

4. The *muscular tissue* of the crayfish always has the form of bands or fibres, of very various thickness, marked, when viewed by transmitted light, by alternate darker and

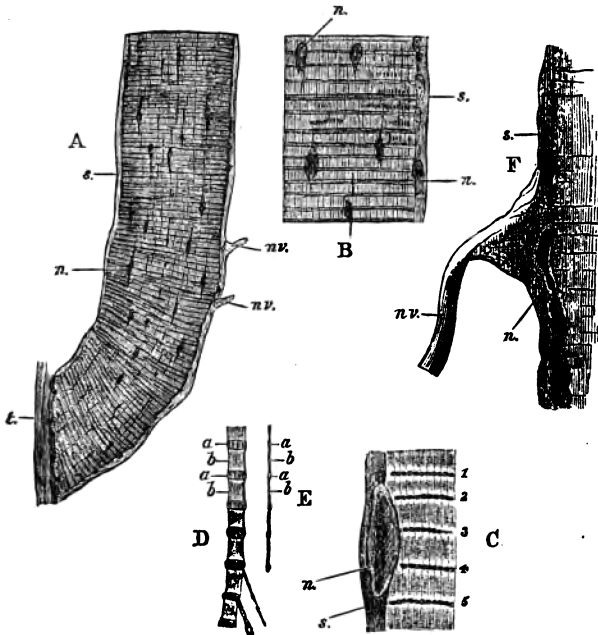


FIG. 52.—*Astacus fluviatilis*.—A, a single muscular fibre, transverse diameter $\frac{1}{10}$ th of an inch; B, a portion of the same more highly magnified; C, a smaller portion treated with alcohol and acetic acid still more highly magnified; D and E, the splitting up of a part of a fibre, treated with picro-carmin, into fibrillæ; F, the connection of a nervous with a muscular fibre which has been treated with alcohol and acetic acid. *a*, darker, and *b*, clearer portions of the fibrillæ; *n*, nuclei; *nv*, nerve fibre; *s*, sarcolemma; *t*, tendon; 1—5, successive dark granular striæ answering to the granular portions, *a*, of each fibrilla.

lighter striæ, transversely to the axis of the fibres (fig. 52 A). The distance of the transverse striæ from one another varies with the condition of the muscle, from 1-4,000th of an inch in the quiescent state to as little as 1-30,000th of an inch in that of extreme contraction. The more delicate muscular fibres, like those of the heart and those of the intestine, are imbedded in the connective tissue of the organ, but have no special sheaths.

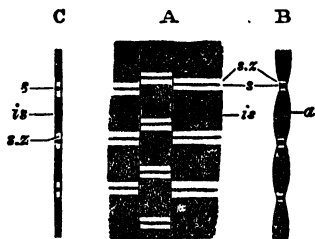


FIG. 53.—*Astacus fluviatilis*.—A, living muscular fibres very highly magnified; B, a fibrilla treated with solution of sodium chloride; C, a fibrilla treated with strong nitric acid. *s*, septal lines; *s.z.*, septal zones; *is*, interseptal zones; *a*, transverse line in the interseptal zone.

The fibres which make up the more conspicuous muscles of the trunk and limbs, on the other hand, are much larger, and are invested by a thin, transparent, structureless sheath, which is termed the *sarcolemma*. Nuclei are scattered, at intervals, through the striated substance of the muscle; and, in the larger muscular fibres, a layer of nucleated protoplasm lies between the sarcolemma and the striated muscle substance.

. This much is readily seen in a specimen of muscular fibre taken from any part of the body, and whether alive or dead. But the results of the ultimate optical analysis of these appearances, and the conclusions respecting the normal structure of striped muscle which may be legitimately drawn from them, have been the subjects of much controversy.

Quiescent muscular fibres from the chela of the forceps of a crayfish, examined while still living, without the addition of any extraneous fluid, and with magnifying powers of not less than seven or eight hundred diameters, exhibit the following appearance. At intervals of about 1-4000th of an inch, very delicate but dark and well-defined transverse lines are visible; and these, on careful focussing, appear beaded, as if they were made of a series of close-set minute granules not more than 1-20,000th to 1-30,000th of an inch in diameter. These may be termed the *septal lines* (fig. 52, D and E, *a*; C, 1-5; fig. 53, *s*). On each side of every septal line there is a very narrow perfectly transparent band, which may be distinguished as the *septal zone* (fig. 53, *sz*). Upon this follows a relatively broad band of a substance which has a semi-transparent aspect, like very finely ground glass, and hence appears somewhat dark relatively to the septal zone. Upon this *inter-septal zone* (*is*) follows another septal zone, then a septal line, another septal zone, an inter-septal zone, and so on throughout the whole length of the fibre.

In the perfectly unaltered state of the muscle no other transverse markings than these are discernible. But it is always possible to observe certain longitudinal markings; and these are of three kinds. In the first place, the nuclei which, in the perfectly fresh muscle, are delicate transparent oval bodies, are lodged in spaces which taper off at each end into narrow longitudinal clefts (fig. 52, A, B). Prolongations of the protoplasmic sheath of the fibre extend inwards and fill these clefts. Secondly, there are similar clefts interposed between these, but narrow and merely linear throughout. Sometimes these clefts contain fine granules. Thirdly, even in the perfectly fresh muscle, extremely faint parallel longitudinal striæ 1-7,000th of an inch, or thereabouts, apart, traverse the several zones, so that longer or shorter segments of the successive septal lines are inclosed between them. A transverse section of the muscle appears divided into rounded or polygonal areas of the same diameter, separated from one another here and there by minute interstices. Moreover, on examination of perfectly fresh muscle with high magnifying powers, the septal lines are hardly ever straight for any distance, but are broken up into short lengths, which answer to one or more of the longitudinal divisions, and stand at slightly different heights.

The only conclusion to be drawn from these appearances seems to me to be that the substance of the muscle is composed of distinct *fibrils*; and that the longitudinal

striæ and the rounded aræ of the transverse section are simply the optical expressions of the boundaries of these fibrils. In the perfectly unaltered state of the tissue, however, the fibrils are so closely packed that their boundaries are scarcely discernible.

Thus each muscular *fibre* may be regarded as composed of larger and smaller bundles of *fibrils* imbedded in a nucleated protoplasmic framework which ensheaths the whole and is itself invested by the sarcolemma.

As the fibre dies, the nuclei acquire hard, dark contours and their contents become granular, while at the same time the fibrils acquire sharp and well-defined boundaries. In fact, the fibre may now be readily teased out with needles, and the fibrils isolated.

In muscle which has been treated with various reagents, such as alcohol, nitric acid, or solution of common salt, the fibrils themselves may be split up into filaments of extreme tenuity, each of which appears to answer to one of the granules of the septal lines. Such an isolated *muscle filament* looks like a very fine thread carrying minute beads at regular intervals.

The septal lines resist most reagents, and remain visible in muscular fibres which have been subjected to various modes of treatment; but they may have the appearance of continuous bars, or be more or less completely resolved into separate granules, according to circumstances. On the other hand, what is to be seen in

the interspace between every two septal lines depends upon the reagent employed. With dilute acids and strong solutions of salt, the inter-septal substance swells up and becomes transparent, so that it ceases to be distinguishable from the septal zone. At the same time a distinct but faint transverse line may appear in the middle of its length. Strong nitric acid, on the contrary, renders the inter-septal substance more opaque, and the septal zones consequently appear very well defined.

In living and recently dead muscle, as well as in muscles which have been preserved in spirit or hardened with nitric acid, the inter-septal zones polarize light; and hence, in the dark field of the polarizing microscope, the fibre appears crossed by bright bands, which correspond with the inter-septal zones, or at any rate, with the middle parts of them. The substance which forms the septal zones, on the contrary, produces no such effect, and consequently remains dark; while the septal lines again have the same property as the inter-septal substance, though in a less degree.

In fibres which have been acted upon by solution of salt, or dilute acids, the inter-septal zones have lost their polarizing property. As we know that the reagents in question dissolve the peculiar constituent of muscle, *myosin*, it is to be concluded that the inter-septal substance is chiefly composed of myosin.

Thus a fibril may be considered to be made up of

segments of different material arranged in regular order ; S—sz—IS—sz—S—sz—IS—sz—S : S representing the septal line ; sz, the septal zone ; IS, the inter-septal zone. Of these, IS is the chief if not the only seat of the myosin ; what the composition of sz and of S may be is uncertain, but the supposition, that, in the living muscle, sz is a mere fluid, appears to me to be wholly inadmissible.

When living muscle contracts, the inter-septal zones become shorter and wider and their margins darker, while the septal zones and the septal lines tend to become effaced—as it appears to me simply in consequence of the approximation of the lateral margins of the inter-septal zones. It is probable that the substance of the intermediate zone is the chief, if not the only, seat of the activity of the muscle during contraction.

5. The elements of the *nervous tissue* are of two kinds, *nerve-cells*, and *nerve fibres* ; the former are found in the ganglia, and they vary very much in size (fig. 54, B). Each ganglionic corpuscle consists of a cell body produced into one or more processes which sometimes, if not always, end in nerve fibres. A large, clear spherical nucleus is seen in the interior of the nerve-cell ; and in the centre of this is a well defined, small round particle, the *nucleolus*. The corpuscle, when isolated, is often surrounded by a sort of sheath of small nucleated cells.

