a broad plate, hairy on its inner surface, which enters into the lateral wall of the cardiac chamber. There are various other smaller skeletal parts, but the most im-

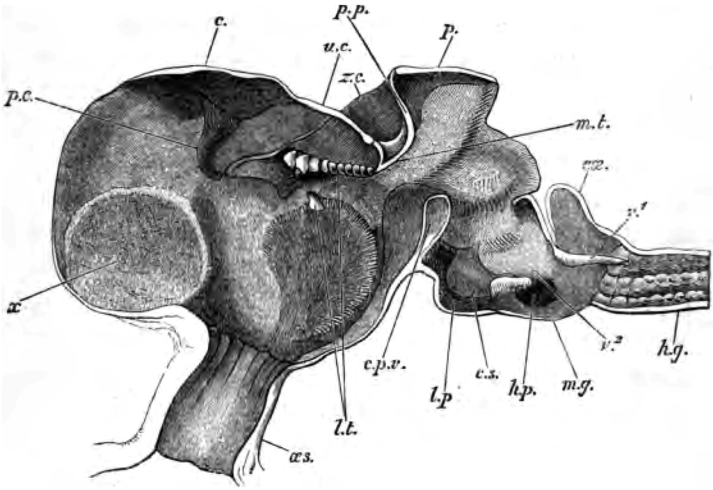

Fig. 10.—*Astacus fluviatilis.*—Longitudinal section of the stomach (× 4). *c*, cardiac ossicle; *cæ*, cæcum; *c.p.v*, cardio-pyloric valve; *cs*, cushion-shaped surface; *hg*, hind-gut; *hp*, aperture of right bile duct; *lp*, lateral pouch; *lt*, lateral teeth; *mg*, mid-gut; *mt*, median tooth; *œs*, œsophagus; *p*, pyloric ossicle; *pc*, pterocardiac ossicles; *pp*, prepyloric ossicle; *uc*, urocardiac process; v^1, median pyloric valve; v^2, lateral pyloric valve; *x*, position of gastrolith; *zc*, zygocardiac ossicle.

portant are those which have been described; and these, from what has been said, will be seen to form a sort of hexagonal frame, with more or less flexible joints at the angles, and having the anterior and the posterior sides connected by a bent jointed middle bar. As all these parts are merely modifications of the hard skeleton, the apparatus is devoid of any power of moving itself. It is set in motion, however, by the same substance as that which gives rise to all the other bodily movements of the crayfish, namely, *muscle*. The chief muscles which move it are four very strong bundles of fibres. Two of these are attached to the front crosspiece, and proceed thence, upwards and forwards, to be fixed to the inner face of the carapace in the front part of the head (figs. 5, 6, and 12, *ag*). The two others, which are fixed into the hinder crosspiece and hinder lateral pieces, pass upwards and backwards, to be attached to the inner face of the carapace in the back part of the head (*pg*). When these muscles shorten, or contract, they pull the front and back crosspieces further away from one another; consequently, the angle between the handles becomes more open and the tooth which is borne on their ends travels downwards and forwards. But, at the same time, the angle between the side bars becomes more open and the lateral tooth of each side moves inwards till it crosses in front of the middle tooth, and strikes against this and the opposite lateral tooth, which has undergone a corresponding change of place. The muscles being now relaxed, the elasticity of the joints suffices to bring the whole apparatus back to its first position, when a new contraction brings about a new clashing of the teeth. Thus, by the alternate contraction and relaxation of these two pair of muscles, the three teeth are made to stir up and crush whatever is contained in the cardiac chamber. When the stomach is removed and the front part of the cardiac chamber is cut away, the front cross-piece may be seized with one pair of forceps and the hind cross-piece with another. On slightly pulling the two, so as to imitate the action of the muscles, the three teeth will be found to come together sharply, exactly in the manner described.

Works on mechanics are full of contrivances for the conversion of motion; but it would, perhaps, be difficult to discover among these a prettier solution of the problem; given a straight pull, how to convert it into three simultaneous convergent movements of as many points.

What I have called the *filter* is constructed mainly out of the chitinous lining of the pyloric chamber. The aperture of communication between this and the cardiac chamber, already narrow, on account of the constriction of the walls of the stomach at this point, is bounded at the sides by two folds; while, from below, a conical tongue-shaped process (figs. 6, 10, and 11, *cpv*), the surface of which is covered with hairs, further obstructs the opening. In the posterior half of the pyloric chamber, its side walls are, as it were, pushed in; and, above, they so nearly meet in the middle line, that a mere vertical chink is left between them; while even this is crossed by hairs set upon the two surfaces. In its lower half, however, each side wall curves outwards, and forms a cushion-shaped surface (fig. 10, *cs*) which looks downwards and inwards. If the floor of the pyloric chamber were flat, a wide triangular passage would thus be left open in its lower half. But, in fact, the floor rises into a ridge in the middle, while, at the sides, it adapts itself to the shape of the two cushion-shaped surfaces; the result of which is that the whole cavity of the posterior part of the pyloric division of the stomach is reduced to a narrow three-rayed fissure. In transverse section, the vertical ray of this fissure is straight, while the two lateral ones are concave upwards (fig. 9, *E*). The cushions of the side walls are covered with short close-set hairs. The corresponding surfaces of the floor are raised into longitudinal parallel ridges, the edge of each of which is fringed with very fine hairs. As everything which passes from the cardiac sac to the intestine must traverse this singular apparatus, only the most finely divided solid matters can escape stoppage, so long as its walls are kept together.

Finally, at the opening of the pyloric sac into the intestine, the chitinous investment terminates in five symmetrically arranged processes, the disposition of which is such that they must play the part of valves in preventing any sudden return of the contents of the intestine to the stomach, while they readily allow of a passage the other way. One of these valvular processes is placed in the middle line above (figs. 10 and 11, v^1). It is longer than the others and concave below. The lateral processes (v^2,) of which there are two on each side, are triangular and flat.

The cuticular lining which gives rise to all the complicated apparatus which has just been described, must

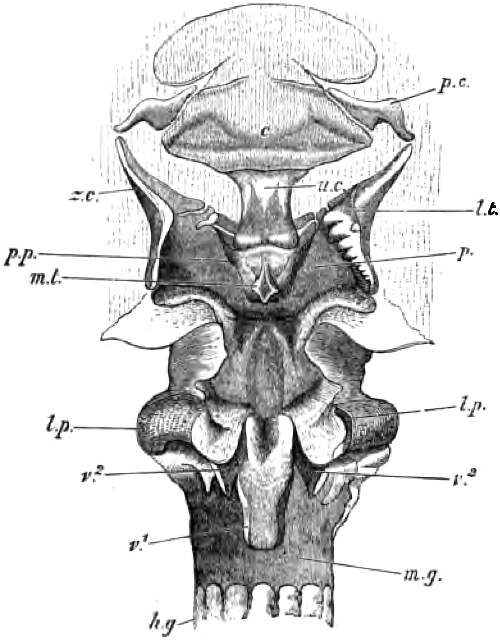

FIG. 11.—*Astacus fluviatilis.*—View of the roof of the stomach, the ventral wall of which, and of the mid-gut, is laid open by a longitudinal incision (× 4). On the right side (the left in the figure), the lateral tooth is cut away, as well as the floor of the lateral pouch. The letters have the same signification as in fig. 10.

not be confounded with the proper wall of the stomach, which invests it, and to which it owes it origin, just as the cuticle of the integument is produced by the soft true skin which lies beneath it. The wall of the stomach is a soft pale membrane containing variously disposed muscular fibres; and, beyond the pylorus, it is continued into the wall of the intestine.

It has already been mentioned that the intestine is a slender and thin-walled tube, which passes straight through the body almost without change, except that it becomes a little wider and thicker-walled near the vent. Immediately behind the pyloric valves, its surface is quite smooth and soft (figs. 9, 10, and 12, *mg*), and its floor presents a relatively large aperture, the termination of the bile duct (fig. 12, *bd*, fig. 10, *hp.*), on each side. The roof is, as it were, pushed out into a short median pouch or *cæcum* (*cæ*). Behind this, its character suddenly changes, and six squarish elevations, covered with a chitinous cuticle, encircle the cavity of the intestine (*r*). From each of these, a longitudinal ridge, corresponding with a fold of the wall of the intestine, takes its rise, and passes, with a slight spiral twist, to its extremity (*hg*). Each of these ridges is beset with small papillæ, and the chitinous lining is continued over the whole to the vent, where it passes into the general cuticle of the integument, just as the lining of the stomach is continuous with the cuticle of the integument at the mouth. The alimentary canal may, therefore, be distinguished into a *fore* and a *hind-gut* (*hg*), which have a thick internal lining of cuticular membrane; and a very short *mid-gut* (*mg*), which has no thick cuticular layer. It will be of

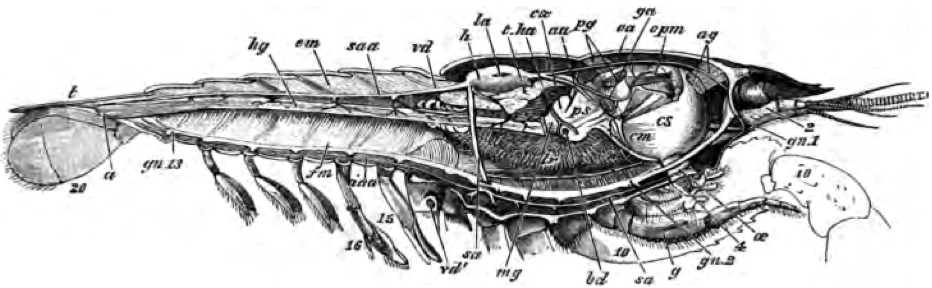

FIG. 12.—*Astacus fluviatilis.*—A dissection of a male specimen from the right side (nat. size). *a*, anus ; *aa*, antennary artery, cut short ; *ag*, anterior gastric muscles, the right cut away to its insertion ; *bd*, aperture of right bile duct ; *cm*, constrictor muscles of stomach ; *cæ*, cæcum ; *cpm*, right cardio-pyloric muscle ; *cs*, cardiac portion of stomach ; *em*, extensor muscles of abdomen ; *fm*, flexor muscles of abdomen ; *ga*, gastric artery ; *gn. 1*, supraœsophageal ganglion ; *gn. 2*, sub-œsophageal ganglion ; *gn. 13*, last abdominal ganglion ; *h*, heart ; *ha*, hepatic artery ; *hg*, hind-gut ; *iaa*, inferior abdominal artery ; *la*, right lateral aperture of heart ; *lr*, left liver ; *mg*, mid-gut ; *oa*, ophthalmic artery ; *æ*, œsophagus ; *pg*, posterior gastric muscles, the right cut away to its insertion ; *ps*, pyloric portion of stomach ; *sa*, sternal artery ; *saa*, superior abdominal artery ; *t* (to the left), telson ; *t* (near the heart), testis ; *vd*, left vas deferens ; *vd'*, aperture of left vas deferens ; *2*, right antennule ; *4*, left mandible ; *9*, left external maxillipede ; *10*, left forceps ; *15*, first, *16*, second, and *20*, sixth abdominal appendages of the left side.

importance to recollect this distinction by-and-by, when the development of the alimentary canal is considered.

