated claws on the one hand and hoofs on the other.

Horns.—These are almost characteristic of ruminants. Paired horns on frontal bones are entirely so at present, although not so in early geological times. Again, frontal horns are of two kinds—viz., solid horns, as in the *Cervidæ* (deer family), and hollow horns, as in the *Bovidæ* and *Ovidæ*—e. g., ox, sheep, goats, etc.

In hollow horns (Fig. 312) we have first a conical projection of the frontal bone, covered as usual with dermis, and this in its turn with active epithelium hardening into horn. About the base there is, as usual, an infolding in which the growth of horn is especially rapid. Successive layers are formed one within another precisely as in claws. The hollow horns are *permanent.*

Fig. 312.—Section through a cow's horn: *c*, cuticle; *hc*, horny cuticle; *ml*, Malpighian layer; *hcr*, horn core; *d*, dermis.

Solid horns, as in the deer, elk, etc., are bosses which grow out from the two frontal bones with great rapidity, and are at first covered with skin and fine hair (so-called velvet). In this condition it is very vascular. In a little while—a month or so—the blood gradually withdraws, the skin dies and is rubbed off, and the antler is really dead though firmly attached to the skull. At the end of the year a separation takes place at the skull, the antler drops, and the skin of the skull grows over and covers the wound. Soon growth begins again at the same place and a new pair of antlers is formed, to pass again through the same annual cycle of changes.

In comparing the antler of a deer with the horn of an ox or sheep it is evident that the mature antler of the former corresponds with the horn core of the latter, while the horny exterior of the latter corresponds to the skin and velvet of the former.

Thus, then, the ruminants are divided into two groups, the hollow-horned and the solid-horned. The horns of the former are *permanent*, those of the latter are *deciduous.* The two grade into one another in the antelopes.

Feathers.—This most wonderful of all skin structures is wholly characteristic of birds.

Structure.—An ordinary quill feather is a marvel of lightness, strength, and elasticity. The *quill* is hollow—a form which gives greatest strength for the same weight of material. The *shaft* may be regarded as a hollow tube filled within with lightest bracing, with the horny envelope thickest on the back, where the strain comes in flight. On each side of the shaft is the *vane.* It will be observed that the two parts of the vane are not equal, the backward *overlapped* part, *p v*, being much the broader. The effect of this is to close up the feathers into a solid plane in the downward blow of the wing, while it opens the feathers and lets the air through in the upstroke (Fig. 313). Again, the vane consists of *barbs*, the shafts of which are broad and therefore strong in a vertical direction, and on these barbs again are a vanelet on each side composed of *barbules*, and finally the barbules are hooked together by little elastic hooks (Fig. 314). In Fig. 315

FIG. 313.—Section through the successive feathers of a bird's wing, showing the mode of overlap: *sh*, shaft; *av*, anterior, and *pv*, posterior vane.

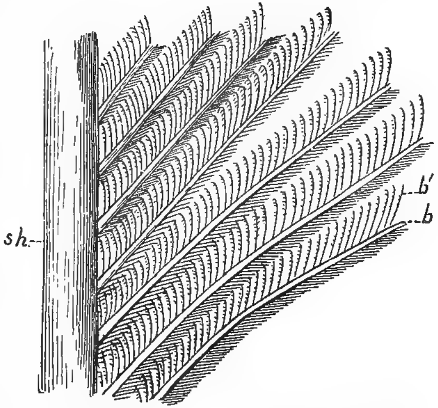

FIG. 314.—Portion of a shaft (*sh*) and vane on one side, showing (*b*) the barbs and (*b′*) the barbules with their hooks.

we give a magnified view of one barb with its barbules and hooks. The object of this structure is to make an impermeable, light, and elastic plane. If these delicate parts are disarranged or ruffled, they are easily rearranged, and hooked together again by preening. So much for the device for making an impermeable plane. Now observe how the plane is set on the fore limb. It is not set on both sides, but only on the *backward* side of the extended arm. The downward stroke of the wing therefore tips up the wing plane behind, so that the same stroke sustains and also drives forward. In Fig. 316, which is a cross section of the wing plane, if 1, 3 represent the whole air pressure in the downstroke, then 1, 2 will be the force which sustains the bird, and 3, 2 that which drives it forward.

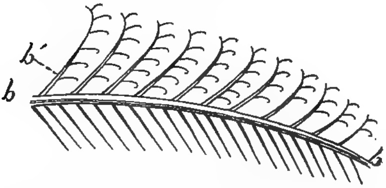

FIG. 315.—A magnified view of one barb (*b b*), with its barbules (*b'*) armed with hooks.

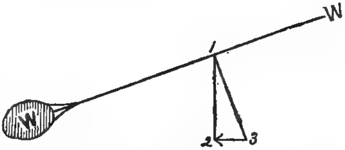

FIG. 316.—Cross section of the wing plane of a bird, showing its action in flying.

How Formed.—We have seen that all these structures thus far are formed in or on a mold, which determines their shape, and from which they are pushed out. Now, the same is true of feathers also. All this complex structure is secreted in an equally complex mold, from which it is necessarily pushed out, and the mold corresponding successively destroyed.

Gradation to Hairs.—We have described the quill feathers of the wings and tail, for these are most complex and characteristic, but all gradations may be traced through the body feathers, down, and plumes, to simple hairs. The plumes of the ostrich have the structure of feathers, except they have no hooklets, and therefore the barbules do not cohere (Fig. 317). Plumes like those of the heron, egret, etc., have no barbules; they are essentially slender, branching hairs (Fig. 318). Again, about the beaks of many birds we find simple hairs (Fig. 319). This would seem to indicate a close relation in this regard between birds and mammals. But birds undoubtedly came from reptiles, and therefore feathers are probably some modification of *scales*. But the gradations here have not been found.

FIG. 317.—Diagram of an ostrich plume, consisting of shaft (*sh*), barbs, and barbules, but no hooks.

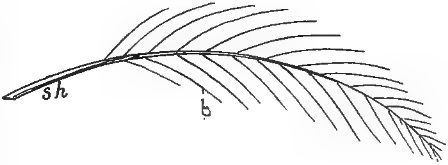

FIG. 318.—Diagram of an egret plume, consisting only of shaft and barbs.

FIG. 319.—Hair about the beak of a bird, consisting of shaft only.

Scales are characteristic of reptiles and fishes, especially the latter.

Fish Scales.—We take these as the type. They cover the whole body. They are formed much like nails—i. e., on the surface of the mucous layer, and especially in pocketlike infoldings. The manner in which from those pockets they grow backward, shingling over one another, is shown in the figure (320), which is taken with some simplification from Owen.