The nerve fibres (fig. 55) of the crayfish are remarkable for the large size which some of them attain. In the central nervous system a few reach as much as 1-200th of an inch in diameter; and fibres of 1-300th or 1-400th of

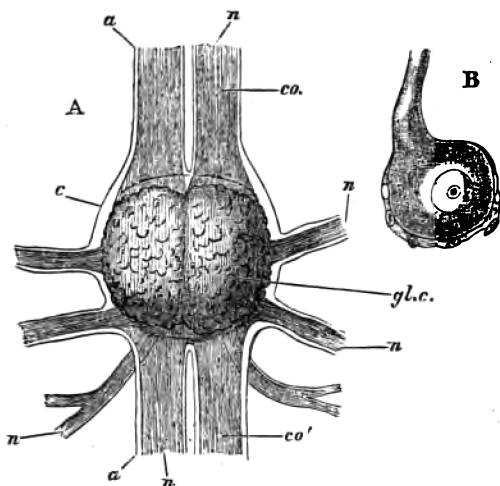


FIG. 54.—*Astacus fluviatilis*.—A, one of the (double) abdominal ganglia, with the nerves connected with it ($\times 25$); B, a nerve cell or ganglionic corpuscle ($\times 250$). *a*, sheath of the nerves; *c*, sheath of the ganglion; *co*, *co'*, commissural cords connecting the ganglia with those in front, and those behind them. *gl.c.* points to the ganglionic corpuscles of the ganglia; *n*, nerve fibres.

an inch in diameter are not rare in the main branches. Each fibre is a tube, formed of a strong and elastic, sometimes fibrillated, sheath, in which nuclei are imbedded at irregular intervals; and, when the nerve trunk gives

off a branch, more or fewer of these tubes divide, sending off a prolongation into each branch.

When quite fresh, the contents of the tubes are perfectly pellucid, and without the least indication of structure; and, from the manner in which the contents

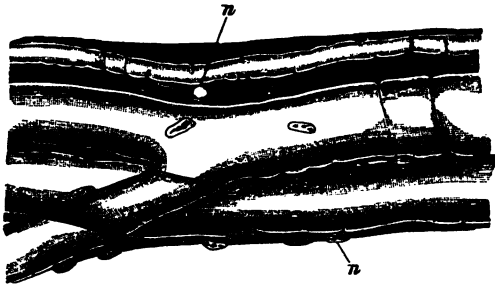


FIG. 55.—*Astacus fluviatilis*.—Three nerve fibres, with the connective tissue in which they are imbedded (magnified about 250 diameters); *n*, nuclei.

exude from the cut ends of the tubes, it is evident that they consist of a fluid of gelatinous consistency. As the fibre dies, and under the influence of water and of many chemical re-agents, the contents break up into globules or become turbid and finely granular.

Where motor nerve fibres terminate in the muscles to which they are distributed, the sheath of each fibre becomes continuous with the sarcolemma of the muscle, and the subjacent protoplasm is commonly raised into a small prominence which contains several nuclei (fig. 52, F). These are called the *terminal* or *motor plates*.

6, 7. The *ova* and the *spermatozoa* have already been described (pp. 132—135).

It will be observed that the blood corpuscles, the epithelial tissues, the ganglionic corpuscles, the *ova* and the *spermatozoa*, are all demonstrably nucleated cells, more or less modified. The first form of connective tissue is so similar to epithelial tissue, that it may obviously be regarded as an aggregate of as many cells as it presents nuclei, the matrix representing the more or less modified and confluent bodies of the cells, or products of these. But if this be so, then the second and third forms have a similar composition, except so far as the matrix of the cells has become fibrillated, or vacuolated, or marked off into masses corresponding with the several nuclei. By a parity of reasoning, muscular tissue may also be considered a cell aggregate, in which the inter-nuclear substance has become converted into striated muscle; while, in the nerve fibres, a like process of metamorphosis may have given rise to the pellucid gelatinous nerve substance. But, if we accept the conclusions thus suggested by the comparison of the various tissues with one another, it follows that every histological element, which has now been mentioned, is either a simple nucleated cell, a modified nucleated cell, or a more or less modified cell aggregate. In other words, every tissue is resolvable into nucleated cells.

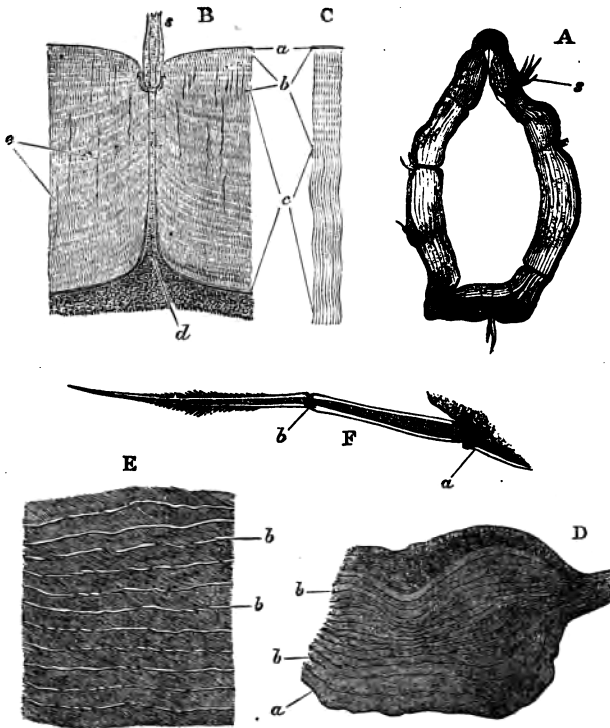


FIG. 56.—*Astacus fluviatilis*.—The structure of the cuticle. *A*, transverse section of a joint of the forceps ($\times 4$); *s*, setæ; *B*, a portion of the same ($\times 30$); *C*, a portion of *B* more highly magnified. *a*, epiostracum; *b*, ectostracum; *c*, endostracum; *d*, canal of seta; *e*, canals filled with air; *s*, seta. *D*, section of an intersternal membrane of the abdomen, the portion to the right in the natural condition, the remainder pulled apart with needles ($\times 20$); *E*, small portion of the same, highly magnified; *a*, intermediate substance; *b*, laminae. *F*, a seta, highly magnified; *a* and *b*, joints.

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A notable exception to this generalisation, however, obtains in the case of the *cuticular structures*, in which no cellular components are discoverable. In its simplest form, such as that presented by the lining of the intestine, the cuticle is a delicate, transparent membrane, thrown off from the surface of the subjacent cells, either by a process of exudation, or by the chemical transformation of their superficial layer. No pores are discernible in this membrane, but scattered over its surface there are oval patches of extremely minute, sharp conical processes, which are rarely more than 1-5,000th of an inch long. Where the cuticle is thicker, as in the stomach and in the exoskeleton, it presents a stratified appearance, as if it were composed of a number of laminae, of varying thickness, which had been successively thrown off from the subjacent cells.

Where the cuticular layer of the integument is uncalcified, for example, between the sterna of the abdominal somites, it presents an external, thin, dense, wrinkled lamina, the *epiostracum*, followed by a soft substance, which, on vertical section, presents numerous alternately more transparent and more opaque bands, which run parallel with one another and with the free surfaces of the slice (fig. 56, D). These bands are very close-set, often not more than 1-5000th of an inch apart near the outer and the inner surfaces, but in the middle of the section they are more distant.

If a thin vertical slice of the soft cuticle is gently

pulled with needles in the direction of its depth, it stretches to eight or ten times its previous diameter, the clear intervals between the dark bands becoming proportionally enlarged, especially in the middle of the slice, while the dark bands themselves become apparently thinner, and more sharply defined. The dark bands may then be readily drawn to a distance of as much as 1-300th of an inch from one another; but if the slice is stretched further, it splits along, or close to, one of the dark lines. The whole of the cuticular layer is stained by such colouring matters as hæmatoxylin; and, as the dark bands become more deeply coloured than the intermediate transparent substance, the transverse stratification is made very manifest by this treatment.

Examined with a high magnifying power, the transparent substance is seen to be traversed by close-set, faint, vertical lines, while the dark bands are shown to be produced by the cut edges of delicate laminæ, having a finely striated appearance, as if they were composed of delicate parallel wavy fibrillæ.

In the calcified parts of the exoskeleton a thin, tough, wrinkled epiostracum (fig. 56, B, *a*), and, subjacent to this, a number of alternately lighter and darker strata are similarly discernible: though all but the innermost laminæ are hardened by a deposit of calcareous salts, which are generally evenly diffused, but sometimes take the shape of rounded masses with irregular contours.

Immediately beneath the epiostracum, there is a zone

which may occupy a sixth or a seventh of the thickness of the whole, which is more transparent than the rest, and often presents hardly any trace of horizontal or vertical striation. When it appears laminated, the strata are very thin. This zone may be distinguished as the *ectostracum* (*b*), from the *endostracum* (*c*), which makes up the rest of the exoskeleton. In the outer part of the endostracum, the strata are distinct, and may be as much as 1-500th of an inch thick, but in the inner part they become very thin, and the lines which separate them may be not more than 1-8000th of an inch apart. Fine, parallel, close-set, vertical striæ (*e*) traverse all the strata of the endostracum, and may usually be traced through the ectostracum, though they are always faint, and sometimes hardly discernible, in this region. When a high magnifying power is employed, it is seen that these striæ, which are about 1-7000th of an inch apart, are not straight, but that they present regular short undulations, the alternate convexities and concavities of which correspond with the light and the dark bands respectively.