If the treatment to which the food is subjected in the alimentary apparatus were of a purely mechanical nature, there would be nothing more to describe in this part of the crayfish's mechanism. But, in order that the nutritive matters may be turned to account, and undergo the chemical metamorphoses, which eventually change them into substances of a totally different character, they must pass out of the alimentary canal into the blood. And they can do this only by making their way through the walls of the alimentary canal; to which end they must either be in a state of extremely fine division, or they must be reduced to the fluid condition. In the case of the fatty matters, minute subdivision may suffice; but the amylaceous substances and the insoluble protein compounds, such as the fibrin of flesh, must be brought into a state of solution. Therefore some substances must be poured into the alimentary canal, which, when mixed with the crushed food, will play the part of a chemical agent, dissolving out the insoluble proteids, changing the amyloids into soluble sugar, and converting all the proteids into those diffusible forms of protein matter, which are known as *peptones*.

The details of the processes here indicated, which may be included under the general name of *digestion*, have only quite recently been carefully investigated in the crayfish; and we have probably still much to learn about them; but what has been made out is very interesting, and proves that considerable differences exist between crayfishes and the higher animals in this respect.

The physiologist calls those organs, the function of which is to prepare and discharge substances of a special character, *glands;* and the matter which they elaborate is termed their *secretion.* On the one side, glands are in relation with the blood, whence they derive the materials which they convert into the substances characteristic of their secretion; on the other side, they have access, directly or indirectly, to a free surface, on to which they pour their secretion as it is formed.

Of such glands, the alimentary canal of the crayfish is provided with a pair, which are not only of very large size, but are further extremely conspicuous, on account of their yellow or brown colour. These two glands (figs. 12 and 13, *lr*) are situated beneath, and on each side of, the stomach and the anterior part of the intestine, and answer in position to the glands termed liver and pancreas in the higher animals, inasmuch as they pour their secretion into the mid-gut. These glands have hitherto always been regarded as the *liver*, and the name may be retained, though their secretion appears rather to correspond with the pancreatic fluid than with the bile of the higher animals.

Each liver consists of an immense number of short tubes, or *cæca,* which are closed at one end, but open at the other into a general conduit, which is termed their *duct.* The mass of the liver is roughly divided into

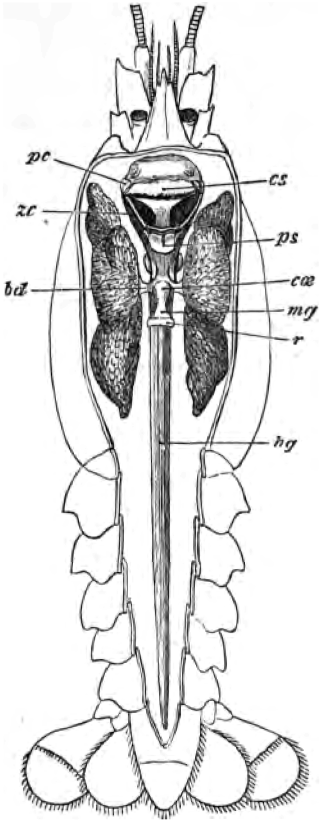

FIG. 13.—*Astacus fluviatilis.*—The alimentary canal and livers seen from above (nat. size). *bd*, bile-duct ; *cæ*, cæcum ; *cs*, cardiac portion of stomach, the line pointing to the cardiac ossicle ; *hg*, hind-gut ; *mg*, mid-gut ; *pc*, pterocardiac ossicle ; *ps*, pyloric portion of stomach, the line pointing to the pyloric ossicle ; *r*, ridge separating mid-gut from hind-gut ; *zc*, zygocardiac ossicle.

three lobes, one anterior, one lateral, and one posterior; and each lobe has its main duct, into which all the tubes composing it open. The three ducts unite together into a wide common duct (*bd*), which opens, just behind the pyloric valves, into the floor of the mid-gut. Hence the apertures of the two *hepatic ducts* are seen, one on each side, in this part of the alimentary canal when it is laid open from above. Every cæcum of the liver has a thin outer wall, lined internally by a layer of cells, constituting what is termed an *epithelium;* and, at the openings of the hepatic ducts, this epithelium passes into a layer of somewhat similar structure, which lines the mid-gut, and is continued through the rest of the alimentary canal, beneath the cuticula. Hence the liver may be regarded as a much divided side pouch of the mid-gut.

The epithelium is made up of *nucleated cells,* which are particles of simple living matter, or *protoplasm,* in the midst of each of which is a rounded body, which is termed the *nucleus.* It is these cells which are the seat of the manufacturing process which results in the formation of the secretion; it is, as it were, their special business to form that secretion. To this end they are constantly being newly formed at the summits of the cæca. As they grow, they pass down towards the duct and, at the same time, separate into their interior certain special products, among which globules of yellow fatty matter are very conspicuous. When these products are fully formed, what remains of the substance of the cells dissolves away, and the yellow fluid accumulating in the ducts passes into the mid-gut. The yellow colour is due to the globules of fat. In the young cells, at the summit of the cæca, these are either absent, or very small, whence the part appears colourless. But, lower down, small yellow granules appear in the cells, and these become bigger and more numerous in the middle and lower parts. In fact, few glands are better fitted for the study of the manner in which secretion is effected than the crayfish's liver.

We may now consider the alimentary machinery, the general structure of which has been explained, in action.

The food, already torn and crushed by the jaws, is passed through the gullet into the cardiac sac, and there reduced to a still more pulpy state by the gastric mill. By degrees, such parts as are sufficiently fluid are drained off into the intestine, through the pyloric strainer, while the coarser parts of the useless matters are probably rejected by the mouth, as a hawk or an owl rejects his casts. There is reason to believe, though it is not certainly known, that fluids from the intestine mix with the food while it is undergoing trituration, and effect the transformation of the starchy and the insoluble protein compounds into a soluble state. At any rate, as soon as the strained-off fluid passes into the mid-gut it must be mixed with the secretion of the liver, the action of which is probably similar to that of the pancreatic juice of the higher animals.

The mixture thus produced, which answers to the chyle of the higher animals, passes along the intestine, and the greater part of it, transuding through the walls of the alimentary canal, enters the blood, while the rest accumulates as dark coloured fæces in the hind gut, and

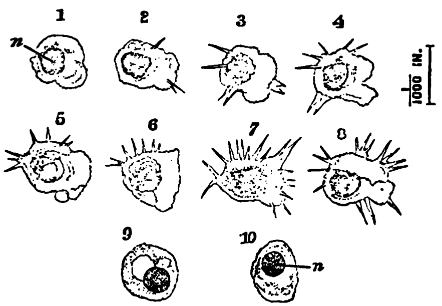

FIG. 14.—*Astacus fluviatilis.*—The corpuscles of the blood (highly magnified). *1–8* show the changes undergone by a single corpuscle during a quarter of an hour; *9* and *10* are corpuscles killed by magenta, and having the nucleus deeply stained by the colouring matter. *n*, nucleus.

is eventually passed out of the body by the vent. The fæcal matters are small in amount, and the strainer is so efficient that they rarely contain solid particles of sensible size. Sometimes, however, there are a good many minute fragments of vegetable tissue.

The blood of which the nutritive elements of the food have thus become integral parts, is a clear fluid, either colourless, or of a pale neutral tint or reddish hue, which, to the naked eye, appears like so much water. But if subjected to microscopic examination, it is found to contain innumerable pale, solid particles, or *corpuscles*, which, when examined fresh, undergo constant changes of form (fig. 14). In fact, they correspond very closely with the colourless corpuscles which exist in our own blood; and, in its general characters, the crayfish's blood is such as ours would be if it were somewhat diluted and deprived of its red corpuscles. In other words, it resembles our lymph more than it does our blood. Left to itself it soon coagulates, giving rise to a pretty firm clot.

The sinuses, or cavities in which the greater part of the blood is contained, are disposed very irregularly in the intervals between the internal organs. But there is one of especially large size on the ventral or sternal side of the thorax (fig. 15, *sc*), into which all the blood in the body sooner or later makes its way. From this *sternal sinus* passages (*av*) lead to the gills, and from these again six canals (*bcv*), pass up on the inner side of the inner wall of each branchial chamber to a cavity situated in the dorsal region of the thorax, termed the *pericardium* (*p*), into which they open.

The blood of the crayfish is kept in a state of constant circulating motion by a pumping and distributing machinery, composed of the *heart* and of the *arteries*, with

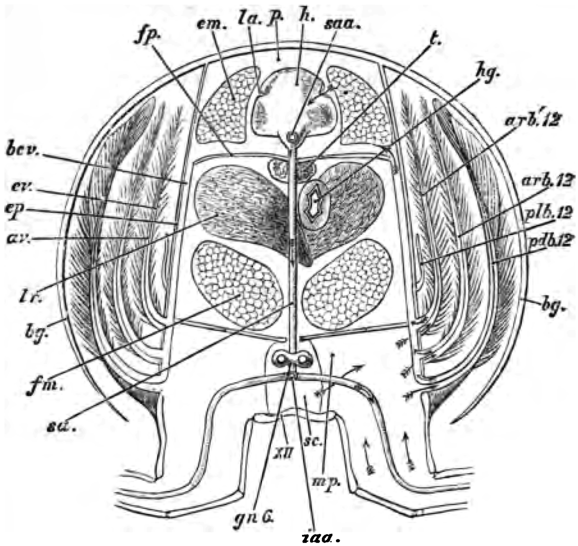

FIG. 15.—*Astacus fluviatilis.*—A diagrammatic transverse section of the thorax through the twelfth somite, showing the course of the circulation of the blood (× 3). *arb. 12*, the anterior or lower, and *arb'*. 12, the posterior or upper arthrobranchia of the twelfth somite ; *av*, afferent branchial vessel ; *bcv*, branchio-cardiac vein ; *bg*, branchiostegite ; *em*, extensor muscles of abdomen ; *ep*, epimeral wall of thoracic cavity ; *cv*, efferent branchial vessel ; *fm*, flexor muscles of abdomen ; *fp*, floor of pericardium ; *gn. 6*, fifth thoracic ganglion ; *h*, heart ; *hg*, hind-gut ; *iaa*, inferior abdominal artery, in cross section ; *la*, lateral valvular apertures of heart ; *lr*, liver ; *mp*, indicates the position of the mesophragm by which the sternal canal is bounded laterally ; *p*, pericardial sinus ; *pdb. 12*, podobranchia, and *plb. 12*, pleurobranchia of the twelfth somite ; *sa*, sternal artery ; *saa*, superior abdominal artery ; *sc*, sternal canal ; *t*, testis ; XII., sternum of twelfth somite. The arrows indicate the direction of the blood flow.

their larger and smaller branches, which proceed from it and ramify through the body, to terminate eventually in the blood sinuses, which represent the veins of the higher animals.