Classification of Fishes by Scales.—Agassiz divided fishes by the character of their scales into four orders—viz., the *Ctenoids*, the *Cycloids*, the *Ganoids*, and the *Placoids*. Ctenoid scales are pectinate on their posterior or exposed margin (Fig. 321, A). Cycloid scales are smooth and rounded on this margin (Fig. 321, B). Ganoid scales are bony, enameled, and usually rhomboidal, close fitting, and not shingling (Fig. 321, C). Placoid scales are very small, with outsticking sharp points (Fig. 321, D). The first two are *horny*, the last

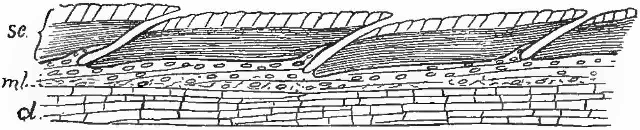

FIG. 320.—Section through skin of a fish: *d*, dermis; *ml*, Malpighian layer; *sc*, scale. (From Owen.)

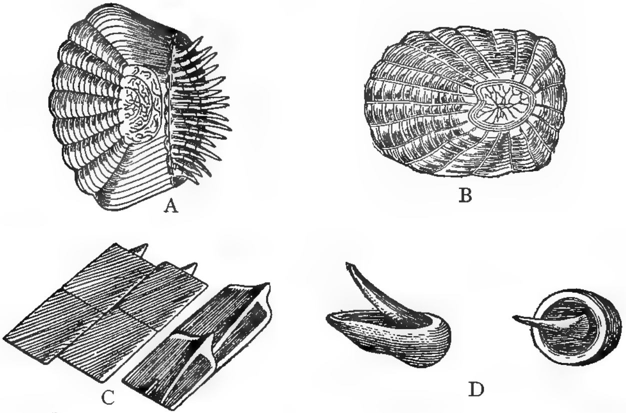

FIG. 321.—Fish scales, illustrating Agassiz's classification.

two are *bony*. The *Ctenoids* are spine-rayed fishes, like the perch, etc.; the *Cycloids* are soft-rayed fishes, like the cod; the *Ganoids* are sturgeons and bony pikes or *gars*; the *Placoids* are sharks, skates, and rays. If we make the *Ctenoids* and *Cycloids* subdivisions of *teleosts* or ordinary typical fishes, then the classification is a good one as far as it goes, and has done good service in geology, for it is the scales which, together with the teeth, are most apt to be preserved.

Reptile Scales.—We have taken fish scales as the type; but scales are found also in reptiles, and even in mammals. In reptiles they may be horny, as in snakes and lizards, or bony scutes, as in *Crocodilia*, or a combination of those two, as in the shells of tortoises and turtles. Scutes differ from scales proper in involving the dermis as well as the epidermis.

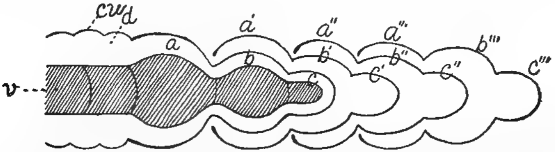

FIG. 322.—Diagram showing structure and mode of formation of a rattlesnake's rattle: $a\ b\ c$, horny cuticle of last joints of the vertebra (v); $a'\ b'\ c'$, that of last year slipped back and caught; $a''\ b''\ c''$, and $a'''\ b'''\ c'''$, are still earlier cuticles.

In *snakes* the horny, scaly cuticle is shed every year, and a new one is formed by the mucous layer. This annual skin shedding gives rise in an interesting way to the rattle of the rattlesnake. The few last joints of the vertebral column (a, b, c) are enlarged and consolidated into an irregular mass, and covered with a horny scale thicker than elsewhere on the body (Fig. 322). With the skin shedding this loosens, and is shed like the rest of the skin, but, being elastic, it slips back and catches on the neck of the next joint. In the next year's skin shedding the horny covering of this part slips back again, and is caught in the same way, and so on. Thus is formed a series of molds of the three consolidated joints loosely caught together. Every year adds another to the chain, and, if not broken or worn off, the number indicates the number of skin sheddings, and therefore the age of the snake.

Turtle Shell.—Turtles are incased in an immovable shell. The dorsal part is called the *carapace*, the ventral part the *plastron.* Where, then, is the jointed backbone characteristic of vertebrates? Their structure seems to violate the vertebrate plan. But not so. It is only an extreme modification of that plan, and is an admirable illustration of *adaptive modification* underlying homology (page 246). If we look into the interior of the carapace of a complete skeleton of a turtle we see a continuous series of vertebræ, consolidated with one another and with the shell in the region of the trunk, but movable in the neck and tail. The shell of a turtle or tortoise is indeed a very complex structure, consisting of three parts—*skeletal*, *dermal*, and *epidermal.* The spinous processes of the vertebræ expand at the top into broad flat plates, which unite with one another to form the *ridge* or central row of plates of the carapace. The ribs also expand into broad plates, which, uniting, form the sloping under-roof on each side. Then the dermis over all this is ossified into bony plates, which unite with the skeleton proper to form the main part of the carapace. Lastly, the *epidermis* completes the structure by forming the horny covering over all. This last is the so-called *tortoise shell* so much prized. Between this and the bony shell, of course, there is a *Malpighian layer*, which by transformation forms the horny layer. Similarly the plastron is formed by the union of dermal bony plates with the *ventral ribs* (like those of an alligator), and covered with epidermal horn. In both the carapace and the plastron the epidermal horny plates do not correspond with the bony plates beneath, but *break joints* with them.

Mammalian Shell.—At the present time shells are found only in the armadillos and pangolins, but in early times—Quaternary—armored mammals were numerous and of great size.

Endoskeleton and Exoskeleton.—Thus, even in mammals and much more in reptiles, we begin to have the distinction between an exterior shell and interior skeleton, or *exoskeleton* and *endoskeleton*. In vertebrates the exoskeleton is purely *protective*, but in invertebrates, which have no endoskeleton, it becomes *locomotive* as well as protective. This brings us naturally to the invertebrates.

SECTION II.

Invertebrates.

ARTHROPODS.

Insects.—Arthropods are all covered with an efficient exoskeleton, both protective and locomotive. In insects it is composed of chitin (a partly calcified horny substance). As this is usually rigid and unyielding and is not shed, insects can not grow after they have once put on this coat of mail. Therefore the whole growth must take place in the soft larval condition. Neither butterflies, nor beetles, nor flies, nor bees and ants, etc., grow. They finish their growth in the form of caterpillar or grub. Many extremely beautiful and curious appendages are found on insects in the form of elaborately sculptured scales, and the splendid colors of insects are mainly due to these. Such are the scales which give color to butterflies, and the gorgeous iridescent green-gold hues to some beetles.

The Higher Crustaceans are equally incased in an unyielding shell more calcified than that of insects; and yet *they grow.* This is possible, however, only by a periodic shedding of the shell, which leaves them for a time almost helpless for want of a rigid skeleton until a new one is formed by deposit of carbonate of lime in the skin.