If the hard exoskeleton has been allowed to become partially or wholly dry before the section is made, the latter will look white by reflected and black by transmitted light, in consequence of the places of the striæ being taken by threads of air of such extreme tenuity, that they may measure not more than 1-30,000th of an inch in diameter. It is to be concluded, therefore, that

the striæ are the optical indications of parallel undulating canals which traverse the successive strata of the cuticle, and are ordinarily occupied by a fluid. When this dries up, the surrounding air enters, and more or less completely fills the tubes. And that this is really the case may be proved by making very thin sections parallel with the face of the exoskeleton, for these exhibit innumerable minute perforations, set at regular distances from one another, which correspond with the intervals between the striæ in the vertical section; and sometimes the contours of the areæ which separate the apertures are so well defined as to suggest a pavement of minute angular blocks, the corners of which do not quite meet.

When a portion of the hard exoskeleton is decalcified, a chitinous substance remains, which presents the same structure as that just described, except that the epiostracum is more distinct; while the ectostracum appears made up of very thin laminæ, and the tubes are represented by delicate striæ, which appear coarser in the region of the dark zones. As in the naturally soft parts of the exoskeleton, the decalcified cuticle may be split into flakes, and the pores are then seen to be disposed in distinct areæ circumscribed by clear polygonal borders. These perforated areæ appear to correspond with individual cells of the ectoderm, and the canals thus answer to the so-called "pore-canals," which are common in cuticular structures and in the walls of many cells which bound free surfaces.

The whole exoskeleton of the crayfish is, in fact, produced by the cells which underlie it, either by the exudation of a chitinous substance, which subsequently hardens, from them; or, as is more probable, by the chemical metamorphosis of a superficial zone of the bodies of the cells into chitin. However this may be, the cuticular products of adjacent cells at first form a simple, continuous, thin pellicle. A continuation of the process by which it was originated increases the thickness of the cuticle; but the material thus added to the inner surface of the latter is not always of the same nature, but is alternately denser and softer. The denser material gives rise to the tough laminæ, the softer to the intermediate transparent substance. But the quantity of the latter is at first very small, whence the more external laminæ are in close apposition. Subsequently the quantity of the intermediate substance increases, and gives rise to the thick stratification of the middle region, while it remains insignificant in the inner region of the exoskeleton.

The cuticular structures of the crayfish differ from the nails, hairs, hoofs, and similar hard parts of the higher animals, insomuch as the latter consist of aggregations of cells, the bodies of which have been metamorphosed into horny matter. The cuticle, with all its dependencies, on the contrary, though no less dependent on cells for its existence, is a derivative product, the formation of which does not involve the complete meta-

morphosis and consequent destruction of the cells to which it owes its origin.

The calcareous salts by which the calcified exoskeleton is hardened can only be supplied by the infiltration of a fluid in which they are dissolved from the blood; while the distinctive structural characters of the epiostracum, the ectostracum, and the endostracum, are the results of a process of metamorphosis which goes on *pari passu* with this infiltration. To what extent this metamorphosis is a properly vital process; and to what extent it is explicable by the ordinary physical and chemical properties of the animal membrane on the one hand, and the mineral salts on the other, is a curious, and at present, unsolved problem.

The outer surface of the cuticle is rarely smooth. Generally it is more or less obviously ridged or tuberculated; and, in addition, presents coarser or finer hair-like processes which exhibit every gradation from a fine microscopic down to stout spines. As these processes, though so similar to hairs in general appearance, are essentially different from the structures known as hairs in the higher animals, it is better to speak of them as *setæ*.

These *setæ* (fig. 56, F) are sometimes short, slender, conical filaments, the surface of which is quite smooth; sometimes the surface is produced into minute serrations, or scale-like prominences, disposed in two or more series; in other *setæ*, the axis gives off slender lateral

branches; and in the most complicated form the branches are ornamented with lateral branchlets. For a certain distance from the base of the seta, its surface is usually smooth, even when the rest of its extent is ornamented with scales or branches. Moreover, the basal part of the seta is marked off from its apical moiety by a sort of joint which is indicated by a slight constriction, or by a peculiarity in the structure of the cuticula at this point. A seta almost always takes its origin from the bottom of a depression or pit of the layer of cuticle, from which it is developed, and at its junction with the latter it is generally thin and flexible, so that the seta moves easily in its socket. Each seta contains a cavity, the boundaries of which generally follow the outer contours of the seta. In a good many of the setæ, however, the parietes, near the base of the seta, are thickened in such a manner as almost, or completely, to obliterate the central cavity. However thick the cuticle may be at the point from which the setæ take their origin, it is always traversed by a funnel-shaped canal (fig. 56, B, *d*), which usually expands beneath the base of the seta. Through this canal the subjacent ectoderm extends up to the base of the seta, and can even be traced for some distance into its interior.

It has already been mentioned that the apodemata and the tendons of the muscles are infoldings of the cuticle, embraced and secreted by corresponding involutions of the ectoderm.

Thus the body of the crayfish is resolvable, in the first place, into a repetition of similar segments, the *metameres*, each of which consists of a somite and two appendages; the metameres are built up out of a few simple *tissues*; and, finally, the tissues are either aggregates of more or less modified nucleated *cells*, or are products of such cells. Hence, in ultimate morphological analysis, the crayfish is a multiple of the histological unit, the nucleated cell.

What is true of the crayfish, is certainly true of all animals, above the very lowest. And it cannot yet be considered certain that the generalization fails to hold good even of the simplest manifestations of animal life; since recent investigations have demonstrated the presence of a nucleus in organisms in which it had hitherto appeared to be absent.

However this may be, there is no doubt that in the case of man and of all vertebrated animals, in that of all arthropods, mollusks, echinoderms, worms, and inferior organisms down to the very lowest sponges, the process of morphological analysis yields the same result as in the case of the crayfish. The body is built up of tissues, and the tissues are either obviously composed of nucleated cells; or, from the presence of nuclei, they may be assumed to be the results of the metamorphosis of such cells; or they are cuticular structures.

The essential character of the nucleated cell is that it consists of a protoplasmic substance, one part of which differs somewhat in its physical and chemical characters

from the rest, and constitutes the nucleus. What part the nucleus plays in relation to the functions, or vital activities, of the cell is as yet unknown; but that it is the seat of operations of a different character from those which go on in the body of the cell is clear enough. For, as we have seen, however different the several tissues may be, the nuclei which they contain are very much alike; whence it follows, that if all these tissues were primitively composed of simple nucleated cells, it must be the bodies of the cells which have undergone metamorphosis, while the nuclei have remained relatively unchanged.

On the other hand, when cells multiply, as they do in all growing parts, by the division of one cell into two, the signs of the process of internal change which ends in fission are apparent in the nucleus before they are manifest in the body of the cell; and, commonly, the division of the former precedes that of the latter. Thus a single cell body may possess two nuclei, and may become divided into two cells by the subsequent aggregation of the two moieties of its protoplasmic substance round each of them, as a centre.

In some cases, very singular structural changes take place in the nuclei in the course of the process of cell-division. The granular or fibrillar contents of the nucleus, the wall of which becomes less distinct, arrange themselves in the form of a spindle or double cone, formed of extremely delicate filaments; and in the plane

of the base of the double cone the filaments present knots or thickenings, just as if they were so many threads with a bead in the middle of each. When the nuclear spindle is viewed sideways, these beads or thickenings give rise to the appearance of a disk traversing the centre of the spindle. Soon each bead separates into two, and these move away from one another, but remain connected by a fine filament. Thus the structure which had the form of a double cone, with a disk in the middle, assumes that of a short cylinder, with a disk and a cone at each end. But as the distance between the two disks increases, the uniting filaments lose their parallelism, converge in the middle, and finally separate, so that two separate double cones are developed in place of the single one. Along with these changes in the nucleus, others occur in the protoplasm of the cell body, and its parts commonly display a tendency to arrange themselves in radii from the extremities of the cones as a centre; while, as the separation of the two secondary nuclear spindles becomes complete, the cell body gradually splits from the periphery inwards, in a direction at right angles to the common axis of the spindles and between their apices. Thus two cells are formed, where, previously, only one existed; and the nuclear spindles of each soon revert to the globular form and confused arrangement of the contents, characteristic of nuclei in their ordinary state. The formation of these nuclear spindles is very beautifully seen in the epithelial cells of the testis of the

crayfish (fig. 33, p. 132); but I have not been able to find distinct evidence of it elsewhere in this animal; and although the process has now been proved to take place in all the divisions of the animal kingdom, it would seem that nuclei may, and largely do, undergo division, without becoming converted into spindles.

The most cursory examination of any of the higher plants shows that the vegetable, like the animal body, is made up of various kinds of tissues, such as pith, woody fibre, spiral vessels, ducts, and so on. But even the most modified forms of vegetable tissue depart so little from the type of the simple cell, that the reduction of them all to that common type is suggested still more strongly than in the case of the animal fabric. And thus the nucleated cell appears to be the morphological unit of the plant no less than of the animal. Moreover, recent inquiry has shown that in the course of the multiplication of vegetable cells by division, the nuclear spindles may appear and run through all their remarkable changes by stages precisely similar to those which occur in animals.

The question of the universal presence of nuclei in cells may be left open in the case of Plants, as in that of Animals; but, speaking generally, it may justly be affirmed that the nucleated cell is the morphological foundation of both divisions of the living world; and the great generalisation of Schleiden and Schwann, that there is a fundamental agreement in structure and

development between plants and animals, has, in substance, been merely confirmed and illustrated by the labours of the half century which has elapsed since its promulgation.