When the carapace is removed from the middle of the region which lies behind the cervical groove, that is, when the dorsal or *tergal* wall of the thorax is taken away, a spacious chamber is laid open which is full of blood. This is the cavity already mentioned as the *pericardium* (fig. 15, *p*), though, as it differs in some respects from that which is so named in the higher animals, it will be better to term it the *pericardial sinus.*

The heart (fig. 15, *h*), lies in the midst of this sinus. It is a thick muscular body (fig. 16), with an irregularly hexagonal contour when viewed from above, one angle of the hexagon being anterior and another posterior. The lateral angles of the hexagon are connected by bands of fibrous tissue (*ac*) with the walls of the pericardial sinus. Otherwise, the heart is free, except in so far as it is kept in place by the arteries which leave it and traverse the walls of the pericardium. One of these arteries (figs. 5, 12, and 16, *saa*), starting from the hinder part of the heart, of which it is a sort of continuation, runs along the middle line of the abdomen above the intestine, to which it gives off many branches. A second large artery starts from a dilatation, which is common to it with the foregoing, but passing directly downwards (figs. 12 and 15, *sa*, and fig. 16, *st. a*), either on the right or on the left side of the intestine, traverses the nervous cord (figs. 12 and 15), and divides into an anterior (fig. 12, *sa*) and a posterior (*iaa*) branch, both of which run beneath and parallel with that cord.

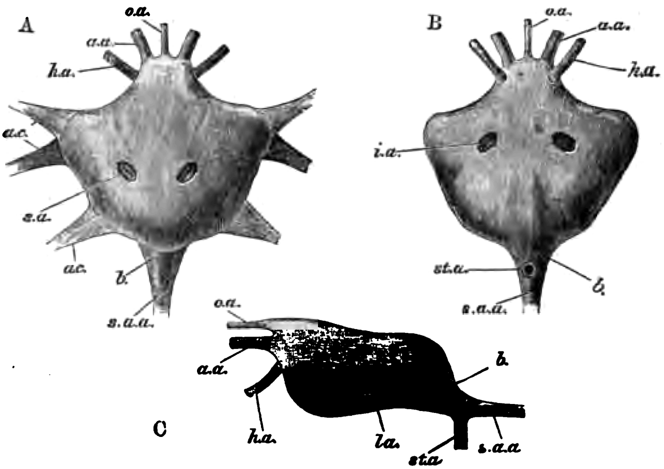

FIG. 16.—*Astacus fluviatilis.*—The heart (× 4). A, from above; B, from below; C, from the left side. *aa*, antennary artery; *ac*, alæ cordis, or fibrous bands connecting the heart with the walls of the pericardial sinus; *b*, bulbous dilatation at the origin of the sternal artery; *ha*, hepatic artery; *la*, lateral valvular apertures; *oa*, ophthalmic artery; *s.a*, superior valvular apertures; *s.a.a*, superior abdominal artery; *st.a*, sternal artery, in B cut off close to its origin.

A third artery runs, from the front part of the heart, forwards in the middle line, over the stomach, to the eyes and fore part of the head (figs. 5, 12, and 16, *oa*); and two others diverge one on each side of this, and sweep round the stomach to the antennæ (*aa*). Behind these, yet two other arteries are given off from the under side of the heart, and supply the liver (*ha*). All these arteries branch out and eventually terminate in fine, so-called *capillary*, ramifications.

In the dorsal wall of the heart two small oval apertures are visible, provided with valvular lips (fig. 16, *sa*), which open inwards, or towards the internal cavity of the heart. There is a similar aperture in each of the lateral faces of the heart (*la*), and two others in its inferior face (*ia*), making six in all. These apertures readily admit fluid into the heart, but oppose its exit. On the other hand, at the origins of the arteries, there are small valvular folds, directed in such a manner as to permit the exit of fluid from the heart, while they prevent its entrance.

The walls of the heart are muscular, and, during life, they contract at intervals with a regular rhythm, in such a manner as to diminish the capacity of the internal cavity of the organ. The result is, that the blood which it contains is driven into the arteries, and necessarily forces into their smaller ramifications an equivalent amount of the blood which they already contained; whence, in the long run, the same amount of blood passes out of the ultimate capillaries into the blood sinuses. From the disposition of the blood sinuses, the impulse thus given to the blood which they contain is finally conveyed to the blood in the branchiæ, and a proportional quantity of that blood leaves the branchiæ and passes into the sinuses which connect them with the pericardial sinus (fig. 15, *bcv*), and thence into that cavity. At the end of the contraction, or *systole*, of the heart, its volume is of course diminished by the volume of the blood forced out, and the space between the walls of the heart and those of the pericardial sinus is increased to the same extent. This space, however, is at once occupied by the blood from the branchiæ, and perhaps by some blood which has not passed through the branchiæ, though this is doubtful. When the systole is over, the *diastole* follows; that it to say, the elasticity of the walls of the heart and that of the various parts which connect it with the walls of the pericardium, bring it back to its former size, and the blood in the pericardial sinus flows into its cavity by the six apertures. With a new systole the same process is repeated, and thus the blood is driven in a circular course through all parts of the body.

It will be observed that the branchiæ are placed in the course of the current of blood which is returning to the heart; which is the exact contrary of what happens in fishes, in which the blood is sent from the heart to the branchiæ, on its way to the body. It follows, from this arrangement, that the blood which goes to the branchiæ is blood in which the quantity of oxygen has undergone a diminution, and that of carbonic acid an increase, as compared with the blood in the heart itself. For the activity of all the organs, and especially of the muscles, is inseparably connected with the absorption of oxygen and the evolution of carbonic acid; and the only source from which the one can be derived, and the only receptacle into which the other can be poured, is the blood which bathes and permeates the whole fabric to which it is distributed by the arteries.

The blood, therefore, which reaches the branchiæ has lost oxygen and gained carbonic acid; and these organs constitute the apparatus for the elimination of the injurious gas from the economy on the one hand, and, on the other, for the taking in of a new supply of the needful "vital air," as the old chemists called it. It is thus that the branchiæ subserve the respiratory function.

The crayfish has eighteen perfect and two rudimentary branchiæ in each branchial chamber, the boundaries of which have been already described.

Of the eighteen perfect branchiæ, six (*podobranchiæ*) are attached to the basal joints of the thoracic limbs, from the last but one to the second (second maxillipede) inclusively (fig. 4, p. 26, *pdb*, and fig. 17, A, B); and eleven (*arthrobranchiæ*) are fixed to the flexible interarticular membranes, which connect these basal joints with the parts of the thorax to which they are articulated (fig. 4, *arb*, *arb'*, fig. 17, C). Of these eleven branchiæ, two are attached to the interarticular membranes of all the ambulatory legs but the last, (=6) and to those of the pincers and of the external maxillipedes, (=4) and one to that of the

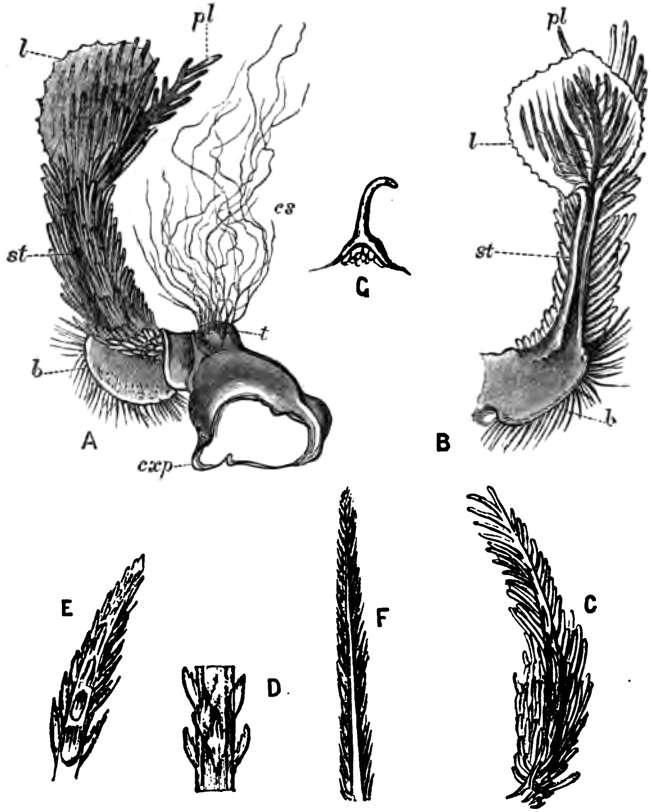

FIG. 17.—*Astacus fluviatilis.*—A, one of the podobranchiæ from the outer side; B, the same from the inner side; C, one of the arthrobranchiæ; D, a part of one of the coxopoditic setæ; E, extremity of the same seta; F, extremity of a seta from the base of the podobranchia; G, hooked seta of the lamina; (A—C, × 3; D—G, highly magnified). *b*, base of podobranchia; *cs*, coxopoditic setæ; *cxp*, coxopodite; *l*, lamina, *pl*, plume, and *st*, stem of podobranchia; *t*, tubercle on the coxopodite, to which the setæ are attached.

second maxillipede. The first maxillipede and the last ambulatory limb have none. Moreover, where there are two arthrobranchiæ, one is more or less in front of and external to the other.

These eleven arthrobranchiæ are all very similar in structure (fig. 17, C). Each consists of a stem which contains two canals, one external and one internal, separated by a longitudinal partition. The stem is beset with a great number of delicate *branchial filaments*, so that it looks like a plume tapering from its base to its summit. Each filament is traversed by large vascular channels, which break up into a net-work immediately beneath the surface. The blood driven into the external canals of the stem (fig. 15, *av*) is eventually poured into the inner canal (*ev*), which again communicates with the channels (*bcv*) which lead to the pericardial sinus (*p*). In its course, the blood traverses the branchial filaments, the outer investment of each of which is an excessively thin chitinous membrane, so that the blood contained in them is practically separated by a mere film from the aërated water in which the gills float. Hence, an exchange of gaseous constituents readily takes place, and as much oxygen is taken in as carbonic acid is given out.