In lower crustaceans the shell is chitinous, like that of insects. Thus crustaceans have been divided by their shell substance into a lower group (*Entomostraca*), insect-shelled or chitinous-shelled, and a higher group (*Malacostraca*), mollusk-shelled or calcareous-shelled.

MOLLUSKS.

These are *par excellence* shell-covered animals, and their classification is largely based on the character of their shells.

Acephala have two shells, a right and a left, hinged along the back—*bivalves.* *Gastropods* have but one, usually much coiled shell—*univalves.* *Cephalopods*, when they have a shell at all, are distinguished by their *many-chambered* structure. The animal lives only in the large outer chamber. All the other chambers are closed and filled with air, and a slender membranous tube—the *siphuncle*—runs from the animal through all these chambers, but not opening into them (Fig. 325).

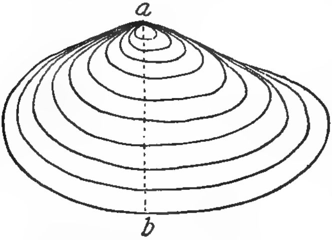

FIG. 323.—Surface view of a bivalve, showing lines of growth or successive sizes of the shell.

Growth of Shell.—The shell is a calcareous secretion by the skin of the mantle. *In bivalves* (see Figs. 280

and 281, pages 401 and 402) the mantle covers the interior of the shell to the very edge, and forms the shell in its epidermic cells, layer by layer, each on the inside of the last, and extending a little beyond it, by the growth of the animal. The successive growths are easily seen on the outside of the shell (Fig. 323; on section, Fig. 324). If a small object like a coin be slipped between the mantle and the shell it will soon be covered by a secretion from the mantle, and finally inclosed in the thickness of the shell.

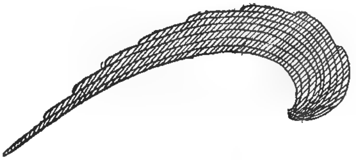

FIG. 324.—Section along the line *a b* of previous figure, showing structure.

The subdivisions of the *Acephala* are seen in the shells. The *Monomyaria* have one muscular impression on the shell, as in the oyster; the *Dimyaria* have two muscular impressions, as in the clam or the river-mussel, etc.

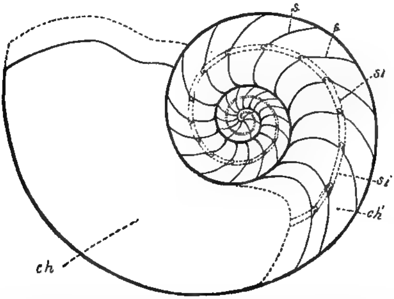

FIG. 325.—Section through a nautilus shell: *ch*, living chamber; *ch'*, empty chamber; *si si*, siphuncle; *s s*, septa. A new septum to be formed and an extension of the outer chamber is shown by the dotted lines.

The *gastropod* shell grows in a similar way, and the successive shell margins can generally be recognized, and often form conspicuous ornaments on the shell.

Cephalopods live, as already said, in the larger outer chamber, all the others being empty and connected with one another in the living animal by the siphuncle (Fig.

325). As the animal grows, the extending mantle adds to the length and size of the outer chamber until finally the animal withdraws from contact with the last chamber wall and secretes another partition, and thus adds another to the series of empty chambers. Cephalopods are classified into two groups—viz., the naked, like squids and cuttlefish, and the shelled, like the nautilus; the former have two gills (dibranchs), the latter four gills (tetrabranchs).

The exquisite beauty and variegated iridescent luster of molluscous shells when polished is the result of the superposition of extremely thin, translucent plates and the interference of light thus produced. The play of color becomes more splendid if the plates are corrugated, as in the abalone (*Haliotus*).

ECHINODERMS.

The shell of a sea urchin is a wonderful structure when examined under a microscope. Imagine a calcareous shell composed of several layers, each layer a reticulation of calcareous fibers, the several layers separated from one another by calcareous pillars, but the openings or mesh of the several layers *not coinciding*—and we have a structure which is a marvel of lightness and strength combined with perfect permeability. This structure is easily seen under the microscope, and the skin structures of echinoderms generally furnish some of the most beautiful of microscopic preparations, and are very characteristic of the several orders.

CORALS.

The deposits of coralline limestone in corals are somewhat peculiar, yet, as they are formed by epidermal cells, like epithelial cells, and therefore are of similar origin, they may well be treated under this head. Everywhere the deposit is in the epidermis; for even the partitions are infoldings of the epiderm.

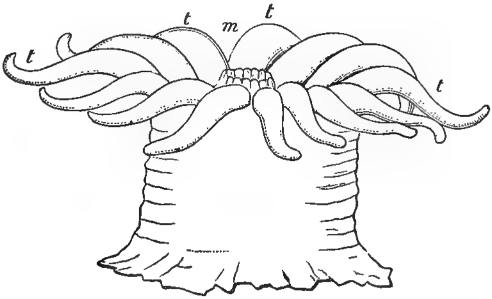

FIG. 326.—Simplified figure of an actinia.

We recall, then, the structure of the soft polyp, with its radiating partitions, and reproduce the figure showing it (Fig. 326). Now, in corals, the structure is the

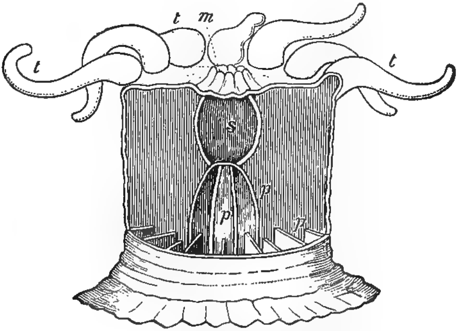

FIG. 327.—Ideal section, vertical and horizontal, showing structure: *t*, tentacles; *s*, stomach; *p p*, partitions.

same, except that deposits of lime carbonate are formed in the lower part—i. e., in the foot disk, the walls, and the partitions to more than midway up the animal, but leaving the upper part of the wall, partitions, and the tentacles soft and free (Fig. 327). When the coral seems to disappear, as in a cell, it is simply the withdrawal of the soft upper parts into the lower calcareous part or theca. In the dead coral the organic matter disappears and leaves the cuplike theca showing the radiated structure of the animal (Fig. 328, *a* and *b*).

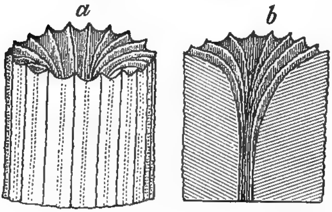

FIG. 328.—*a*, stony part of a single coral; *b*, section of same, showing structure.