Not only is it true that the minute structure of the crayfish is, in principle, the same as that of any other animal, or of any plant, however different it may be in detail ; but, in all animals (save some exceptional forms) above the lowest, the body is similarly composed of three layers, ectoderm, mesoderm, and endoderm, disposed around a central alimentary cavity. The ectoderm and the endoderm always retain their epithelial character ; while the mesoderm, which is insignificant in the lower organisms, becomes, in the higher, far more complicated even than it is in the crayfish.

Moreover, in the whole of the *Arthropoda*, and the whole of the *Vertebrata*, to say nothing of other groups of animals, the body, as in the crayfish, is susceptible of distinction into a series of more or less numerous segments, composed of homologous parts. In each segment these parts are modified according to physiological requirements ; and by the coalescence, segregation, and change of relative size and position of the segments, well characterized regions of the body are marked out. And it is remarkable that precisely the same principles are illustrated by the morphology of plants. A flower with its whorls of sepals, petals, stamens and carpels has the same relation to a stem

with its whorls of leaves, as a crayfish's head has to its abdomen, or a dog's skull to its thorax.

It may be objected, however, that the morphological generalisations which have now been reached, are to a considerable extent of a speculative character; and that, in the case of our crayfish, the facts warrant no more than the assertion that the structure of that animal may be consistently interpreted, on the supposition that the body is made up of homologous somites and appendages, and that the tissues are the result of the modification of homologous histological elements or cells; and the objection is perfectly valid.

There can be no doubt that blood corpuscles, liver cells, and ova are all nucleated cells; nor any that the third, fourth, and fifth somites of the abdomen are constructed upon the same plan; for these propositions are mere statements of the anatomical facts. But when, from the presence of nuclei in connective tissue and muscles, we conclude that these tissues are composed of modified cells; or when we say that the ambulatory limbs of the thorax are of the same type as the abdominal limbs, the exopodite being suppressed, the statement, as the evidence stands at present, is no more than a convenient way of interpreting the facts. The question remains, has the muscle actually been formed out of nucleated cells? Has the ambulatory limb ever possessed an exopodite, and lost it?

The answer to these questions is to be sought in the facts of individual and ancestral development.

An animal not only is, but becomes ; the crayfish is the product of an egg, in which not a single structure visible in the adult animal exists : in that egg the different tissues and organs make their appearance by a gradual process of evolution ; and the study of this process can alone tell us whether the unity of composition suggested by the comparison of adult structures, is borne out by the facts of their development in the individual or not. The hypothesis that the body of the crayfish is made up of a series of homologous somites and appendages, and that all the tissues are composed of nucleated cells, might be only a permissible, because a useful, mode of colligating the facts of anatomy. The investigation of the actual manner in which the evolution of the body of the crayfish has been effected, is the only means of ascertaining whether it is anything more. And, in this sense, development is the criterion of all morphological speculations.

The first obvious change which takes place in an impregnated ovum is the breaking up of the yelk into smaller portions, each of which is provided with a nucleus, and is termed a *blastomere*. In a general morphological sense, a blastomere is a nucleated cell, and differs from an ordinary cell only in size, and in the usual, though by no means invariable, abundance of granular contents ; and blastomeres insensibly pass into ordinary cells, as

the process of division of the yelk into smaller and smaller portions goes on.

In a great many animals, the splitting-up into blastomeres is effected in such a manner that the yelk is, at first, divided into equal, or nearly equal, masses; that each of these again divides into two; and that the number of blastomeres thus increases in geometrical progression until the entire yelk is converted into a mulberry-like body, termed a *morula*, made up of a great number of small blastomeres or nucleated cells. The whole organism is subsequently built up by the multiplication, the change of position, and the metamorphosis of these products of yelk division.

In such a case as this, yelk division is said to be *complete*. An unessential modification of complete yelk division is seen when, at an early period, the blastomeres produced by division are of unequal sizes; or when they become unequal in consequence of division taking place much more rapidly in one set than in another.

In many animals, especially those which have large ova, the inequality of division is pushed so far that only a portion of the yelk is affected by the process of fission, while the rest serves merely as *food-yelk*, for nutriment to the blastomeres thus produced. Over a greater or less extent of the surface of the egg, the protoplasmic substance of the yelk segregates itself from the rest, and, constituting a *germinal layer*, breaks up into the blastomeres, which multiply at the expense of the food-

yelk, and fabricate the body of the embryo. This process is termed *partial* or *incomplete* yelk division.

The crayfish is one of those animals in the egg of which the yelk undergoes partial division. The first steps of the process have not yet been thoroughly worked out, but their result is seen in ova which have been but a short time laid (fig. 57, A). In such eggs, the great mass of the substance of the vitellus is destined to play the part of food-yelk; and it is disposed in conical masses, which radiate from a central spheroidal portion to the periphery of the yelk (*v*). Corresponding with the base of each cone, there is a clear protoplasmic plate, which contains a nucleus; and as these bodies are all in contact by their edges, they form a complete, though thin, investment to the food-yelk. This is termed the *blastoderm* (*bl*).

Each nucleated protoplasmic plate adheres firmly to the corresponding cone of granular food-yelk, and, in all probability, the two together represent a blastomere; but, as the cones only indirectly subserve the growth of the embryo, while the nucleated peripheral plates form an independent spherical sac, out of which the body of the young crayfish is gradually fashioned, it will be convenient to deal with the latter separately.

Thus, at this period, the body of the developing crayfish is nothing but a spherical bag, the thin walls of which are composed of a single layer of nucleated cells, while its cavity is filled with food-yelk. The first modification

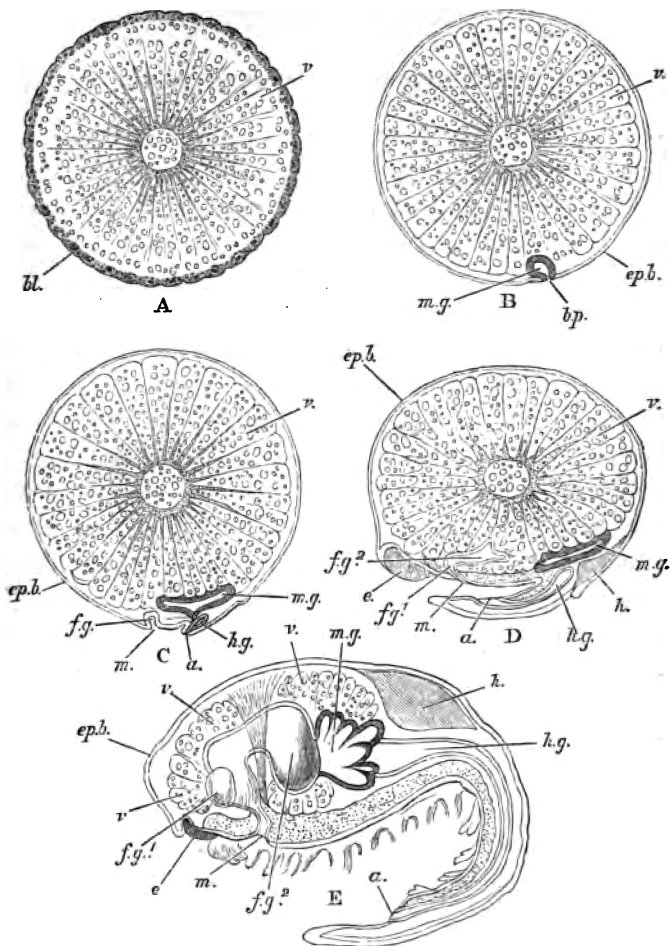


FIG. 57.—*Astaenus furciculatus*.—Diagrammatic sections of embryos; partly after Reichenbach, partly original ($\times 20$). A. An ovum in which the blastoderm is just formed. B. An ovum in which the invagination of the blastoderm to constitute the hypoblast or rudiment of the mid-gut has taken place. (This nearly answers to the stage represented in fig. 58, A.) C. A longitudinal section of an ovum, in which the rudiments of the abdomen, of the hind-gut, and of the fore-gut have appeared. (This nearly answers to the stage represented in fig. 58, E.) D. A similar section of an embryo in nearly the same stage of development as that represented in C, fig. 59. E. An embryo just hatched, in longitudinal section; *a*, anus; *bl.*, blastoderm; *bp.*, blastopore; *e*, eye; *ep.b.*, epiblast; *fg.*, fore-gut; *fg.¹*, its oesophageal, and *fg.²*, its gastric portion; *h.*, heart; *h.g.*, hind-gut; *m.*, mouth; *m.g.*, hypoblast, archenteron, or mid-gut; *v.*, yolk. The dotted portions in D and E represent the nervous system.

which is effected in the vesicular blastoderm manifests itself on that face of it which is turned towards the pedicle of the egg. Here the layer of cells becomes thickened throughout an oval area about 1-25th of an inch in diameter. Hence, when the egg is viewed by reflected light, a whitish patch of corresponding form and size appears in this region. This may be termed the *germinal disk*. Its long axis corresponds with that of the future crayfish.

Next, a depression (fig. 58, A, *bp*) appears in the hinder third of the germinal disk, in consequence of this part of the blastoderm growing inwards, and thus giving rise to a small wide-mouthed pouch, which projects into the food-yolk with which the cavity of the blastoderm is filled (fig. 57, B, *mg*). As this infolding, or invagination of the blastoderm, goes on, the pouch thus produced increases, while its external opening, termed the *blastopore* (fig. 57, B, and 58, A—E, *bp*), diminishes in size. Thus the body of the embryo crayfish, from being a simple bag becomes a double bag, such as might be produced by pushing in the wall of an incompletely distended india-rubber ball with the finger. And, in this case, if the interior of the bag contained porridge, the latter would very fairly represent the food-yolk.