The six podobranchiæ, or gills which are attached to the basal joints of the legs, play the same part, but differ a good deal in the details of their structure from those which are fixed to the interarticular membranes. Each consists of a broad *base* (fig. 17, A and B; *b*) beset with many fine straight hairs, or *setæ* (F), whence a narrow *stem* (*st*) proceeds. At its upper end this stem divides into two parts, that in front, the *plume* (*pl*), resembling the free end of one of the gills just described, while that behind, the *lamina* (*l*), is a broad thin plate, bent upon itself longitudinally in such a manner that its folded edge lies forwards, and covered with minute hooked setæ (G). The gill which follows is received into the space included between the two lobes or halves of the folded lamina (fig. 4, p. 26). Each lobe is longitudinally plaited into about a dozen folds. The whole front and outer face of the stem is beset with branchial filaments; hence, we may compare one of these branchiæ to one of the preceding kind, in which the stem has become modified and has given off a large folded lamina from its inner and posterior face.

The branchiæ now described are arranged in sets of three for each of the thoracic limbs, from the third maxillipede to the last but one ambulatory limb, and two for the second maxillipede, thus making seventeen in all ($3 \times 5 + 2 = 17$); and, between every two there is found a bundle of long twisted hairs (fig. 17, A, *cx.s*; D and E), which are attached to a small elevation (*t*) on the basal joint of each limb. These *coxopoditic setæ*, no doubt, serve to prevent the intrusion of parasites and other foreign matters into the branchial chamber. From the mode of attachment of the six branchiæ it is obvious that they must share in the movements of the basal joints of the legs; and that, when the crayfish walks, they must be more or less agitated in the branchial chamber.

The eighteenth branchia resembles one of the eleven arthrobranchiæ in structure; but it is larger, and it is attached neither to the basal joint of the hindermost ambulatory limb, nor to its interarticular membrane, but to the sides of the thorax, above the joint. From this mode ot attachment it is distinguished from the others as a *pleurobranchia* (fig. 4, *plb. 14*).

Finally, in front of this, fixed also to the walls of the thorax, above each of the two preceding pairs of ambulatory limbs, there is a delicate filament, about a sixteenth of an inch long, which has the structure of a branchial filament, and is, in fact, a rudimentary pleurobranchia (fig. 4, *plb. 12*, *plb. 13*).

The quantity of water which occupies the space left in the branchial chamber by the gills is but small, and as the respiratory surface offered by the gills is relatively very large, the air contained in this water must be rapidly exhausted, even when the crayfish is quiescent; while, when any muscular exertion takes place, the quantity of carbonic acid formed, and the demand for fresh oxygen, is at once greatly increased. For the efficient performance of the function of respiration, therefore, the water in the branchial chamber must be rapidly renewed, and there must be some arrangement by which the supply of fresh water may be proportioned to the demand. In many animals, the respiratory surface is covered with rapidly vibrating filaments, or *cilia*, by means of which a current of water is kept continually flowing over the gills, but there are none of these in the crayfish. The same object is attained, however, in another way. The anterior boundary of the branchial chamber corresponds with the cervical groove, which, as has been seen, curves downwards and then forwards, until it terminates at the sides of the space occupied by the jaws. If the branchiostegite is cut away along the groove, it will be found that it is attached to the sides of the head, which project a little beyond the anterior part of the thorax, so that there is a depression behind the sides of the head—just as there is a depression, behind a man's jaw, at the sides of the neck. Between this depression in front, the walls of the thorax internally, the branchiostegite externally, and the bases of the forceps and external foot-jaws below, a curved canal is included, by which the branchial cavity opens forwards as by a funnel. Attached to the base of the second maxilla there is a wide curved plate (fig. 4, *6*) which fits against the projection of the head, as a shirt collar might do, to carry out our previous comparison; and this scoop-shaped plate (termed the *scaphognathite*), which is concave forwards and convex backwards, can be readily moved backwards and forwards.

If a living crayfish is taken out of the water, it will be found that, as the water drains away from the branchial cavity, bubbles of air are forced out of its anterior opening.

Again, if, when a crayfish is resting quietly in the water, a little coloured fluid is allowed to run down towards the posterior opening of the branchial chamber, it will very soon be driven out from the anterior aperture, with considerable force, in a long stream. In fact, as the scaphognathite vibrates not less than three or four times in a second, the water in the funnel-shaped front passage of the branchial cavity is incessantly baled out; and, as fresh water flows in from behind to make up the loss, a current is kept constantly flowing over the gills. The rapidity of this current naturally depends on the more or less quick repetition of the strokes of the scaphognathite; and hence, the activity of the respiratory function can be accurately adjusted to the wants of the economy. Slow working of the scaphognathite answers to ordinary breathing in ourselves, quick working to panting.

A further self-adjustment of the respiratory apparatus is gained by the attachment of the six gills to the basal joints of the legs. For, when the animal exerts its muscles in walking, these gills are agitated, and thus not only bring their own surfaces more largely in contact with the water, but produce the same effect upon the other gills.

The constant oxidation which goes on in all parts of the body not only gives rise to carbonic acid; but, so far as it affects the proteinaceous constituents, it produces compounds which contain nitrogen, and these, like other waste products, must be eliminated. In the higher animals, such waste products take the form of urea, uric acid, hippuric acid, and the like; and are got rid of by the kidneys. We may, therefore, expect to find some organ which plays the part of a kidney in the crayfish; but the position of the structure, which there is much reason for regarding as the representative of the kidney, is so singular that very different interpretations have been put upon it.

On the basal joint of each antenna it is easy to see a small conical eminence with an opening on the inner side of its summit (fig. 18). The aperture (x) leads by a short canal into a spacious sac, with extremely delicate walls (s), which is lodged in the front part of the head, in front of and below the cardiac division of the stomach (cs). Beneath this, in a sort of recess, which corresponds with the epistoma, and with the base of the antenna, there is a discoidal body of a dull green colour, in shape somewhat like one of the fruits of the mallow, which is known as the *green gland* (gg). The sac narrows below like a wide funnel, and the edges of its small end are continuous with the walls of the green gland; they surround an aperture which leads into the interior of the latter structure, and conveys its products into the sac, whence they are excreted by the opening in the antennary papilla. The green gland is said to contain a substance termed *guanin* (so named because it is found in the *guano* which is the accumulated excrement of birds), a nitrogenous body analogous in some respects to uric acid, but less highly oxidated;

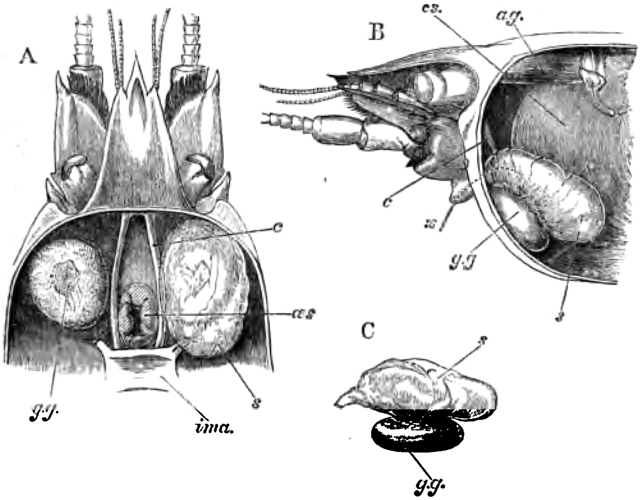

FIG. 18.—*Astacus fluviatilis.*—A, the anterior part of the body, with the dorsal portion of the carapace removed to show the position of the green glands; B, the same, with the left side of the carapace removed; C, the green gland removed from the body (all × 2). *ag*, left anterior gastric muscle; *c*, circumœsophageal commissures; *cs*, cardiac portion of stomach; *gg*, green gland, exposed in A on the left side by the removal of its sac; *ima*, intermaxillary or cephalic apodeme; *œs*, œsophagus seen in transverse section in A, the stomach being removed; *s*, sac of green gland; *x*, bristle passed from the aperture in the basal joint of the antenna into the sac.

and if this be the case, there can be little doubt that the green gland represents the kidney, and its secretion the urinary fluid, while the sac is a sort of urinary bladder.

Restricting our attention to the phenomena which have now been described, and to a short period in the life of the crayfish, the body of the animal may be regarded as a factory, provided with various pieces of machinery, by means of which certain nitrogenous and other matters are extracted from the animal and vegetable substances which serve for food, are oxidated, and are then delivered out of the factory in the shape of carbonic acid gas, guanin, and probably some other products, with which we are at present unacquainted. And there is no doubt, that if the total amount of products given out could be accurately weighed against the total amount of materials taken in, the weight of the two would be found to be identical. To put the matter in its most general shape, the body of the crayfish is a sort of focus to which certain material particles converge, in which they move for a time, and from which they are afterwards expelled in new combinations. The parallel between a whirlpool in a stream and a living being, which has often been drawn, is as just as it is striking. The whirlpool is permanent, but the particles of water which constitute it are incessantly changing. Those which enter it, on the one side, are whirled around and temporarily constitute a part of its individuality; and as they leave it on the other side, their places are made good by new comers.

Those who have seen the wonderful whirlpool, three miles below the Falls of Niagara, will not have forgotten the heaped-up wave which tumbles and tosses, a very embodiment of restless energy, where the swift stream hurrying from the Falls is compelled to make a sudden turn towards Lake Ontario. However changeful in the contour of its crest, this wave has been visible, approximately in the same place, and with the same general form, for centuries past. Seen from a mile off, it would appear to be a stationary hillock of water. Viewed closely, it is a typical expression of the conflicting impulses generated by a swift rush of material particles.

Now, with all our appliances, we cannot get within a good many miles, so to speak, of the crayfish. If we could, we should see that it was nothing but the constant form of a similar turmoil of material molecules which are constantly flowing into the animal on the one side, and streaming out on the other.

The chemical changes which take place in the body of the crayfish, are doubtless, like other chemical changes, accompanied by the evolution of heat. But the amount of heat thus generated is so small and, in consequence of the conditions under which the crayfish lives, it is so easily carried away, that it is practically insensible. The crayfish has approximately the temperature of the surrounding medium, and it is, therefore, reckoned among the cold-blooded animals.