Theca.—Only recently has the origin of the theca been well understood. It was formerly supposed that the coral limestone was deposited in the substance of the tissues, and therefore constituted a sort of *endoskeleton*. But now it is known to be a true *exoskeleton* or an epidermal structure. The mode of formation seems to be as follows: (1) The basal

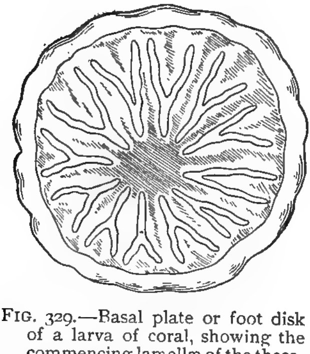

FIG. 329.—Basal plate or foot disk of a larva of coral, showing the commencing lamellæ of the theca. (After Sedgwick.)

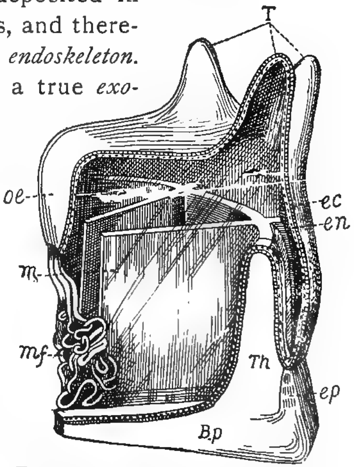

FIG. 330.—Diagram showing structure of the theca; the white in section is coral limestone: *Bp*, basal plate; *Th*, theca; *ep*, epitheca; *ec*, ectoderm or epiderm; *en*, endoderm; *T*, tentacles; *œ*, œsophagus; *m*, mesentery; *mf*, mesenteric filaments. (After Sedgwick.)

plate forms radiating upgrowths by the infolding from below of the epiderm and deposit of calcareous matter in the folds (Fig. 329); (2) the outer margins of the radiating calcareous septa unite to form the outer wall of the theca; (3) the body wall by downfolding grows over this outer wall, inclosing and covering it and adding to it by calcareous deposit, and thus completing the outer surface (Fig. 330).

SPONGES.

The skeletal deposits in sponges also are formed by the agency of unmodified cells, and therefore may be brought under this head. What we call a *sponge* is the horny skeleton of the animal of the same name, and deposited within its tissues in the most intricate way. The glass sponge, such as the Venus's flower-basket—*Euplectella*—with its beautiful and intricate mesh of glass fibers, is similarly produced by a deposit of silica in the tissues of the animal. The classification of sponges is based on the character of the skeleton. There are horny sponges, glass sponges, and calcareous sponges.

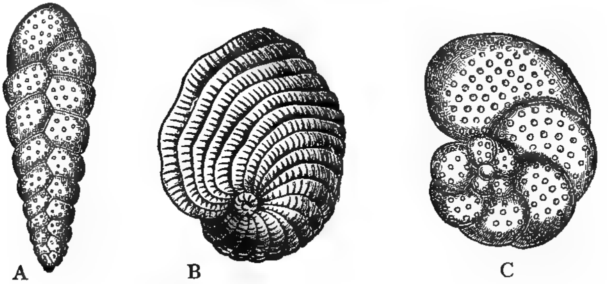

FIG. 331.—Shells of living foraminifera: A, textularia variabilis; B, peneroplis planatus; C, rotalia concamerata. (After Williamson.) The figures are greatly enlarged.

RHIZOPODS.

Many rhizopods have no hard parts, but others, especially *Foraminifera* and *Radiolaria*, form calcareous or siliceous skeletons of exquisite beauty and complexity. They form the most beautiful objects under the microscope. These skeletons are also very characteristic of the various orders (Fig. 331).

CHAPTER VI.

GEOGRAPHICAL DISTRIBUTION OF ORGANISMS.

THIS subject is not directly connected with physiology, although it is with morphology, but its extreme interest and importance in connection with evolution justifies its treatment with some fullness.

It is well known that the observant traveler from one continent to another—as, for example, to take an extreme case, from Europe or the United States to Australia—finds all the animals and plants entirely different from those he has been accustomed to see at home. The same is true in less degree in going from America to Europe, or even from the Atlantic to the Pacific side of our own continent. Until comparatively recently the facts of this distribution of species were a mere chaotic mass without a guiding principle. The theory of evolution has brought law and order into this chaos. All we can do here is to give a bare outline of the general laws of this distribution and their explanation.

Fauna and Flora.—In popular language fauna and flora means the group of animals and plants inhabiting any place; but in scientific language it is a natural group of organisms differing from other natural groups and separated from them by geographical boundaries, or by temperature or climate, or physical conditions of some sort, and in harmonic relations with one another and with the environment.

Illustrations of Harmonic Relations.—The complexity of the harmonic relations of all members of a group of organisms is such that if one element is altered a wave of change, often of the most unexpected kind, is propagated through the group until a new harmonic relation is established. It was Darwin who first drew attention to the relation of *cats* to the flourishing of clover. The fertilization of clover flowers is dependent on the presence of *bumble bees*, but the nests of these are destroyed by *field mice*, and field mice are destroyed by *cats*. Professor Morgan somewhat humorously extends the complex relation by adding that cats are cherished by old maids. Thus the presence of old maids is favorable to the growth of clover. The most unexpected results often come from interference with these natural relations. Farmers to protect crops destroy birds, and insects injurious to crops increase. Sportsmen introduce English rabbits into Australia and New Zealand, and the governments of those countries have spent millions of pounds in vain attempts to destroy them.

In a word, every species in order to continue to exist must be in harmonic relation with the environment both physical and organic. Now, the physical environment consists of soil, climate, and geographical barriers. Among these the simplest and the most universal is *temperature*. We will therefore speak first of *temperature regions*. And among organisms the simplest in their relations are *plants*. Therefore we speak first of all of

Botanical Temperature Regions.—As we travel from equator to pole we pass through successive zones of temperature ranging from 80° to 0° F. These zones are characterized predominantly by different groups of plants. We have first a region of palms and tree ferns, corresponding with the intertropical zone; then a region of evergreen hard-wood trees corresponding with the warm temperate zone; then a region of deciduous hardwood trees, corresponding with the full temperate zone; then a region of conifers and birches, corresponding to the cold temperate or subarctic zone; then a treeless region, corresponding to the arctic or circumpolar zone; and finally a plantless or nearly plantless region, occupied by the polar ice cap (Fig. 332).

Qualification.—1. By the terms region of palms, region of pines, etc., we mean only that these kinds of trees by their abundance give character to the aspect of field and forest.

2. We have drawn *lines* separating these regions, but in fact they shade completely into one another.

3. We have drawn the separating lines regular, like lines of latitude, but, in fact, they are irregular, like isothermal lines.