By this invagination a most important step has been taken in the development of the crayfish. For, though the pouch is nothing but an ingrowth of part of the blastoderm, the cells of which its wall is composed

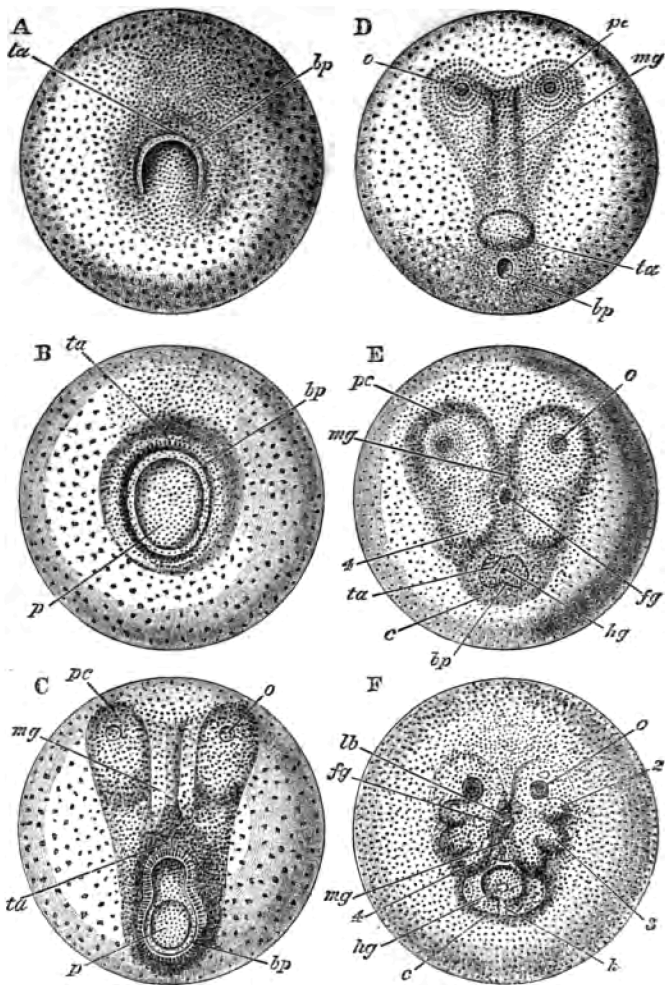


FIG. 58.—*Astacus fluviatilis*.—Surface views of the earlier stages in the development of the embryo, from the appearance of the blastopore (A) to the assumption of the nauplius form (F) (after Reichenbach, \times about 23). *bp*, blastopore; *c*, carapace; *fg*, fore-gut involution; *h*, heart; *hg*, hind-gut involution; *lb*, labrum; *mg*, medullary groove; *o*, optic pit; *p*, endodermal plug partly filling up the blastopore; *pc*, procephalic processes; *ta*, abdominal elevation; *z*, antennules; *s*, antenna; *l*, mandibles.

henceforward exhibit different tendencies from those which are possessed by the rest of the blastoderm. In fact, it is the primitive alimentary apparatus or *archenteron*, and its wall is termed the *hypoblast*. The rest of the blastoderm, on the contrary, is the primitive epidermis, and receives the name of *epiblast*. If the food-yolk were away, and the archenteron enlarged until the hypoblast came in contact with the epiblast, the entire body would be a double-walled sac, containing an alimentary cavity, with a single external aperture. This is the *gastrula* condition of the embryo; and some animals, such as the common fresh-water polype, are little more than permanent *gastrulae*.

Although the *gastrula* has not the slightest resemblance to a crayfish, yet, as soon as the hypoblast and the epiblast are thus differentiated, the foundations of some of the most important systems of organs of the future crustacean are laid. The hypoblast will give rise to the epithelial lining of the mid-gut; the epiblast (which answers to the ectoderm in the adult) to the epithelia of the fore-gut and hind-gut, to the epidermis, and to the central nervous system.

The mesodermal structures, that is to say the connective tissue, the muscles, the heart and vessels, and the reproductive organs, which lie between the ectoderm and the endoderm, are not derived directly from either the epiblast or the hypoblast, but have a *quasi*-independent origin, from a mass of cells which first makes its appear-

ance in the neighbourhood of the blastopore, between the hypoblast and the epiblast, though they are probably derived from the former. From this region they gradually spread, first over the sternal, and then on to the tergal aspect of the embryo, and constitute the *mesoblast*.

Epiblast, hypoblast, and mesoblast are at first alike constituted of nothing but nucleated cells, and they increase in dimensions by the continual fission and growth of these cells. The several layers become gradually modelled into the organs which they constitute, before the cells undergo any notable modification into tissues. A limb, for example, is, at first, a mere cellular outgrowth, or bud, composed of an outer coat of epiblast with an inner core of mesoblast; and it is only subsequently that its component cells are metamorphosed into well-defined epidermic and connective tissues, vessels and muscles.

The embryo crayfish remains only a short while in the gastrula stage, as the blastopore soon closes up, and the archenteron takes the form of a sac, flattened out between the epiblast and the food-yelk, with which its cells are in close contact (fig. 57, C and D).* Indeed, as development proceeds, the cells of the hypoblast actually feed upon the substance of the food-yelk, and turn it to account for the general nutrition of the body.

* Whether, as some observers state, the hypoblastic cells grow over and inclose the food-yelk or not, is a question that may be left open. I have not been able to satisfy myself of this fact.

The sternal area of the embryo gradually enlarges until it occupies one hemisphere of the yolk; in other words, the thickening of the epiblast gradually extends outwards. Just in front of the blastopore, as it closes, the middle of the epiblast grows out into a rounded elevation (fig. 58, *ta*; fig. 59, *ab*), which rapidly increases in length, and at the same time turns forwards. This is the rudiment of the whole abdomen of the crayfish. Further forwards, two broad and elongated, but flatter thickenings appear; one on each side of the middle line (fig. 58, *pc*). As the free end of the abdominal papilla now marks the hinder extremity of the embryo, so do these two elevations, which are termed the *procephalic lobes*, define its anterior termination. The whole sternal region of the body will be produced by the elongation of that part of the embryo which lies between these two limits.

A narrow longitudinal groove-like depression appears on the surface of the epiblast, in the middle line, between the procephalic lobes and the base of the abdominal papilla (fig. 58, C—F, *mg*). About its centre, this groove becomes further depressed by the ingrowth of the epiblast, which constitutes its floor, and gives rise to a short tubular sac, which is the rudiment of the whole fore-gut (fig. 57, C, and fig. 58, E, *fg*). At first, this epiblastic ingrowth does not communicate with the archenteron, but, after a while, its blind end combines with the front and lower part of the hypoblast, and an opening is formed by

which the cavity of the fore-gut communicates with that of the mid-gut (fig. 57, E). Thus a gullet and stomach, or rather the parts which will eventually give rise to all these, are constituted. And it is important to remark that, in comparison with the mid-gut, they are, at first, very small.

In the same way, the epiblast covering the sternal face of the abdominal papilla undergoes invagination and is converted into a narrow tube which is the origin of the whole hind-gut (fig. 57, C, and fig. 58, E, *hg*). This, like the fore-gut, is at first blind; but the shut front end soon applying itself to the hinder wall of the archenteric sac, the two coalesce and open into one another (fig. 57, E). Thus the complete alimentary canal, consisting of a very narrow, tubular, fore- and hind-gut, derived from the epiblast, and a wider and more sac-like mid-gut, formed of the whole hypoblast, is constituted.

The procephalic lobes become more convex; while, behind them, the surface of the epiblast rises into six elevations disposed in pairs, one on each side of the median groove. The hindermost of these, which lie at the sides of the mouth, are the rudiments of the mandibles (fig. 58, E and F, *4*); the other two become the antennæ (*β*) and the antennules (*α*), while, at a later period, processes of the procephalic lobes give rise to the eyestalks.

A short distance behind the abdomen, the epiblast rises into a transverse ridge, which is concave forwards,

while its ends are prolonged on each side nearly as far as the mouth. This is the commencement of the free edge of the carapace (fig. 58, E and F, and fig. 59, A, c) —the lateral parts of which, greatly enlarging, become the branchiostegites (fig. 59, D, c).

In many animals allied to crayfish, the young, when it has reached a stage in its development, which answers to this, undergoes rapid changes of outward form and of internal structure, without making any essential addition to the number of the appendages. The appendages which represent the antennules, the antennæ, and the mandibles elongate and become oar-like locomotive organs; a single median eye is developed, and the young leaves the egg as an active larva, which is known as a *Nauplius*. The crayfish, on the other hand, is wholly incapable of an independent existence at this stage, and continues its embryonic life within the egg case; but it is a remarkable circumstance that the cells of the epiblast secrete a delicate cuticula, which is subsequently shed. It is as if the animal symbolized a nauplius condition by the development of this cuticle, as the foetal whalebone whale symbolizes a toothed condition by developing teeth which are subsequently lost and never perform any function.