If our investigation of the results of the process of alimentation in a well-fed Crayfish were extended over a longer time, say a year or two, we should find that the products given out were no longer equal to the materials taken in, and the balance would be found in the increase of the animal's weight. If we inquired how the balance was distributed, we should find it partly in store, chiefly in the shape of fat; while, in part, it had been spent in increasing the plant and in enlarging the factory. That is to say, it would have supplied the material for the animal's growth. And this is one of the most remarkable respects in which the living factory differs from those which we construct. It not only enlarges itself, but, as we have seen, it is capable of executing its own repairs to a very considerable extent.

CHAPTER III.

THE PHYSIOLOGY OF THE CRAYFISH—THE MECHANISM BY WHICH THE LIVING ORGANISM ADJUSTS ITSELF TO SURROUNDING CONDITIONS AND REPRODUCES ITSELF.

If the hand is brought near a vigorous crayfish, free to move in a large vessel of water, it will generally give a vigorous flap with its tail, and dart backwards out of reach; but if a piece of meat is gently lowered into the vessel, the crayfish will sooner or later approach and devour it.

If we ask why the crayfish behaves in this fashion, every one has an answer ready. In the first case, it is said that the animal is aware of danger, and therefore hastens away; in the second, that it knows that meat is good to eat, and therefore walks towards it and makes a meal. And nothing can seem to be simpler or more satisfactory than these replies, until we attempt to conceive clearly what they mean; and, then, the explanation, however simple it may be admitted to be, hardly retains its satisfactory character.

For example, when we say that the crayfish is "aware of danger," or "knows that meat is good to eat," what do we mean by "being aware" and "knowing"? Certainly it cannot be meant that the crayfish says to himself, as we do, "This is dangerous," "That is nice;" for the crayfish, being devoid of language, has nothing to say either to himself or any one else. And if the crayfish has not language enough to construct a proposition, it is obviously out of the question that his actions should be guided by a logical reasoning process, such as that by which a man would justify similar actions. The crayfish assuredly does not first frame the syllogism, "Dangerous things are to be avoided; that hand is dangerous; therefore it is to be avoided;" and then act upon the conclusion thus logically drawn.

But it may be said that children, before they acquire the use of language, and we ourselves, long after we are familiar with conscious reasoning, perform a great variety of perfectly rational acts unconsciously. A child grasps at a sweetmeat, or cowers before a threatening gesture, before it can speak; and any one of us would start back from a chasm opening at our feet, or stoop to pick up a jewel from the ground, "without thinking about it." And, no doubt, if the crayfish has any mind at all, his mental operations must more or less resemble those which the human mind performs without giving them a spoken or unspoken verbal embodiment.

If we analyse these, we shall find that, in many cases, distinctly felt sensations are followed by a distinct desire to perform some act, which act is accordingly performed;

while, in other cases, the act follows the sensation without one being aware of any other mental process; and, in yet others, there is no consciousness even of the sensation. As I wrote these last words, for example, I had not the slightest consciousness of any sensation of holding or guiding the pen, although my fingers were causing that instrument to perform exceedingly complicated movements. Moreover, experiments upon animals have proved that consciousness is wholly unnecessary to the carrying out of many of those combined movements by which the body is adjusted to varying external conditions.

Under these circumstances, it is really quite an open question whether a crayfish has a mind or not; moreover, the problem is an absolutely insoluble one, inasmuch as nothing short of being a crayfish would give us positive assurance that such an animal possesses consciousness; and, finally, supposing the crayfish has a mind, that fact does not explain its acts, but only shows that, in the course of their accomplishment, they are accompanied by phenomena similar to those of which we are aware in ourselves, under like circumstances.

So we may as well leave this question of the crayfish's mind on one side for the present, and turn to a more profitable investigation, namely, that of the order and connexion of the physical phenomena which intervene between something which happens in the neighbourhood of the animal and that other something which responds to it, as an act of the crayfish.

Whatever else it may be, this animal, so far as it is acted upon by bodies around it and reacts on them, is a piece of mechanism, the internal works of which give rise to certain movements when it is affected by particular external conditions; and they do this in virtue of their physical properties and connexions.

Every movement of the body, or of any organ of the body, is an effect of one and the same cause, namely, muscular contraction. Whether the crayfish swims or walks, or moves its antennæ, or seizes its prey, the immediate cause of the movements of the parts which bring about, or constitute, these bodily motions is to be sought in a change which takes place in the flesh, or muscle, which is attached to them. The change of place which constitutes any movement is an effect of a previous change in the disposition of the molecules of one or more muscles; while the direction of that movement depends on the connexions of the parts of the skeleton with one another, and of the muscles with them.

The muscle of the crayfish is a dense, white substance; and if a small portion of it is subjected to examination it will be found to be very easily broken up into more or less parallel bundles of fine fibres. Each of these fibres is generally found to be ensheathed in a fine transparent membrane, which is called the *sarcolemma*, within which is contained the proper substance of the muscle. When quite fresh and living, this substance is soft and semi-fluid, but it hardens and becomes solid immediately after death.

Examined, with high magnifying powers, in this

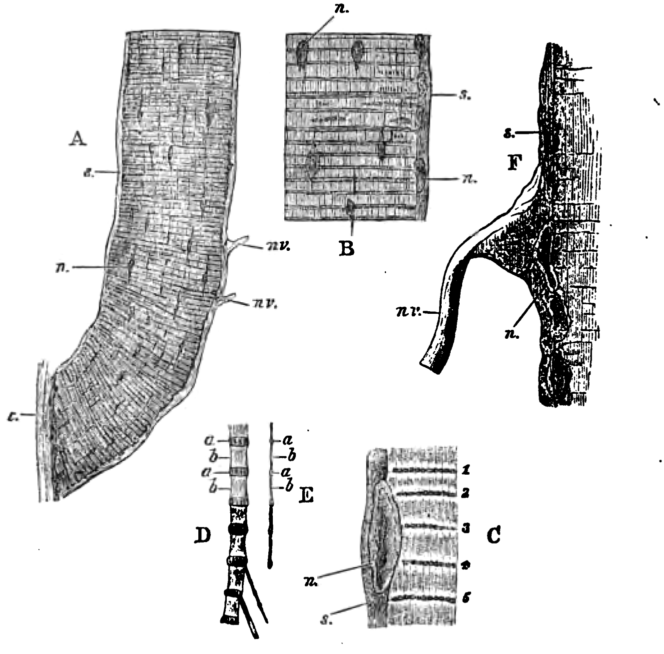

FIG. 19.—*Astacus fluviatilis.*—A, a single muscular fibre; transverse diameter $\frac{1}{110}$th of an inch; B, a portion of the same more highly magnified; C, a smaller portion still more highly magnified; D and E, the splitting up of a part of fibre into fibrillæ; F, the connexion of a nervous with a muscular fibre which has been treated with acetic acid. *a*, darker, and *b*, clearer portions of the fibrillæ; *n*, nucleus of sarcolemma; *nv*, nerve fibre; *s*, sarcolemma; *t*, tendon; 1—5, successive dark bands answering to the darker portions, *a*, of each fibrilla.

condition, the muscle-substance appears marked by very regular transverse bands, which are alternately opaque and transparent; and it is characteristic of the group of animals to which the crayfish belongs that their muscle-substance has this striped character in all parts of the body.

A greater or less number of these fibres, united into one or more bundles, constitutes a muscle; and, except when these muscles surround a cavity, they are fixed at each end to the hard parts of the skeleton. The attachment is frequently effected by the intermediation of a dense, fibrous, often chitinous, substance, which constitutes the *tendon* (fig. 19, A; *t*) of the muscle.

The property of the living muscle, which enables it to be the cause of motion, is this: Every muscular fibre is capable of suddenly changing its dimensions, in such a manner that it shortens and becomes proportionately thicker. Hence the absolute bulk of the fibre remains practically unchanged. From this circumstance, muscular *contraction*, as the change of form of a muscle is called, is radically different from the process which commonly goes by the same name in other things, and which involves a diminution of bulk.

The contraction of muscle takes place with great force, and, of course, if the parts to which its ends are fixed are both free to move, they are brought nearer at the moment of contraction: if one only is free to move that is approximated to the fixed part; and if the muscular fibre surrounds a cavity, the cavity is lessened when the muscle contracts. This is the whole source of motor power in the crayfish machine. The results produced by the exertion of that power depend upon the manner

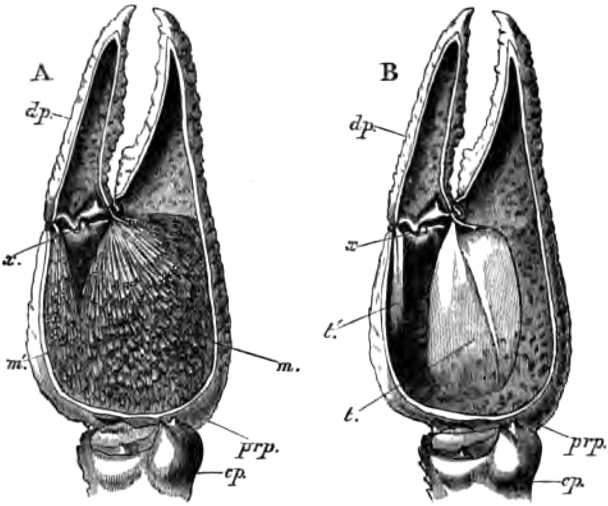

FIG. 20.—*Astacus fluviatilis.*—The chela of the forceps, with one side cut away to show, in A, the muscles, in B, the tendons (× 2). *cp*, carpopodite; *prp*, propodite; *dp*, dactylopodite; *m*, adductor muscle; *m'*, abductor muscle; *t*, tendon of adductor muscle; *t'*, tendon of abductor muscle; *x*, hinge.

in which the parts to which the muscles are attached are connected with one another.

One example of this has already been given in the curious mechanism of the gastric mill. Another may be found in the chela which terminates the forceps. If the articulation of the last joint (fig. 20, *dp*) with the one which precedes it (*prp*) is examined, it will be found that the base of the terminal segment (*dp*) turns on two hinges (*x*), formed by the hard exoskeleton and situated at opposite points of the diameter of the base, on the penultimate segment; and these hinges are so disposed that the last joint can be moved only in one plane, to or from the produced angle of the penultimate segment (*prp*), which forms the fixed claw of the chela. Between the hinges, on both the inner and the outer sides of the articulation, the exoskeleton is soft and flexible, and allows the terminal segment to play easily through a certain arc. It is by this arrangement that the direction and the extent of the motion of the free claw of the chela are determined. The source of the motion lies in the muscles which occupy the interior of the enlarged penultimate segment of the limb. Two muscles, one of very great size (*m*), the other smaller (*m'*), are fastened by one end to the exoskeleton of this segment. The fibres of the larger muscle converge to be fixed into the two sides of a long flat process of the chitinous cuticula, on the inner side of the base of the terminal segment, which serves as a tendon (*t*); while those of the smaller muscle are similarly attached to a like process which proceeds from the outer side of the base of the terminal segment (*t'*). It is obvious that, when the latter muscle shortens it must move the apex of the terminal segment (*dp*) away from the end of the fixed claw; while, when the former contracts, the end of the terminal segment is brought towards that of the fixed claw.