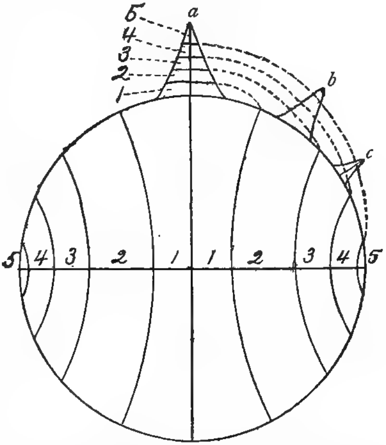

FIG. 332.—Diagram showing temperature zones in latitude and corresponding zones in altitude: 1, tropical; 2, temperate; 3, subarctic; 4, arctic; 5, perpetual snow. *a*, *b*, *c*, mountains in tropical, temperate, and subarctic regions respectively.

Regions in Altitude. — These regions being temperature regions, similar regions are found in ascending mountains (Fig. 332). A mountain in the tropics if it reaches perpetual snow will contain all of them, while mountains in higher latitude only the higher portions of the series. For example, in the Peruvian Andes we have all these regions successively encircling the mountain—

i. e., a region of palms at the base, a region of hard-wood trees higher up, then a region of pines, a treeless region, and a plantless region or perpetual snow. In the *sierra*, which is in the temperate zone, the region of palms is wanting, but all the others are present. To two thousand feet or more hard-wood trees predominate, then pines and spruces up to ten thousand to twelve thousand, then shrubs and flowers, and finally perpetual snow.

Zoölogical Temperature Regions.—Thus far we have spoken only of plants, because their relations are more simple and easily brought out on account of their being fixed to the soil. But the same laws govern animal species also. Animals also have their temperature regions. For example, the great cats, the hyenas, the great pachyderms, the camels, the ostriches, parrots, toucans, the reef-building corals, etc., are tropical, while the polar bear, the civets, martens, seals, walruses, and whales are predominantly arctic.

COMPLETER DEFINITION OF TEMPERATURE REGIONS.

1. The range of any organic form is the extent or area of its distribution. It is most restricted for species; is greater for genera, because when a species ceases the genus may be continued by other species of the same genus. It is still greater for families, because when a genus ceases the family may still continue as other genera of the same family, etc. The range is extensive in proportion to the largeness of the taxonomic group. For example, we have said that the range of the conifers in the *sierra* was from two thousand to ten thousand feet. This is the range of the order, but no species extend so far. If we take the genus *Pinus* we have first the digger pine (*P. sabiniana*), then the yellow pine (*P. ponderosa*), then the sugar pine (*P. Lamberti-*

ana), then the tamarack pine (*P. contorta*), then the *P flexilis*, etc.

2. The ranges of contiguous species shade insensibly into one another by overlapping interpenetration and co-existence on the margins.

Each species is most abundant and vigorous about the middle of its range, and becomes less and less numerous and vigorous on the margins until it ceases and gives place to some other species. Thus, if *a a′* (Fig. 333) be the range of species *A*, and *b b′* of species *B*, then the rising and declining curves represent the relative abundance in different parts of their ranges, and *a′ b* their overlap or area of coexistence on the margins.

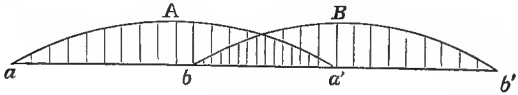

FIG. 333.

3. But species do not *usually* grade into other species, which take their place, in *specific characters*. There is not usually any evidence of transmutation of one species into another. One species seems to be *replaced by*, not *transmuted into*, another species. The change is usually by *substitution*, not by transmutation. I say *usually* because sometimes such gradation in specific characters is found.

Illustrations.—We take for illustration only two examples: (1) The *sequoia*, or big tree, and redwood exist to-day only in California; one (the redwood) confined to the coast range, and the other (the big tree) to the Sierra. Now, in commencing south, wherever found these trees are perfect in all their specific characters of bark, wood, leaf, and fruit. They remain substantially unchanged throughout their range, and stop at their northern limit still unmistakably the same. They do not, and apparently can not, change their specific characters. They die first. (2) Take another example, the sweet gum (liquidambar) of the eastern coast. This remarkably distinct form ranges from Florida to the borders of the Great Lakes. Throughout all this wide range it is precisely the same unmistakable species, characterized by its peculiar starred leaf, winged twigs, spinous burr, and fragrant gum. On the limits of its range it does not change into any other species, but simply dies out and is replaced by others.

These are illustrations of what has been called "*permanence of specific form.*" *It is as if* species originated, no matter how—say, at once by creation—in their present form, somewhere in the region where we find them, and thence spread in all directions as far as physical conditions and struggle for life with other species would allow, interlocking there with other contesting species and coexisting with them on the common border.

4. **Barriers.**—Faunas and floras shade gradually into one another when limited only by temperature conditions; but if there should be an impassable physical barrier, like an east and west mountain range, or a desert or sea, then the fauna and flora on each side of such barrier will differ greatly and *without any shading*. Thus the species north and south of the Himalaya, or north and south of the Sahara, differ conspicuously and trenchantly. It is again *as if* each group of organisms had originated or been created at once out of hand just as they are and where we find them, and spread as far as they could, but could not mingle with the next contiguous group on account of the intervening barrier.

5. **North and South of the Equator.**—Again, there are temperature zones south of the equator as well as north; but none of the species found in temperate or

arctic zones north are the same as those found in similar zones south. It is, again, *as if* each group was created as it is and where we find it, and prevented from passing to similar zone, north or south, by the torrid temperature intervening.

CONTINENTAL FAUNAL REGIONS.

Thus far we have considered only temperature conditions; now we take up other limiting conditions.

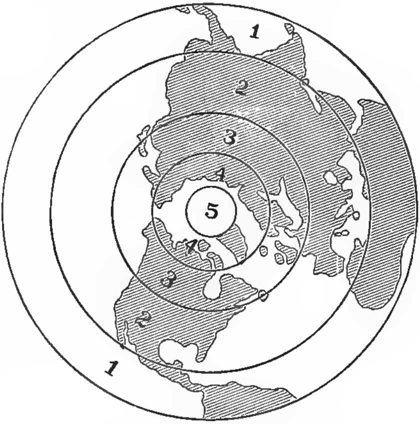

FIG. 334.—Polar projection of the earth: 1, tropical; 2, temperate; 3, subarctic; 4, arctic; 5, polar regions.

If continuous land existed all around the earth, then, barring desert regions, there is no reason to doubt that species would range all around, and there would be a strictly zonal arrangement of species determined by temperature alone. But the continents are widely and impassably separated by oceans. Therefore the species on different continents are wholly different. It is, again, *as if* each continent had been populated by its own inhabitants, suited to its climate, just as we find it now, and had not been able to cross the ocean barrier and mingle.

If we take the facts in detail the case becomes still stronger. Let Fig. 334 represent a north polar projection of the earth. The five zones are represented by corresponding numerals. We may leave out No. 5, as this is unknown and largely uninhabited. In No. 4 the fauna is practically the same all around, because of the close approximation of the lands of the two continents here and the easy communication over the solid ice.