In fact, in the crayfish, the nauplius condition is soon left behind. The sternal disk spreads more and more over the yolk; as the region between the mouth and the root of the abdomen elongates, slight transverse

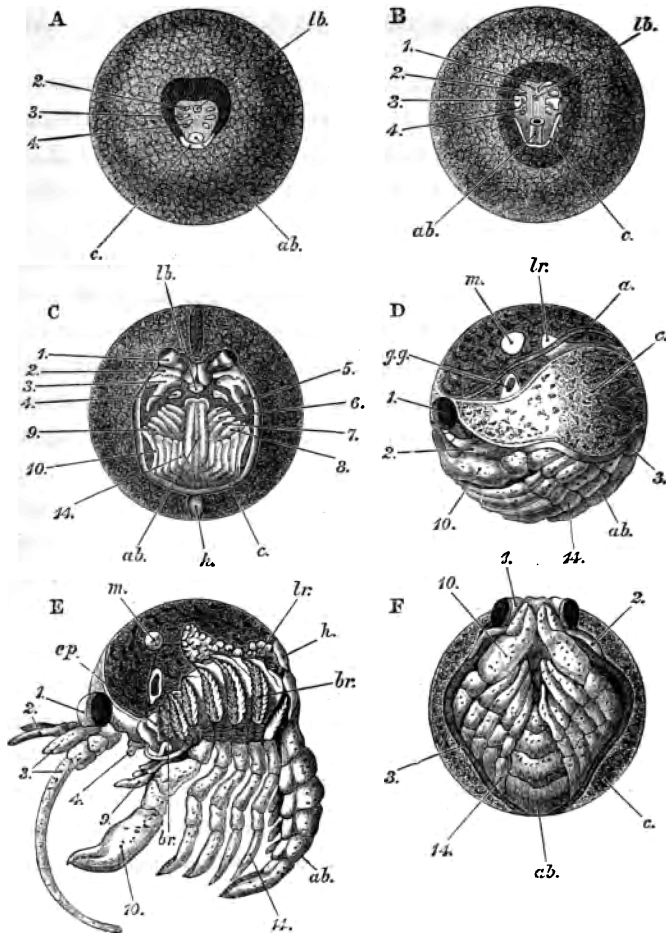


FIG. 59.—*Astacus fluviatilis*.—Ventral (A, B, C, F) and lateral (D, E) views of the embryo in successive stages of development (after Rathke, $\times 15$). A is a little more advanced than the embryo represented in fig. 58. F: D, E, and F are views of the young crayfish when nearly ready to be hatched: in E, the carapace is removed, and the limbs and abdomen are spread out. 1—14, the cephalic and thoracic appendages; ab, abdomen; br, branchiae; c, carapace; cp, epipodite of the first maxillipede; gg, green gland; h, heart; lb, labrum; lr, liver; m, mandibular muscles.

depressions indicate the boundaries of the posterior cephalic and the thoracic somites; and pairs of elevations, similar to the rudiments of the antennules and antennæ, appear upon them in regular order from before backwards (fig. 59, C).

In the meanwhile, the extremity of the abdomen flattens out and takes on the form of an oval plate, the middle of the posterior margin of which is slightly truncated or notched; while, finally, transverse constrictions mark off six segments, the somites of the abdomen, in front of this. Along with these changes, four pairs of tubercles grow out from the sternal faces of the four middle abdominal somites, and constitute the rudiments of the four middle pairs of abdominal appendages. The first abdominal somite exhibits only two hardly perceptible elevations in place of the appendages of the others, while the sixth seems, at first, to have none. The appendages of the sixth somite, however, are already formed, though, singularly enough, they lie beneath the cuticle of the telson and are set free only after the first ecdysis.

The rostrum grows out between the procephalic lobes; it remains relatively very short up to the time that the young crayfish quits the egg, and is directed more downwards than forwards. The lateral portions of the carapacial ridge, becoming deeper, are converted into the branchiostegites, and the cavities which they overarch are the branchial chambers. The transverse portion of

the ridge, on the other hand, remains relatively short, and constitutes the free posterior margin of the carapace.

As these changes take place, the abdomen and the sternal region of the thorax are constantly enlarging in proportion to the rest of the ovum; and the food-yelk which lies in the cephalothorax is, *pari passu*, being diminished. Hence the cephalothorax constantly becomes relatively smaller and the tergal aspect of the carapace less spherical; although, even when the young crayfish is ready to be hatched, the difference between it and the adult in the form of the cephalothoracic region, and in the size of the latter relatively to the abdomen, is very marked.

The simple bud-like outgrowths of the somites, in which all the appendages take their origin, are rapidly metamorphosed. The eyestalks (fig. 59, 1) soon attain a considerable relative size. The extremities of the antennules (2) and of the antennæ (3) become bifurcated; and the two divisions of the antennule remain broad, thick, and of nearly the same size up to birth. On the other hand, the inner or endopoditic division of the antenna becomes immensely lengthened, and at the same time annulated, while the outer or exopoditic division remains relatively short, and acquires its characteristic scale-like form.

The labrum (*l*) arises as a prolongation of the middle sternal region in front of the mouth, while the bilobed metastoma is an outgrowth of the sternal region behind it.

The posterior cephalic and the thoracic appendages (5—14) elongate and gradually approach the form which they possess in the adult. I have not been able to discover, at any period of development, an outer division or exopodite in any of the five posterior thoracic limbs. And this is a very remarkable circumstance, inasmuch as such an exopodite exists in the closely allied lobster in the larval state; and, in many of the shrimp and prawn-like allies of the crayfish, a complete or rudimentary exopodite is found in these limbs, even in the adult condition.

When the crayfish is hatched (fig. 60) it differs from the adult in many ways—not only is the cephalothorax more convex and larger in proportion to the abdomen; but the rostrum is short and bent down between the eyes. The sterna of the thorax are wider relatively, and hence there is a greater interval between the bases of the legs than in the adult. The proportion of the limbs to one another and to the body are nearly the same as in the adult, but the chelæ of the forceps are more slender. The tips of the chelæ are all strongly incurved (fig. 8, B, p. 41), and the dactylopodites of the two posterior thoracic limbs are hook-like. The appendages of the first abdominal somite are undeveloped, and those of the last are inclosed within the telson, which is, as has already been said, of a broad oval form, usually notched in the middle of its hinder margin, and devoid of any indication of transverse division. Its margins are produced into a single series of short conical

processes, and the disposition of the vascular canals in its interior gives it the appearance of being radially striated.

The setæ, so abundant in the adult, are very scanty in the newly hatched young; and the great majority of those which exist are simple conical prolongations of the un-

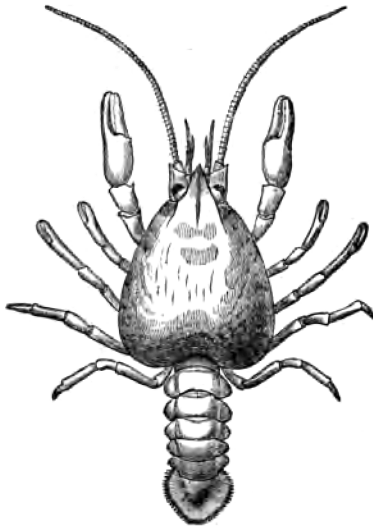


FIG. 60.—*Astacus fluviatilis*.—Newly-hatched young ($\times 6$).

calcified cuticle, the bases of which are not sunk in pits and which are devoid of lateral scales or processes.

The young animals are firmly attached to the abdominal appendages of the parent in the manner already described. They are very sluggish, though they move when touched; and at this period they do not feed, but

are nourished by the food-yelk, of which a considerable store still remains in the cephalothorax.

I imagine that they are set free during the first ecdysis, and that the appendages of the sixth abdominal somite are at that time expanded, but nothing is definitely known at present of these changes.

The foregoing sketch of the general nature of the changes which take place in the egg of the crayfish suffice to show that its development is, in the strictest sense of the word, a process of evolution. The egg is a relatively homogeneous mass of living protoplasmic matter, containing much nutritive material; and the development of the crayfish means the gradual conversion of this comparatively simple body into an organism of great complexity. The yelk becomes differentiated into formative and nutritive portions. The formative portion is subdivided into histological units: these arrange themselves into a blastodermic vesicle; the blastoderm becomes differentiated into epiblast, hypoblast, and mesoblast; and the simple vesicle assumes the gastrula condition. The layers of the gastrula shape themselves into the body of the crayfish and its appendages, while along with this, the cells of which all the parts are built, become metamorphosed into tissues, each with its characteristic properties. And all these wonderful changes are the necessary consequences of the interaction of the molecular forces resident in the substance of the

impregnated ovum, with the conditions to which it is exposed; just as the forms evolved from a crystallising fluid are dependent upon the chemical composition of the dissolved matter and the influence of surrounding conditions.

Without entering into details which lie beyond the scope of the present work, something must be said respecting the manner in which the complicated internal organisation of the crayfish is evolved from the cellular double sac of the gastrula stage.

It has been seen that the fore-gut is at first an insignificant tubular involution of the epiblast in the region of the mouth. It is, in fact, a part of the epiblast turned inwards, and the cells of which it is composed secrete a thin cuticular layer, as do those of the rest of the epiblast, which gives rise to the ectodermal or epidermic part of the integument. As the embryo grows, the fore-gut enlarges much faster than the mid-gut, increasing in height and from before backwards, while its side-walls remain parallel, and are separated by only a narrow cavity. At length, it takes on the shape of a triangular bag (fig. 57, D, *fg*), attached by its narrow end around the mouth and immersed in the food-yelk, which it gradually divides into two lobes, one on the right and one on the left side. At the same time a vertical plate of mesoblastic tissue, from which the great anterior and posterior muscles are eventually developed, connects it with the roof and with the front wall of the carapace.