A living crayfish is able to perform very varied movements with its pincers. When it swims backwards, these limbs are stretched straight out, parallel with one another, in front of the head; when it walks, they are usually carried like arms bent at the elbow, the "forearm" partly resting on the ground; on being irritated, the crayfish sweeps the pincers round in any direction to grasp the offending body; when prey is seized, it is at once conveyed, with a circular motion, towards the region of the mouth. Nevertheless, these very varied actions are all brought about by a combination of simple flexions and extensions, each of which is effected in the exact order, and to the exact extent, needful to bring the chela into the position required.

The skeleton of the stem of the limb which bears the chela is, in fact, divided into four moveable segments; and each of these is articulated with the segments on each side of it by a hinge of just the same character as that which connects the moveable claw of the chela with the penultimate segment, while the basal segment is similarly articulated with the thorax.

If the axes of all these articulations * were parallel, it is obvious that, though the limb might be moved as a whole through a considerable arc, and might be bent in various

* By axis of the articulation is meant a line drawn through the pair of hinges which constitute it.

degrees, yet all its movements would be limited to one plane. But, in fact, the axes of the successive articulations are nearly at right angles to one another; so that, if the segments are successively either extended or flexed, the chela describes a very complicated curve; and by varying the extent of flexion or extension of each segment, this curve is susceptible of endless variation. It would probably puzzle a good mathematician to say exactly what position should be given to each segment, in order to bring the chela from any given position into any other; but if a lively crayfish is incautiously seized, the experimenter will find, to his cost, that the animal solves the problem both rapidly and accurately.

The mechanism by which the retrograde swimming of the crayfish is effected, is no less easily analysed. The apparatus of motion is, as we have seen, the abdomen, with its terminal five-pointed flapper. The rings of the abdomen are articulated together by joints (fig. 21, ×) situated a little below the middle of the height of the rings, at opposite ends of transverse lines, at right angles to the long axis of the abdomen.

Each ring consists of a dorsal, arched portion, called the *tergum* (fig. 21; fig. 36, p. 142, *t. XIX*), and a nearly flat ventral portion, which is the *sternum* (fig. 36, *st. XIX*). Where these two join, a broad plate is sent down on each side, which overlaps the bases of the abdominal appendages, and is known as the *pleuron* (fig. 36, *pl. XIX*).

The sterna are all very narrow, and are connected together by wide spaces of flexible exoskeleton.

When the abdomen is made straight, it will be found that these *intersternal* membranes are stretched as far as they will yield. On the other hand. when the abdomen

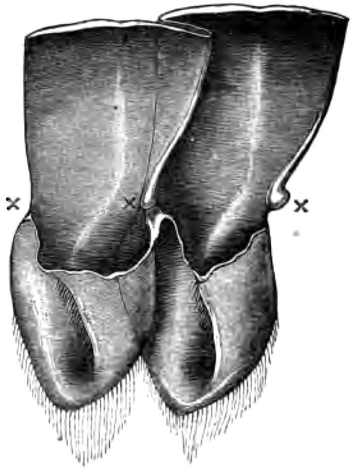

FIG. 21.—*Astacus fluviatilis.*—Two of the abdominal somites, in vertical section, seen from the inner side, to show ×, ×, the hinges by which they are articulated with one another (× 3). The anterior of the two somites is that to the right of the figure.

is bent up as far as it will go, the sterna come close together, and the intersternal membranes are folded.

The terga are very broad; so broad, in fact, that each overlaps its successor, when the abdomen is straightened or extended, for nearly half its length in the middle line; and the overlapped surface is smooth, convex, and marked off by a transverse groove from the rest of the tergum as an *articular facet.* The front edge of the articular facet is continued into a sheet of flexible cuticula, which turns back, and passes as a loose fold to the hinder edge of the overlapping tergum (fig. 21). This tergal *interarticular membrane* allows the terga to move as far as they can go in flexion; whilst, in extreme extension, they are but slightly stretched. But, even if the intersternal membranes presented no obstacle to excessive extension of the abdomen, the posterior free edge of each tergum fits into the groove behind the facet in the next in such a manner, that the abdomen cannot be made more than very slightly concave upwards without breaking.

Thus the limits of motion of the abdomen, in the vertical direction, are from the position in which it is straight, or has even a very slight upward concavity, to that in which it is completely bent upon itself, the telson being brought under the bases of the hinder thoracic limbs. No lateral movement between the somites of the abdomen is possible in any of its positions. For, when it is straight, lateral movement is hindered not only by the extensive overlapping of the terga, but also by the manner in which the hinder edges of the pleura of each of the four middle somites overlap the front edges of their successors. The pleura of the second somite are much larger than any of the others, and their front edges overlap the small pleura of the first abdominal somite; and when the abdomen is much flexed, these pleura even ride over the posterior edges of the branchiostegites. In the position of extension, the overlap of the terga is great, while that of the pleura of the middle somites is small. As the abdomen passes from extension to flexion, the overlap of the terga of course diminishes; but any decrease of resistance to lateral strains which may thus arise, is compensated by the increasing overlap of the pleura, which reaches its maximum when the abdomen is completely flexed.

It is obvious that longitudinal muscular fibres fixed into the exoskeleton, above the axes of the joints, must bring the centres of the terga of the somites closer together, when they contract; while muscular fibres attached below the axes of the joints must approximate the sterna. Hence, the former will give rise to extension, and the latter to flexion, of the abdomen as a whole.

Now there are two pairs of very considerable muscles disposed in this manner. The dorsal pair, or the *extensors* of the abdomen (fig. 22, *e.m*), are attached in front to the side walls of the thorax, thence pass backwards into the abdomen, and divide into bundles, which are fixed to the inner surfaces of the terga of all the somites. The other pair, or the *flexors* of the abdomen (*f.m*) constitute a very much larger mass of muscle, the fibres of which are curiously twisted, like the strands of a rope. The front end of this double rope is fixed to a series of processes of the exoskeleton of the thorax, called *apodemata*, some of which roof over the sternal blood-sinuses and the thoracic part of the nervous system; while, in the abdomen, its strands are attached to the sternal exoskeleton of all the somites and extend, on each side of the rectum, to the telson.

When the exoskeleton is cleaned by maceration, the

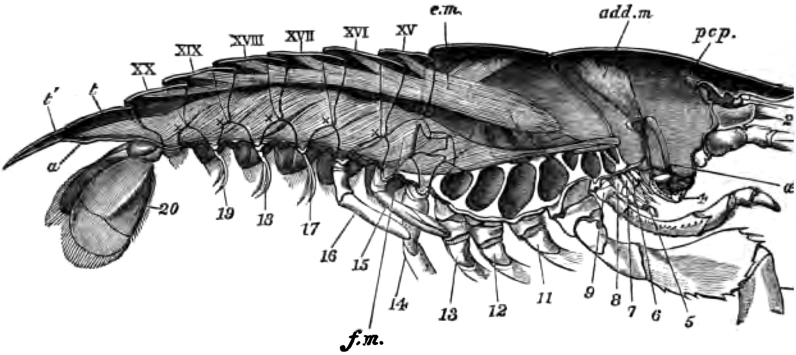

FIG. 22.—*Astacus fluviatilis.*—A longitudinal section of the body to show the principal muscles and their relations to the exoskeleton (nat. size). *a*, the vent; *add.m*, adductor muscle of mandible; *e.m*, extensor, and *f.m*, flexor muscle of abdomen; *œs*, œsophagus; *pcp*, procephalic process; *t,t'*, the two segments of the telson; *XV—XX*, the abdominal somites; *1—20*, the appendages; ×, ×, hinges between the successive abdominal somites.

abdomen has a slight curve, dependent upon the form and the degree of elasticity possessed by its different parts; and, in a living crayfish at rest, it will be observed that the curvature of the abdomen is still more marked. Hence it is ready either for extension or for flexion.

A sudden contraction of the flexor muscles instantly increases the ventral curvature of the abdomen, and throws the tail fin, the two side lobes of which are spread out, forwards; while the body is propelled backwards by the reaction of the water against the stroke. Then the flexor muscles being relaxed, the extensor muscles come into play; the abdomen is straightened, but less violently and with a far weaker stroke on the water, in consequence of the less strength of the extensors and of the folding up of the lateral plates of the fin, until it comes into the position requisite to give full force to a new downward and forward stroke. The tendency of the extension of the abdomen is to drive the body forward; but from the comparative weakness and the obliquity of its stroke, its practical effect is little more than to check the backward motion conferred upon the body by the flexion of the abdomen.

Thus, every action of the crayfish, which involves motion, means the contraction of one or more muscles. But what sets muscle contracting? A muscle freshly removed from the body may be made to contract in various ways, as by mechanical or chemical irritation, or by an electrical shock; but, under natural conditions, there is only one cause of muscular contraction, and that is the activity of a nerve. Every muscle is supplied with one or more nerves. These are delicate threads which, on microscopic examination, prove to be bundles of fine tubular filaments, filled with an apparently structureless substance of gelatinous consistency, the *nerve fibres* (fig. 23). The nerve bundle which passes to a muscle breaks up into smaller bundles and, finally, into separate fibres, each of which ultimately terminates by becoming continuous with the substance of a muscular fibre fig. 19, F.) Now the peculiarity of a muscle nerve, or *motor* nerve, as it is called, is that irritation of the nerve fibre at any part of its length, however distant from the muscle,

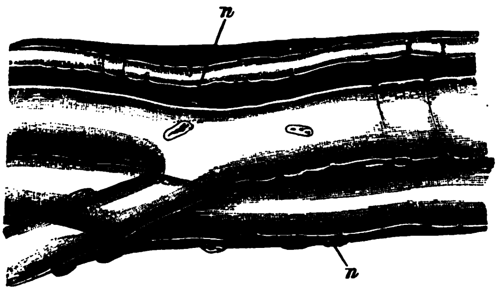

FIG. 23.—*Astacus fluviatilis.*—Three nerve fibres, with the connective tissue in which they are imbedded. (Magnified about 250 diameters.) *n*, nuclei.

brings about muscular contraction, just as if the muscle itself were irritated. A change is produced in the molecular condition of the nerve at the point of irritation; and this change is propagated along the nerve, until it reaches the muscle, in which it gives rise to that change in the arrangement of its molecules, the most obvious effect of which is the sudden alteration of form which we call muscular contraction.