But in Nos. 3 and 2, which include the United States and Europe, we find the species are substantially all different. Even many of the genera and some families are peculiar to each continent. Some species, indeed, are representative or resembling species, but not identical. To this general statement there are some exceptions, but these are of the kind which prove the rule, or rather the principle on which the rule is founded.

Exceptions.—1. *Hardy* or *widely migrating species*, such as geese and ducks. These are the same on the two continents, because they range also into No. 4, and thence go down on either continent.

2. *Introduced species*, such as all the useful plants and domesticated animals and all the noxious weeds and animal pests—flies, rats, etc.—which follow the footsteps of civilization. We not only find these on both continents, but they often do as well, or even better in their new homes than in their native places. They were not in those new homes before only because they could not get there.

3. *Alpine Species.*—It is a curious fact that animals and plants inhabiting the tops of high mountains in Europe and in the United States are extremely similar, and even sometimes identical, even though so widely and impassably separated. The explanation of this will come up later.

In No. 1, or tropic zone, the difference is still greater; not only all the species in South America and Africa are wholly different, but many whole families are entirely peculiar to one or the other continent. For example, the monkeys are found in both, but the tailless monkeys are peculiar to the Old World, while the prehensile tailed monkeys are peculiar to America. The great pachyderms are peculiar to the Old, while the sloths are peculiar to the New. Among birds the great family of humming birds, containing over four hundred species, are peculiar to America, while the true ostriches are confined to Africa. Among plants, the great family of cactuses, with its innumerable species, is peculiar to America.

Nos. 2 and 3, in the southern hemisphere, continue quite distinct in South America and Africa, because these are still widely separated. There are some evidences, however, derived entirely from their faunas and floras, that they were once more approximated than now.

SUBDIVISIONS OF CONTINENTAL FAUNAS.

We have already spoken of subdivisions of these determined by temperature, and in a more marked manner by east and west barriers, such as mountain chains, etc. But they are divided also by north and south barriers. Thus the United States fauna is divided in a very marked way by north and south mountain chains into distinct faunal regions. By the Appalachian range the division is not very marked, because the chain is not very high nor very long, but the Rocky Mountain chain, running the length of the continent, and, together with the intermountain deserts, more than one thousand miles wide, form an insuperable barrier to most species of animals and plants. So that California is a very distinct faunal and floral region. Similarly, but in less degree, the Ural separates a European from an Asiatic fauna and flora.

Special Cases.—1. *Australia.*—We have thus far spoken only of the two great continental masses, eastern and western, but there is another land mass of continental proportions—viz., Australia. This we take as our first example of special cases. It is the most isolated of continents, and the most distinct of all faunal regions. All the animals and plants there are widely different from those of any other region. To show the greatness of this difference we take up more particularly one class only—viz., the mammals.

Mammals are divided into three subclasses: *Eutheria*, or ordinary typical mammals, found everywhere except Australia; *Metatheria*, or marsupials; and *Prototheria*, or monotremes. *Eutheria* are perfect *young-bearers;* the *Prototheria* are perfect *egg-layers;* the *Metatheria* are intermediate. The young of these are born in a very imperfectly organized condition, and embryonic development is finished in the marsupium or pouch. Now, there are about one hundred and fifty species of mammals in Australia, all of which are marsupials and monotremes. Moreover, monotremes are found nowhere else, and of marsupials only a few opossums are found elsewhere, viz., in America, North and South. The only exception to this sweeping difference is the existence of a few bats and a few rats —animals especially liable to dispersal by means of floating logs, etc., and therefore to accidental introduction.

2. *Madagascar.*—This very large island off the east coast of Africa is separated from the latter by the wide and deep Mozambique Channel. Next to Australia, it is perhaps the most distinct of all faunal regions. It may be called the home of the lemurs, and has besides many curious forms. All the mammals are peculiar, except such as have been introduced. But it is well to remember that whatever distant resemblances they have are mostly with those of South Africa.

3. *Galapagos.*—These islands, off the west coast of South America, strongly attracted the attention of Darwin during his voyage on the Beagle on account of the singularity of their fauna. They have been visited by many other naturalists for the same reason. There are no mammals or amphibians, and the species of other groups are all peculiar. Among them are found many very large lizards and several species of gigantic land tortoises. These islands are separated from South America by deep water.

4. *River Mussels.*—We might multiply examples indefinitely. We take one more. In the Altamaha River, Georgia, among other shells found there is one, *Unio spinosus*, with needlelike spines an inch and a half long. This species is not found elsewhere on the face of the earth. How did it get there?

In all these cases it would seem *as if* the groups of animals and plants had been made and put there where we find them, and are not found elsewhere because they could not get away.

Marine Faunas.—Thus far we have spoken only of land organisms, but the same laws are true in less degree for marine species.

Temperature Regions.—Here, also, of course, we have temperature regions, and consequent gradations by change of species as we go north or south. Here, also, at certain places we may have more abrupt changes. For example, on the east coast of the United States we have two abrupt changes of coast fauna, one at Cape Cod and the other at Cape Hatteras. Scarcely a single species passes from north to south of these points, or *vice versa.* The cause is found in the marine currents off the coast. The warm Gulf waters coming through the straits of Florida hug the coast and warm the shore waters as far as Cape Hatteras (*a*, Fig. 336), and then leave the coast. The icy-cold waters coming out of Baffin's Bay hug the New England coast as far as Cape Cod, *b*, giving it its peculiarly harsh climate, and then disappear and become a deep current. Thus the subtropical fauna is carried beyond its limits to Cape Hatteras, while the arctic shore fauna is carried beyond its natural limits as far south as Cape Cod, making three sharply defined shore faunas.

Continental Shore Faunas.—The richest marine faunas are along the shores of continents. The deep sea is an impassable barrier to these. Therefore the faunas along the two shores, European and American, of the Atlantic are almost wholly different. The continent itself is, of course, a still more effectual barrier, and therefore our Atlantic shore species and Pacific shore species are wholly different.

Pelagic Fauna.—Many marine species swim or float freely in the open sea, and are much more widely diffused, being limited by temperature alone. These are called pelagic species.

Abyssal Fauna.—Again, certain species live only at very great depths. These are abyssal species.

Special Cases.—There are special cases here also —that is., the species found along the shores of isolated islands, as about Australia, Madagascar, Galapagos, etc.

Primary Divisions of Land Faunas.—Thus, then, organic forms are limited in range in every direction by many kinds of physical conditions. They are limited north and south by temperature, and in all directions by barriers such as mountain chains, deserts, and oceans. Besides these, climate and soils limit especially plants, and these limit animals. Thus the whole earth is divided into a few great primary *faunal regions*, and these are subdivided into *provinces*, etc. Many schemes of primary and secondary divisions have been proposed. I give that which is most generally adopted—viz., that of Mr. Sclater and Mr. Wallace. According to this scheme there are *six* primary regions, each subdivided into four provinces. The primary regions are: 1. *Palearctic*, including the whole of the Old World north of Sahara and the Himalayas. 2. *Ethiopian*, including Africa south of Sahara. 3. *Oriental*, including Asia south of the Himalayas, together with the adjacent islands, Ceylon, Java, Borneo, Philippines, etc. 4. *Australian*, including Australia, New Guinea, New Zealand, and Polynesia. 5. *Neotropic*, including South America, Central America, and the Antilles. 6. *Nearctic*, including all North America north of Mexico. These regions are shown on map (Fig. 335).