Becoming constricted in the middle, the fore-gut next appears to consist of two dilatations of about equal size, connected by a narrower passage (fig. 57, E, *fg*¹, *fg*²). The front dilatation becomes the œsophagus and the cardiac division of the stomach; the hinder one, the pyloric division. At the sides of the front end of the cardiac division two small pouches are formed shortly after birth; in each of these a thick laminated deposit of chitin takes place, and constitutes a minute crab's-eye or gastrolith, which has the same structure as in the adult, and is largely calcified. This fact is the more remarkable as, at this time, the exoskeleton contains very little calcareous deposit. In the position of the gastric teeth, folds of the cellular wall of corresponding shape are formed, and the chitinous cuticle of which the teeth are composed is, as it were, modelled upon them.

The hind-gut occupies the whole length of the abdomen, and its cells early arrange themselves into six ridges, and secrete a cuticular layer.

The mid-gut, or hypoblastic sac, very soon gives off numerous small prolongations on each side of its hinder extremity, and these are converted into the cæca of the liver (fig. 57, E, *mg*). The cells of its tergal wall are in close contact with the adjacent masses of food-yolk; and it is probable that the gradual absorption of the food-yolk is chiefly effected by these cells. At birth, however, the lateral lobes of the food-yolk are still large, and occupy the space left between the stomach and liver

on the one hand, and the cephalic integument on the other.

The mesoblastic cells give rise to the layer of connective tissue which forms the deeper portion of the integument, and to that which invests the alimentary canal; to all the muscles; and to the heart, the vessels, and the corpuscles of the blood. The heart appears very early as a solid mass of mesoblastic cells in the tergal region of the thorax, just in front of the origin of the abdomen (figs. 57, 58, 59, *h*). It soon becomes hollow, and its walls exhibit rhythmical contractions.

The branchiæ are, at first, simple papillæ of the integument of the region from which they take their rise. These papillæ elongate into stems, which give off lateral filaments. The podobranchiæ are at first similar to the arthrobranchiæ, but an outgrowth soon takes place near the free end of the stem, and becomes the lamina, while the attached end enlarges into the base.

The renal organ is stated to arise by a tubular involution of the epiblast, which soon becomes convoluted, and gives rise to the green gland.

The central nervous system is wholly a product of the epiblast. The cells which lie at the sides of the longitudinal groove already mentioned (fig. 58, *mg*), grow inwards, and give rise to two cords which are at first separate from one another and continuous with the rest of the epiblast. At the front end of the groove a

depression arises, and its cells form a mass which connects these two cords in front of the mouth, and gives rise to the cerebral ganglia. The epiblastic linings of two small pits (fig. 58, *o*) which appear very early on the surface of the procephalic lobes, are also carried inwards in the same way, and, uniting with the foregoing, produce the optic ganglia.

The cells of the longitudinal cords become differentiated into nerve fibres and nerve cells, and the latter, gathering towards certain points, give rise to the ganglia which eventually unite in the middle line. By degrees, the ingrowth of epiblastic cells, from which all these structures are developed, becomes completely separated from the rest of the epiblast, and is invested by mesoblastic cells. The central nervous system, therefore, in a crayfish, as in a vertebrated animal, is at first, as a part of the ectoderm, morphologically one with the epidermis; and the deep and protected position which it occupies in the adult is only a consequence of the mode in which the nervous portion of the ectoderm grows inwards and becomes detached from the epidermic portion.

The visual rods of the eye are merely modified cells of the ectoderm. The auditory sac is formed by an involution of the ectoderm of the basal joint of the antennule. At birth it is a shallow wide-mouthed depression, and contains no otoliths.

Lastly, the reproductive organs result from the segregation and special modification of cells of the mesoblast

behind the liver. Rathke states that the sexual apertures are not visible until the young crayfish has attained the length of an inch; and that the first pair of abdominal appendages of the male appear still later in the form of two papillæ, which gradually elongate and take on their characteristic forms.

CHAPTER V.

THE COMPARATIVE MORPHOLOGY OF THE CRAYFISH.—THE STRUCTURE AND THE DEVELOPMENT OF THE CRAYFISH COMPARED WITH THOSE OF OTHER LIVING BEINGS.

Up to this point, our attention has been directed almost exclusively to the common English crayfish. Except in so far as the crayfish is dependent for its maintenance upon other animals, or upon plants, we might have ignored the existence of all living things except crayfishes. But, it is hardly necessary to observe, that innumerable hosts of other forms of life not only tenant the waters and the dry land, but throng the air; and that all the crayfishes in the world constitute a hardly appreciable fraction of its total living population.

Common observation leads us to see that these multitudinous living beings differ from not-living things in many ways; and when the analysis of these differences is pushed as far as we are at present able to carry it, it shews us that all living beings agree with the crayfish and differ from not-living things in the same particulars. Like the crayfish, they are constantly wasting away by

oxidation, and repairing themselves by taking into their substance the matters which serve them for food ; like the crayfish, they shape themselves according to a definite pattern of external form and internal structure ; like the crayfish, they give off germs which grow and develop into the shapes characteristic of the adult. No mineral matter is maintained in this fashion ; nor grows in the same way ; nor undergoes this kind of development ; nor multiplies its kind by any such process of reproduction.

Again, common observation early leads to the discrimination of living things into two great divisions. Nobody confounds ordinary animals with ordinary plants, nor doubts that the crayfish belongs to the former category and the waterweed to the latter. If a living thing moves and possesses a digestive receptacle, it is held to be an animal ; if it is motionless and draws its nourishment directly from the substances which are in contact with its outer surface, it is held to be a plant. We need not inquire, at present, how far this rough definition of the differences which separate animals from plants holds good. Accepting it for the moment, it is obvious that the crayfish is unquestionably an animal,—as much an animal as the vole, the perch, and the pond-snail, which inhabit the same waters. Moreover, the crayfish has, in common with these animals, not merely the motor and digestive powers characteristic of animality, but they all, like it, possess a complete alimentary canal ; special appa-

ratus for the circulation and the aëration of the blood; a nervous system with sense-organs; muscles and motor mechanisms; reproductive organs. Regarded as pieces of physiological apparatus, there is a striking similarity between all three. But, as has already been hinted in the preceding chapter, if we look at them from a purely morphological point of view, the differences between the crayfish, the perch, and the pond-snail, appear at first sight so great, that it may be difficult to imagine that the plan of structure of the first can have any relation to that of either of the last two. On the other hand, if the crayfish is compared with the water-beetle, notwithstanding wide differences, many points of similarity between the two will manifest themselves; while, if a small lobster is set side by side with a crayfish, an unpractised observer, though he will readily see that the two animals are somewhat different, may be a long time in making out the exact nature of the differences.

Thus there are degrees of likeness and unlikeness among animals, in respect of their outward form and internal structure, or, in other words, in their morphology. The lobster is very like a crayfish, the beetle is remotely like one; the pond-snail and the perch are extremely unlike crayfishes. Facts of this kind are commonly expressed in the language of zoologists, by saying that the lobster and the crayfish are closely allied forms; that the beetle and the crayfish present a remote affinity; and that there is no affinity between the

crayfish and the pond-snail, or the crayfish and the perch.

The exact determination of the resemblances and differences of animal forms by the comparison of the structure and the development of one with those of another, is the business of comparative morphology. Morphological comparison, fully and thoroughly worked out, furnishes us with the means of estimating the position of any one animal in relation to all the rest; while it shews us with what forms that animal is nearly, and with what it is remotely, allied: applied to all animals, it furnishes us with a kind of map, upon which animals are arranged in the order of their respective affinities; or a classification, in which they are grouped in that order. For the purpose of developing the results of comparative morphology in the case of the crayfish, it will be convenient to bring together, in a summary form, those points of form and structure, many of which have already been referred to and which characterise it as a separate kind of animal.

Full-grown English crayfishes usually measure about three inches and a half from the extremity of the rostrum in front to that of the telson behind. The largest specimen I have met with measured four inches.* The

* The dimensions of crayfishes at successive ages given at p. 31, beginning at the words "By the end of the year," refer to the "*écrevisse à pieds rouges*" of France; not to the English crayfish, which is

males are commonly somewhat larger, and they almost always have longer and stronger forceps than the females. The general colour of the integument varies from a light reddish-brown to a dark olive-green; and the hue of the tergal surface of the body and limbs is always deeper than that of the sternal surface, which is often light yellowish-green, with more or less red at the extremities of the forceps. The greenish hue of the sternal surface occasionally passes into yellow in the thorax and into blue in the abdomen.

The distance from the orbit to the posterior margin of the carapace is nearly equal to that from the posterior margin of the carapace to the base of the telson, when the abdomen is fully extended, but this measurement of the carapace is commonly greater than that of the abdomen in the males and less in the females.

The general contour of the carapace (fig. 61), without the rostrum, is that of an oval, truncated at the ends: the anterior end being narrower than the posterior. Its surface is evenly arched from side to side. The greatest breadth of the carapace lies midway between the cervical groove and its posterior edge. Its greatest vertical depth is on a level with the transverse portion of the cervical groove.

The length of the rostrum, measured from the orbit

considerably smaller. Doubtless, the proportional rate of increment is much the same, in the two kinds; but in the English crayfish it has not been actually ascertained.

to its extremity, is greater than half the distance from the orbit to the cervical groove. It is trihedral in section, and its free end is slightly curved upwards (fig. 41). It gradually becomes narrower for about three-fourths of its whole length. At this point it has rather less than half the width which it has at its base (fig. 61, A); and its raised, granular and sometimes distinctly serrated margins are produced into two obliquely directed spines, one on each side. Beyond these, the rostrum rapidly narrows to a fine point; and this part of the rostrum is equal in length to the width between the two spines.