If we follow the course of the motor nerves in a direction away from the muscles to which they are distributed, they will be found, sooner or later, to terminate in *ganglia* (fig. 24 A. *gl.c;* fig. 25, *gn. 1—13.*) A ganglion is a body which is in great measure composed of

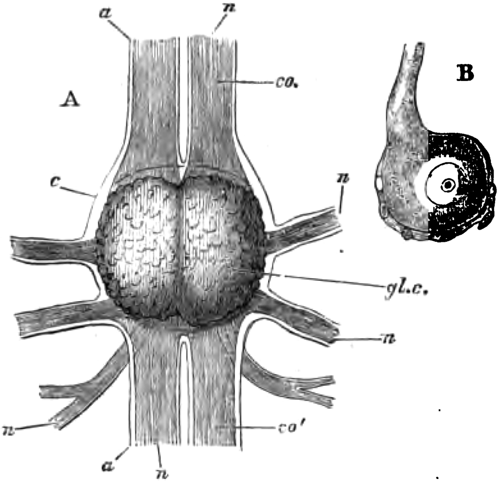

FIG. 24.—*Astacus fluviatilis.*—A, one of the (double) abdominal ganglia, with the nerves connected with it (× 25); B, a nerve cell or ganglionic corpuscle (× 250). *a*, sheath of the nerves; *c*, sheath of the ganglion; *co*, *co'*, commissural cords connecting the ganglia with those in front, and those behind them. *gl.c.* points to the ganglionic corpuscles of the ganglia; *n*, nerve fibres.

nerve fibres; but, interspersed among these, or disposed around them, there are peculiar structures, which are termed *ganglionic corpuscles*, or *nerve cells* (fig. 24, B.) These are nucleated cells, not unlike the epithelial cells which have been already mentioned, but which are larger

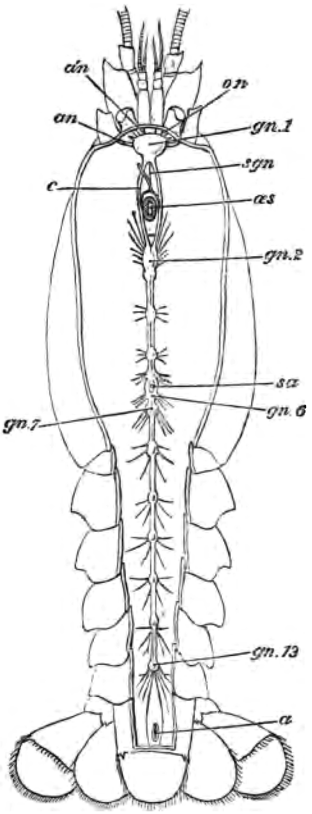

FIG. 25.—*Astacus fluviatilis.*—The central nervous system seen from above (nat. size). *a*, vent; *an*, antennary nerve; *a'n*, antennulary nerve; *c*, circumœsophageal commissures; *gn.* 1, supraœsophageal ganglion; *gn.* 2, infraœsophageal ganglion; *gn.* 6, fifth thoracic ganglion; *gn.* 7, last thoracic ganglion; *gn.* 13, last abdominal ganglion; *œs*, œsophagus in cross section; *on*, optic nerve; *sa*, sternal artery in cross section; *sgn*, stomatogastric nerve.

and often give off one or more processes. These processes, under favourable circumstances, can be traced into continuity with nerve fibres.

The chief ganglia of the crayfish are disposed in a longitudinal series in the middle line of the ventral aspect of the body close to the integument (fig. 25). In the abdomen, for example, six ganglionic masses are readily observed, one lying over the sternum of each somite, connected by longitudinal bands of nerve fibres, and giving off branches to the muscles. On careful examination, the longitudinal connecting bands, or *commissures* (fig. 24, *co*), are seen to be double, and each mass appears slightly bilobed. In the thorax, there are six, larger, double ganglionic masses, likewise connected by double commissures; and the most anterior of these, which is the largest (fig. 25, *gn.* 2), is marked at the sides by notches, as if it were made up of several pairs of ganglia, run together into one continuous whole. In front of this, two commissures (*c*) pass forwards, separating widely, to give room for the gullet (*œs*), which passes between them; while in front of the gullet, just behind the eyes, they unite with a transversely elongated mass of ganglionic substance (*gn.* 1), termed the *brain*, or *cerebral ganglion*.

All the motor nerves, as has been said, are traceable, directly or indirectly, to one or other of these thirteen sets of ganglia; but other nerves are given off from the ganglia, which cannot be followed into any muscle. In fact, these nerves go either to the integument or to the organs of sense, and they are termed *sensory nerves.*

When a muscle is connected by its motor nerve with a ganglion, irritation of that ganglion will bring about the contraction of the muscle, as well as if the motor nerve itself were irritated. Not only so; but if a sensory nerve, which is in connexion with the ganglion, is irritated, the same effect is produced; moreover, the sensory nerve itself need not be excited, but the same result will take place, if the organ to which it is distributed is stimulated. Thus the nervous system is fundamentally an apparatus by which two separate, and it may be distant, parts of the body, are brought into relation with one another; and this relation is of such a nature, that a change of state arising in the one part is followed by the propagation of changes along the sensory nerve to the ganglion, and from the ganglion to the other part; where, if that part happens to be muscle, it produces contraction. If one end of a rod of wood, twenty feet long, is applied to a sounding-board, the sound of a tuning-fork held against the opposite extremity will be very plainly heard. Nothing can be seen to happen in the wood, and yet its molecules are certainly set vibrating, at the same rate as the tuning-fork vibrates; and when, after travelling rapidly along the wood, these vibrations affect the sounding-board, they give rise to vibrations of the molecules of the air, which reaching the ear, are converted into an audible note. So in the nerve tract:

no apparent change is effected in it by the irritation at one end; but the rate at which the molecular change produced travels can be measured; and, when it reaches the muscle, its effect becomes visible in the change of form of the muscle. The molecular change would take place just as much if there were no muscle connected with the nerve, but it would be no more apparent to ordinary observation than the sound of the tuning-fork is audible in the absence of the sounding-board.

If the nervous system were a mere bundle of nerve fibres extending between sensory organs and muscles, every muscular contraction would require the stimulation of that special point of the surface on which the appropriate sensory nerve ended. The contraction of several muscles at the same time, that is, the combination of movements towards one end, would be possible only if the appropriate nerves were severally stimulated in the proper order, and every movement would be the direct result of external changes. The organism would be like a piano, which may be made to give out the most complicated harmonies, but is dependent for their production on the depression of a separate key for every note that is sounded. But it is obvious that the crayfish needs no such separate impulses for the performance of highly complicated actions. The simple impression made on the organs of sensation in the two examples with which we started, gives rise to a train of complicated and accurately co-ordinated muscular contractions. To carry the analogy of the musical instrument further, striking a single key gives rise, not to a single note, but to a more or less elaborate tune; as if the hammer struck not a single string, but pressed down the stop of a musical box.

It is in the ganglia that we must look for the analogue of the musical box. A single impulse conveyed by a sensory nerve to a ganglion, may give rise to a single muscular contraction, but more commonly it originates a series of such, combined to a definite end.

The effect which results from the propagation of an impulse along a nerve fibre to a ganglionic centre, whence it is, as it were, reflected along another nerve fibre to a muscle, is what is termed a *reflex action*. As it is by no means necessary that sensation should be a concomitant of the first impulse, it is better to term the nerve fibre which carries it *afferent* rather than sensory; and, as other phenomena besides those of molar motion may be the ultimate result of the reflex action, it is better to term the nerve fibre which transmits the reflected impulse *efferent* rather than motor.

If the nervous commissures between the last thoracic and the first abdominal ganglia are cut, or if the thoracic ganglia are destroyed, the crayfish is no longer able to control the movements of the abdomen. If the forepart of the body is irritated, for example, the animal makes no effort to escape by swimming backwards. Nevertheless, the abdomen is not paralysed, for, if it be irritated, it will flap vigorously. This is a case of pure reflex action. The stimulus is conveyed to the abdominal ganglia through afferent nerves, and is reflected from them, by efferent nerves, to the abdominal muscles.

But this is not all. Under these circumstances it will be seen that the abdominal limbs all swing backwards and forwards, simultaneously, with an even stroke; while the vent opens and shuts with a regular rhythm. Of course, these movements imply correspondingly regular alternate contractions and relaxations of certain sets of muscles; and these, again, imply regularly recurring efferent impulses from the abdominal ganglia. The fact that these impulses proceed from the abdominal ganglia, may be shown in two ways: first, by destroying these ganglia in one somite after another, when the movements in each somite at once permanently cease; and, secondly, by irritating the surface of the abdomen, when the movements are temporarily inhibited by the stimulation of the afferent nerves. Whether these movements are properly reflex, that is, arise from incessant new afferent impulses of unknown origin, or whether they depend on the periodical accumulation and discharge of nervous energy in the ganglia themselves, or upon periodical exhaustion and restoration of the irritability of the muscles, is unknown. It is sufficient for the present purpose to use the facts as evidence of the peculiar co-ordinative function of ganglia.

The crayfish, as we have seen, avoids light; and the slightest touch of one of its antennæ gives rise to active motions of the whole body. In fact, the animal's position and movements are largely determined by the influences received through the feelers and the eyes. These receive their nerves from the cerebral ganglia; and, as might be expected, when these ganglia are extirpated, the crayfish exhibits no tendency to get away from the light, and the feelers may not only be touched, but sharply pinched, without effect. Clearly, therefore, the cerebral ganglia serve as a ganglionic centre, by which the afferent impulses derived from the feelers and the eyes are transmuted into efferent impulses. Another very curious result follows upon the extirpation of the cerebral ganglia. If an uninjured crayfish is placed upon its back, it makes unceasing and well-directed efforts to turn over; and if everything else fails, it will give a powerful flap with the abdomen, and trust to the chapter of accidents to turn over as it darts back. But the brainless crayfish behaves in a very different way. Its limbs are in incessant motion, but they are "all abroad;" and if it turns over on one side, it does not seem able to steady itself, but rolls on to its back again.

If anything is put between the chelæ of an uninjured crayfish, while on its back, it either rejects the object at once, or tries to make use of it for leverage to turn over. In the brainless crayfish a similar operation gives rise to a very curious spectacle.* If the object, whatever it be

* My attention was first drawn to these phenomena by my friend Dr. M. Foster, F.R.S., to whom I had suggested the desirableness of an experimental study of the nerve physiology of the crayfish.