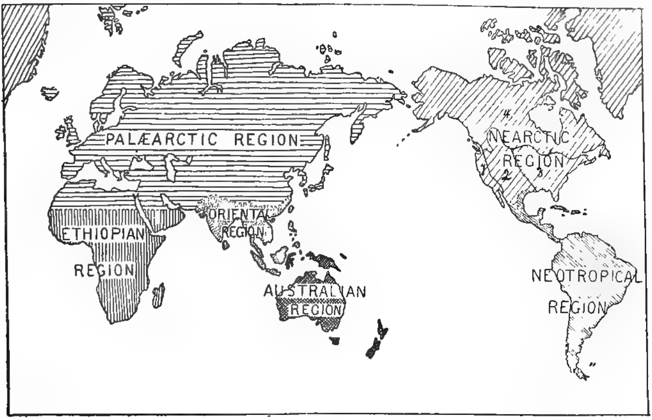

FIG. 335.—Map of the world, showing the six primary regions of Mr. Wallace.

These are each subdivided into four provinces, as shown in the following schedule; but we will give more particularly only those of our own Nearctic region.

1. Palearctic	1. European.
	2. Mediterranean.
	3. Siberian.
	4. Manchurian.
2. Ethiopian	1. Eastern.
	2. Western.
	3. Southern.
	4. Malagasian.
3. Oriental	1. Indian.
	2. Ceylonese.
	3. Indo-Chinese.
	4. Indo-Malayan.
4. Australian.	1. Austro-Malayan.
	2. Australian
	3. New Zealandian.
	4. Polynesian.
5. Neotropic	1. Chilian.
	2. Brazilian.
	3. Mexican.
	4. Antillean.
6. Nearctic	1. Californian.
	2. Rocky Mountain.
	3. Alleghanian.
	4. Canadian.

The subdivisions of the Nearctic are given in Fig. 336. They are: 1. *California*, including the Pacific border from Vancouver Island to the borders of Mexico. 2. *Rocky Mountains*, including all the mountains and desert region, and extending into the Mexican plateau. 3. *Alleghanian*, including all the United States east of the plains and south of the Great Lakes. 4. *Canadian*, including all north of 1, 2, and 3.

Primary Divisions of Marine Faunas.—Sclater makes of these also six. But in the present imperfect state of knowledge the simpler classification proposed by Gill seems preferable. Gill divides marine faunas into three great realms: 1. North Polar or *Arctalian*. 2. *Tropicalian*. 3. South Polar, or *Notalian*.

Theories of the Origin of the Distribution of Organisms.—We have given in outline the facts. The question is, "How came it so?" Before the advent of the theory of evolution the most rational theory was based on the ideas of *permanence of specific types and centers of specific origin*, as if each species was made in its present form and its present place, and thence spread as far as it could without changing its character. It did not deny some variation, but always within certain limits. If the centre of a circle represents a specific type, then radii will represent the variation in all directions, and the circumference the limit of variations. Some species are more and some less variable; the circle may be larger or smaller, but in all there is a limiting line beyond which it is impossible to go without destroying the

Fig. 336.

species. Or, again, permanence may be compared to a right cylinder standing on end. It may lean in any direction to a limit and right itself, but pressed too far it is overthrown, and the species is destroyed. Within these limits species are made according to a plan or type at once, and these continued by generation unchanged. They are, as it were, struck from the same die, until the die is broken or worn out and another made. Thus the process goes on by an alternation of supernatural and natural means. The origin was supernatural, the continuance by natural process of generation. The making of dies was supernatural, the coinage was natural.

This *old* theory, as already shown, explains many of the phenomena given above, *but not all.* For example: 1. If each species were made especially for a certain place and environment, then it ought to be more perfectly adapted to that place than any other, but, on the contrary, *introduced species often flourish better in their new than in their old homes.* 2. Again, if species are made each in its own place and spread as far as they can and wherever they can—as indeed they do—then the amount of difference between faunas of different places ought to be in strict proportion to the impassableness of the barriers between. This is indeed largely true, but not the whole truth. There is another element which is left out—viz., the element of *time.* The difference is proportioned to the impassableness of the barrier and *the time since the barrer was set up.* This element of time connects the subject with the idea of evolution of organic forms throughout all geological time. In a word, the old theory was well enough for the present condition of things, though not perfect even there, but fails entirely to connect present faunas and their distribution with those of previous times. The study of the present alone is but a *flash-light view* of the world, and therefore the world seems to *stand still*, and organic forms seem to be *permanent.* Geology alone shows us the world in continuous motion, in continuous change by evolution.

In the *new* and now universally adopted view there are four principles to be borne in mind: 1. The origin of organic forms "by descent with modifications"—i. e., by evolution—and the steady forward march of evolution everywhere and through all time. If this were all, there would be no geographical diversity at all. 2. In different places, with different environments and isolated from one another, evolution *took different directions*, and faunas became more and more different as long as the isolation continued. If this had been all, geographical diversity would by this time have been far more extreme than we find it anywhere. 3. But from time to time, at long intervals in geological history, there occurred widespread changes in physical geography and climate by which barriers were removed and new barriers set up. The result was wide migration and mingling and conflict of faunas, and consequently more rapid evolution, but at the same time a decrease of geographical diversity. 4. A re-isolation in new localities, and a commencing process of divergence which is still going on.

Now, the last of these periods of great changes, climatic and geographic, and of extensive migrations and minglings and conflict of faunas, and therefore of rapid evolution, was the glacial epoch, or *ice age.* It is evident, then, that the geographic and climatic changes of the glacial epoch furnish the key to the present distribution of species, and, conversely, the present geographic distribution of species furnishes a key to the direction of migrations of that time.

A full discussion of this interesting subject should be preceded by a course in geology, but an outline may be brought out by means of illustrative examples.

1. *Alpine Species.*—We have already spoken of the remarkable fact that alpine species of plants and of insects are very similar (though not usually identical) in Europe and America, although so widely separated and completely isolated. The key to the explanation is found in the additional fact that they are both similar to arctic species, and the explanation of both is found in the migrations of the glacial epoch.