—a bit of metal, or wood, or paper, or one of the animal's own antennæ—is placed between the chelæ of the forceps, it is at once seized by them, and carried backwards; the chelate ambulatory limbs are at the same time advanced, the object seized is transferred to them, and they at once tuck it between the external maxillipedes, which, with the other jaws, begin vigorously to masticate it. Sometimes the morsel is swallowed; sometimes it passes out between the anterior jaws, as if deglutition were difficult. It is very singular to observe that, if the morsel which is being conveyed to the mouth by one of the forceps is pulled back, the forceps and the chelate ambulatory limbs of the other side are at once brought forward to secure it. The movements of the limbs are, in short, adjusted to meet the increased resistance.

All these phenomena cease at once, if the thoracic ganglia are destroyed. It is in these, therefore, that the simple stimulus set up by the contact of a body with, for example, one of the forceps, is translated into all the surprisingly complex and accurately co-ordinated movements, which have been described. Thus the nervous system of the crayfish may be regarded as a system of co-ordinating mechanisms, each of which produces a certain action, or set of actions, on the receipt of an appropriate stimulus.

When the crayfish comes into the world, it possesses in its neuro-muscular apparatus certain innate potentialities of action, and will exhibit the corresponding acts, under the influence of the appropriate stimuli. A large proportion of these stimuli come from without through the organs of the senses. The greater or less readiness of each sense organ to receive impulses, of the nerves to transmit them, and of the ganglia to give rise to combined impulses, is dependent at any moment upon the physical condition of these parts; and this, again, is largely modified by the amount and the condition of the blood supplied. On the other hand, a certain number of these stimuli are doubtless originated by changes within the various organs which compose the body, including the nerve centres themselves.

When an action arises from conditions developed in the interior of an animal's body, inasmuch as we cannot perceive the antecedent phenomena, we call such an action "spontaneous;" or, when in ourselves we are aware that it is accompanied by the idea of the action, and the desire to perform it, we term the act "voluntary." But, by the use of this language, no rational person intends to express the belief that such acts are uncaused or cause themselves. "Self-causation" is a contradiction in terms; and the notion that any phenomenon comes into existence without a cause, is equivalent to a belief in chance, which one may hope is, by this time, finally exploded.

In the crayfish, at any rate, there is not the slightest reason to doubt that every action has its definite physical cause, and that what it does at any moment would be as clearly intelligible, if we only knew all the internal and external conditions of the case, as the striking of a clock is to any one who understands clockwork.

The adjustment of the body to varying external conditions, which is one of the chief results of the working of the nervous mechanism, would be far less important from a physiological point of view than it is, if only those external bodies which come into direct contact with the organism * could affect it; though very delicate influences of this kind take effect on the nervous apparatus through the integument.

It is probable that the *setæ*, or hairs, which are so generally scattered over the body and the appendages, are delicate tactile organs. They are hollow processes of the chitinous cuticle, and their cavities are continuous with narrow canals, which traverse the whole thickness of the cuticle, and are filled by a prolongation of the subjacent proper integument. As this is supplied with nerves, it is likely that fine nerve fibres reach the bases of the hairs, and are affected by anything which stirs these delicately poised levers.

* It may be said that, strictly speaking, only those external bodies which are in direct contact with the organism do affect it—as the vibrating ether, in the case of luminous bodies; the vibrating air or water, in the case of sonorous bodies; odorous particles, in the case of odorous bodies: but I have preferred the ordinary phraseology to a pedantically accurate periphrasis.

There is much reason to believe that odorous bodies affect crayfish; but it is very difficult to obtain experi-

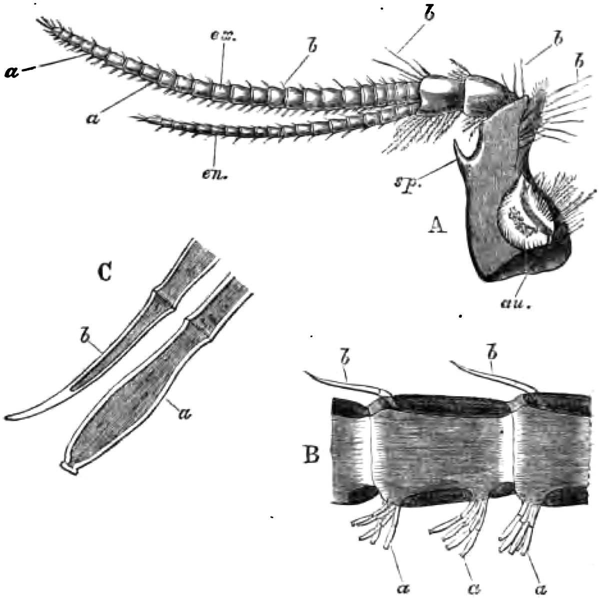

FIG. 26.—*Astacus fluviatilis*.—A, the right antennule seen from the inner side (× 5); B, a portion of the exopodite enlarged; C, olfactory appendage of the exopodite; *a*, front view; *b*, side view (× 300); *a*, olfactory appendages; *au*, auditory sac, supposed to be seen through the wall of the basal joint of the antennule; *b*, setæ; *en*, endopodite; *ex*, exopodite; *sp*. spine of the basal joint.

mental evidence of the fact. However, there is a good deal of analogical ground for the supposition that some peculiar structures, which are evidently of a sensory nature, developed on the under side of the outer branch of the antennule, play the part of an olfactory apparatus.

Both the outer (fig. 26 A. *ex*) and the inner (*en*) branches of the antennule are made up of a number of delicate ring-like segments, which bear fine setæ (*b*) of the ordinary character.

The inner branch, which is the shorter of the two, possesses only these setæ; but the under surface of each of the joints of the outer branch, from about the seventh or eighth to the last but one, is provided with two bundles of very curious appendages (fig. 27, A, B, C, *a*), one in front and one behind. These are rather more than 1-200th of an inch long, very delicate, and shaped like a spatula, with a rounded handle and a flattened somewhat curved blade, the end of which is sometimes truncated, sometimes has the form of a prominent papilla. There is a sort of joint between the handle and the blade, such as is found between the basal and the terminal parts of the ordinary setæ, with which, in fact, these processes entirely correspond in their essential structure. A soft granular tissue fills the interior of each of these problematical structures, to which Leydig, their discoverer, ascribes an olfactory function.

It is probable that the crayfish possesses something analogous to taste, and a very likely seat for the organ of this function is in the upper lip and the metastoma; but if the organ exists it possesses no structural peculiarities by which it can be identified.

There is no doubt, however, as to the special recipients of sonorous and luminous vibrations; and these are of particular importance, as they enable the nervous machinery to be affected by bodies indefinitely remote from it, and to change the place of the organism in relation to such bodies.

Sonorous vibrations are enabled to act as the stimulants of a special nerve (fig. 25, *a′n*) connected with the brain, by means of the very curious *auditory sacs* (fig. 26, A, *au*) which are lodged in the basal joints of the antennules.

Each of these joints is trihedral, the outer face being convex; the inner, applied to its fellow, flat; and the upper, on which the eyestalk rests, concave. On this upper face there is a narrow elongated oval aperture, the outer lip of which is beset with a flat brush of long close-set setæ, which lie horizontally over the aperture, and effectually close it. The aperture leads into a small sac (*au*) with delicate walls formed by a chitinous continuation of the general cuticula. The inferior and posterior wall of the sac is raised up along a curved line into a ridge which projects into its interior (fig. 27, A, *r*). Each side of this ridge is beset with a series of delicate setæ (*as*), the longest of which measures about $\frac{1}{10}$th of an inch; they thus form a longitudinal band bent upon itself. These *auditory setæ* project into the fluid contents of the sac, and their apices are for the most part imbedded in a gelatinous mass, which contains irregular particles of sand

and sometimes of other foreign matter. A nerve (*n n′*,) is distributed to the sac, and its fibres enter the bases of the hairs, and may be traced to their apices, where they end in peculiar elongated rod-like bodies (fig. 27, C). Here is an auditory organ of the simplest description.

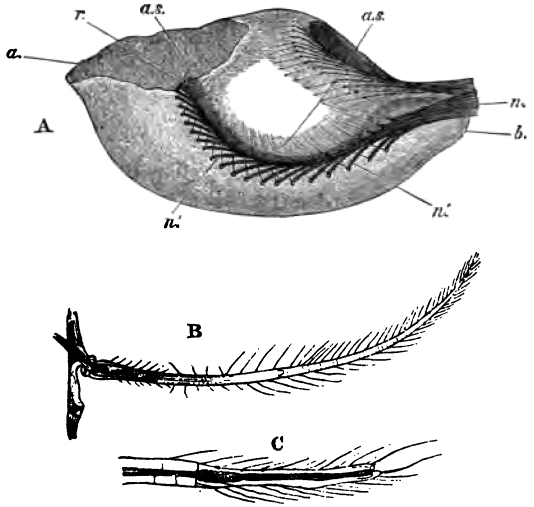

FIG. 27.—*Astacus fluviatilis.* A, the auditory sac detached and seen from the outside (× 15) ; B, auditory hair (× 100) ; C, the distal extremity of the same more highly magnified. *a*, aperture of sac ; *as*, auditory setæ ; *b*, its inner or posterior extremity ; *n n′*, nerves ; *r*, ridge.

It retains, in fact, throughout life, the condition of a simple sac or involution of the integument, such as is that of the vertebrate ear in its earliest stage.

The sonorous vibrations transmitted through the water in which the crayfish lives to the fluid and solid contents of the auditory sac are taken up by the delicate hairs of the ridge, and give rise to molecular changes which traverse the auditory nerves and reach the cerebral ganglia.

The vibrations of the luminiferous ether are brought to bear upon the free ends of two large bundles of nerve fibres, termed the optic nerves (fig. 25, *on*), which proceed directly from the brain, by means of a highly complex *eye*. This is an apparatus, which, in part, sorts out the rays of light into as many very small pencils as there are separate endings of the fibres of the optic nerve, and, in part, serves as the medium by which the luminous vibrations are converted into molecular nerve changes.

The free extremity of the eyestalk presents a convex, soft, and transparent surface, limited by an oval contour. The cuticle in this region, which is termed the *cornea*, (fig. 28, *a*), is, in fact, somewhat thinner and less distinctly laminated than in the rest of the eyestalk, and it contains no calcareous matter. But it is directly continuous with the rest of the exoskeleton of the eyestalk, to which it stands in somewhat the same relation as the soft integument of an articulation does to the adjacent hard parts.

The *cornea* is divided into a great number of minute, usually square facets, by faint lines, which cross it from side