We have already seen that arctic species are the same on the two continents, because they are *circumpolar* and in substantial connection all around. Now, as the glacial cold came on, the ice sheet advanced southward, driving the arctic species before it on both continents, until they invaded and occupied all America to the Gulf and all Europe to the Mediterranean. As the ice sheet retreated, arctic species followed it, step by step, back to their present arctic home. But many individuals sought arctic conditions by retreating up the slopes of mountains, and were left stranded there on both continents. Since then they have been changed somewhat in different directions by isolation, but *the time has not been long enough* for great divergence. There is some difference, but not so great as the wide separation would lead us to expect.

2. *Australia.*—Of all known faunas and floras, this is the most distinct. It is so because *longest isolated.* We have seen that all its mammals are nonplacentals—i. e., marsupials and monotremes—except a few introduced accidentally or by man. Furthermore, that monotremes are found nowhere else, and marsupials nowhere else, except a few opossums in America. But this has not always been so. In Jurassic (middle geological) times the earth was everywhere abundantly inhabited by marsupials and monotremes, but not by eutheres or typical mammals. These last were introduced subsequently in

the Tertiary. Therefore we conclude that Australia was connected with other continents during middle geological times, and, in common with other lands, was inhabited by metatheres and prototheres, but that before or about the beginning of the Tertiary it was separated, and has remained so ever since. Therefore, when, by struggle, migrations, and conflicts on the great theater of evolution *Arctogæa* (Eurasia and North America), eutheres were evolved at the beginning of the Tertiary, Australia was already isolated, and they never got there.

3. *Africa.*—The fauna of Africa south of Sahara is very distinct, though less so than that of Australia. The mammals of Africa are of two groups: (1) A group of large, powerful animals somewhat like the Eurasians, but especially like the Pliocene Eurasians. (2) A group of small animals of low organization (mostly insectivores and lemurs) very peculiar to Africa, but more like those of Madagascar than any other. These latter we shall call *indigenes* or natives, the former group we will call *invaders*.

Explanation.—In preglacial times Africa south of Sahara was isolated, and inhabited *only by the indigenes.* Then came the glacial elevation, opening Africa to migrations from the north, and the glacial cold, driving Pliocene mammals southward into Africa, where they were shut up by subsequent changes in physical geography. Then came the struggle between the invaders and the natives. Both were sorely changed, the invaders mainly by the new environment, the natives mainly by the struggle for life. The final result was the mixture of the two groups, but the invaders greatly predominated. (See Wallace's Geographical Distribution of Animals.)

Island Faunas.—We have spoken thus far of *continental* faunas, but island faunas are peculiarly interesting. Islands are of two kinds—continental islands and oceanic islands. Continental islands are outliers of continents, separated from them only by subsidence. They have a geological structure similar to the mother continent. Oceanic islands are those which have no connection with any continent, but have been built up from the ocean bed by volcanic eruption in comparatively recent geological times. The fauna of continental islands is always related to that of the mother continent, differing from it in proportion to the width of ocean separating and the *time* of separation. The fauna of oceanic islands have no such evident relation to any continent. As examples of the former group we have Ceylon, Java, Borneo, Sumatra, Japan, etc., as appendages of Asia; Madagascar, of Africa; the British Isles, of Europe; the West Indies, of North America, etc. Of oceanic islands we have as examples the Bermudas and Azores in the Atlantic, and all the Polynesian Islands in the Pacific.

4. *Madagascar.*—We have already seen that the mammals of Madagascar differ greatly from those of any other country, but that their nearest alliance is with those of Africa. We now add that this alliance, however, is only with those we called the *indigenes*, and not at all with the invaders.

Explanation.—In preglacial times, when Africa was isolated from the rest of the world, Madagascar was connected with it, and both were inhabited by the indigenes. Before the glacial epoch, and therefore before the invasion of Pliocene mammals, Madagascar was separated from the continent by subsidence, and these isolated indigenes were spared the invasion and conflict. Since that time divergence has gone on until now the fauna is very peculiar. In the fauna of Madagascar we probably have a nearer approach to the original inhabitants of both than we now have in the African indigenous group. For although both have changed with time, yet the African, more than the Malagasian, because of the struggle which the former alone suffered.

5. *British Isles.*—The fauna of the British Isles is substantially the same as that of the European continent, but there are some very significant differences. (1) It is far *poorer* in species, and this is especially true of Ireland. For example, of mammals—Europe has ninety species, England forty, and Ireland only twenty-two. Of reptiles and amphibians Europe has twenty-two species, England thirteen, and Ireland four. (2) In many cases there is a difference, but not sufficient to make species; the differences are varietal instead of specific. Such are the facts.

Explanation.—In preglacial times the British Isles were a part of the continent and inhabited by the same animals. In glacial times they were covered by the ice sheet and all animals were destroyed or driven southward. After glacial times and the withdrawal of the ice sheet they became again a part of the continent and were recolonized from Europe. But the time of connection with Europe after the withdrawal of the ice sheet was too short for complete colonization, especially of extreme Ireland. Some species had not colonized at all and more had not yet reached Ireland, when by subsidence the islands were cut off from the continent, and at the same time Ireland from England. This entirely explains the comparative poverty of the fauna. Now the slight differences. The time has been too short and isolation too imperfect for great divergence. Divergence has commenced, but has gone only to varietal and not to specific differences.

6. *California Coast Islands.*—Heretofore I have spoken almost wholly of faunas. In this case I will deal with the flora. But the principles are the same.

The large islands off the coast of southern California have all the characters of continental islands. They have been separated from California in comparatively recent times. The flora of these islands is very peculiar. Out of three hundred species described, at least fifty are found nowhere else. The others are similar to those in California. But in the California flora it is necessary to distinguish two groups—viz., a distinctively Californian group and a group which is more widely diffused. The former I shall call indigenes or natives; the latter are probably invaders. Now, it is the distinctively Californian group only that is found on the islands. These are the facts. Now the

Explanation.—Before the glacial epoch the islands were a part of the mainland and all had a common flora—viz., the group I have called indigenes. Then came the separation by subsidence and the isolation of many indigenes on the islands. Then came the glacial cold and the invasion of California by a northern flora, the struggle between invaders and natives, the destruction of some native species, and the modification of both natives and invaders by new environment and by conflict. The final result was the California flora of to-day. The island flora was spared the invasion and the conflict. It has been changed less than the native Californian. We have in them a nearer approach to the preglacial flora of both.

7. *Oceanic Islands and their Fauna.*—Oceanic islands are built up from the sea bottom mostly by volcanic action, and have never had any connection with a continent. We see these forming now. When first formed they are, of course, *uninhabited.* They receive their species, animals and plants, as gifts from the sea—mere floating *waifs* brought by waves and currents. Their fauna and flora are always peculiar because isolated,

but with affinities connecting with several different lands. The predominance of affinities will depend partly on proximity and partly on the direction of winds and currents. Mammals (except bats) and amphibians are entirely wanting (unless introduced by man) because these are not apt to be drifted on logs, as are some reptiles.

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New York: D. APPLETON & CO., 72 Fifth Avenue.