The tergal surface of the rostrum is flattened and slightly excavated from side to side, except in its anterior half, where it presents a granular or finely serrated median ridge, which gradually passes into a low elevation in the posterior half, and, as such, may generally be traced on to the cephalic region of the carapace. The inclined sides of the rostrum meet ventrally in a sharp edge, convex from before backwards; the posterior half of this edge gives rise to a small, usually bifurcated, spine, which descends between the eye-stalks (fig. 41). The raised and granulated lateral margins of the rostrum are continued back on to the carapace for a short distance, as two linear ridges (fig. 61, A). Parallel with each of these ridges, and close to it, there is another longitudinal elevation (*a*, *b*), the anterior end of which is raised into a prominent spine (*a*), which is situated immediately behind the orbit, and may, therefore, be termed the *post-orbital*

spine. The elevation itself may be distinguished as the *post-orbital ridge*. The flattened surface of this ridge is marked by a longitudinal depression or groove. The

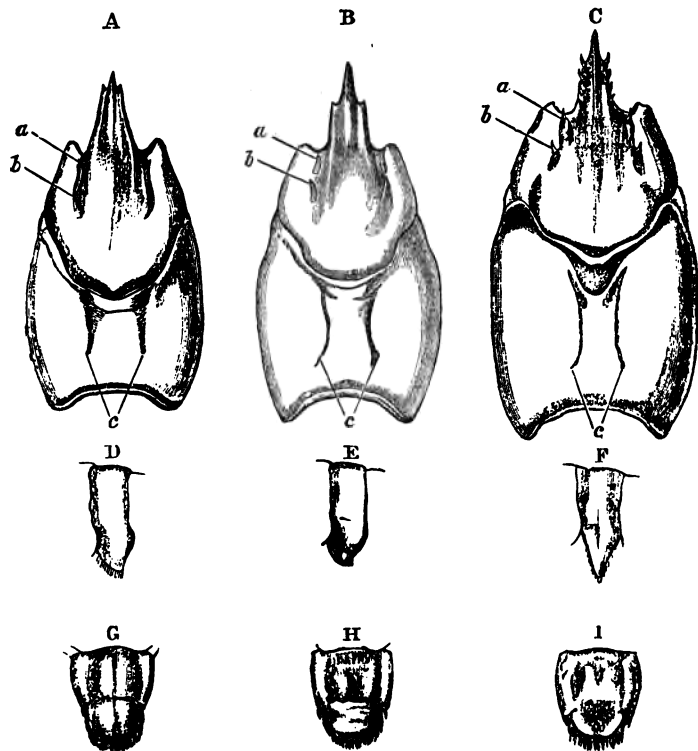


FIG. 61.—A, D, & G, *Astacus torrentium*; B, E, & H, *A. nobilis*; C, F, & I, *A. nigrescens* (nat. size). A—C, Dorsal views of carapace; D—F, side views of third abdominal somites; G—I, Dorsal views of telson. *a*, *b*, post-orbital ridge and spines; *c*, branchio-cardiac grooves inclosing the areola.

posterior end of the ridge passes into a somewhat broader and less marked elevation, the hinder end of which turns inwards, and then comes to an end at a point midway between the orbit and the cervical groove. Generally this hinder elevation appears like a mere continuation of the post-orbital ridge; but, sometimes, the two are separated by a distinct depression. I have never seen any prominent spine upon the posterior elevation, though it is sometimes minutely spinulose. The post-orbital ridges of each side, viewed together, give rise to a characteristic lyrate mark upon the cephalic region of the carapace.

A faintly marked, curved, linear depression runs from the hinder end of the post-orbital ridge, at first directly downwards, and then curves backwards to the cervical groove. It corresponds with the anterior and inferior boundary of the attachment of the adductor muscle of the mandible.

Below the level of this, and immediately behind the cervical groove, there are usually three spines, arranged in a series, which follow the cervical groove. The points of all are directed obliquely forwards, and the lowest is the largest. Sometimes there is only one prominent spine, with one or two very small ones; sometimes there are as many as five of these *cervical spines*.

The cardiac region is marked out by two grooves which run backwards from the cervical groove (fig. 61, A, c), and terminate at a considerable distance from the posterior

edge of the carapace. Each groove runs, at first, obliquely inwards, and then takes a straight course parallel with its fellow. The area thus defined is termed the *areola*; its breadth is equal to about one-third of the total transverse diameter of the carapace in this region.

No such distinct lines indicate the lateral boundary of the region in front of the cervical groove which answers to the stomach. But the middle part of the carapace, or that which is comprised in the gastric and cardiac regions, has its surface sculptured in a different way from the branchiostegites and the lateral regions of the head. In the former, the surface is excavated by shallow pits, separated by relatively broad flat-topped ridges; but, in the latter, the ridges become more prominent, and take the form of tubercles, the apices of which are directed forwards. Minute setæ spring from the depressions between these tubercles.

The branchiostegite has a thickened rim, which is strongest below and behind (fig. 1). The free edge of this rim is fringed with close-set setæ.

The pleura of the second to the sixth abdominal somites are broadly lanceolate and obtusely pointed at their free ends (fig. 61, D); the anterior edge is longer and more convex than the posterior edge. In the females, the pleura are larger, and are directed more outwards and less downwards than in the males. The pleura of the second somite are much larger than the rest, and overlap the very small pleura of the first somite (fig. 1). The

pleura of the sixth somite are narrow, and their posterior edges are concave.

The pits and setæ of the cuticle which clothes the tergal surfaces of the abdominal somites are so few and scattered, that the latter appear almost smooth. In the telson, however, especially in its posterior division, the markings are coarser and the setæ more apparent.

The telson (fig. 61, G) presents an anterior quadrate division and a posterior half-oval part, the free curved edge of which is beset with long setæ, and is sometimes slightly notched in the middle. The posterior division is freely movable upon the anterior, in consequence of the thinness and pliability of the cuticle along a transverse line which joins the postero-external angles of the anterior division, each of which is produced into two strong spines, of which the outer is the longer. The length of the posterior division of the telson, measured from the middle of the suture, is equal to, or but very little less than, that of the anterior division.

On the under side of the head, the basal joints of the antennules are visible, internal to those of the antennæ, but the attachment of the latter is behind and below that of the former (fig. 3, A). Behind these, and in front of the mouth, the epistoma (fig. 39, A, II, III) presents a broad area of a pentagonal form. The posterior boundary of this area is formed by two thickened transverse ridges, which meet on the middle line at a very open angle, the apex of which is turned forwards.

The posterior edges of these ridges are continuous with the labrum. The anterior margin is produced in the middle into a *fleur de lys* shaped process, the summit of which terminates between the antennules. At the sides of this process, the anterior margin of the epistoma is deeply excavated to receive the basal joints of the antennæ. Following the contours of these excavated margins, the surface of the epistoma presents two lateral convexities. The widest and most prominent part of each of these lies towards the outer edge of the epistoma, and is produced into a conical spine. Sometimes there is a second smaller spine beside the principal one. Between the two convexities lies a triangular median depressed area.

The distance from the apex of the anterior median process to the posterior ridge is equal to a little more than half the width of the epistoma.

The corneal surface of the eye is transversely elongated and reniform, and its pigment is black. The eye-stalks are much broader at their bases than at their corneal ends (fig. 48, A). The antennules are about twice as long as the rostrum. The tergal surface of the trihedral basal joint of the antennule, on which the eye-stalk rests, is concave; the outer surface is convex, the inner flat (figs. 26, A, and 48, B). Near the anterior end of the sternal edge which separates the two latter faces, there is a strong curved spine directed forwards (fig. 48, B, a). When the setæ, which proceed from the outer edge of

the auditory aperture and hide it, are removed, it is seen to be a wide, somewhat triangular cleft, which occupies the greater part of the hinder half of the tergal surface of the basal joint (fig. 26, A).

The exopodites, or squames, of the antennæ extend as far as the apex of the rostrum, or even project beyond it, when they are turned forwards, while they reach to the commencement of the filament of the endopodite (*Frontis-piece*). The squame is fully twice as long as it is broad, with a general convexity of its tergal and concavity of its sternal surface. The outer edge is straight and thick, the inner, which is fringed with long setæ, is convex and thin (fig. 48, C). Where these two edges join in front, the squame is produced into a strong spine. A thick outer portion of the squame is marked off from the thinner inner portion by a longitudinal groove on the tergal side, and by a strong ridge on the sternal side. One or two small spines generally project from the posterior and external angle of the squame; but they may be very small or absent in individual specimens. Close beneath these, the outer angle of the next joint is produced into a strong spine. When the abdomen is straightened out, if the antennæ are turned back as far as they will go without damage, the ends of their filaments usually reach the tergum of the third somite of the abdomen (*Frontis-piece*). I have not observed any difference between the sexes in this respect.

The inner edge of the ischiopodite of the third maxilli-

pede is strongly serrated and wider in front than behind (fig. 44); the meropodite possesses four or five spines in the same region; and there are one or two spines at the distal end of the carpopodite. When straightened out, the maxillipedes extend as far as, or even beyond, the end of the rostrum.

The inner or sternal edge of the ischiopodite of the forceps is serrated; that of the meropodite presents two rows of spines, the inner small and numerous, the outer large and few. There are several strong spines at the anterior end of the outer or tergal face of this joint. The carpopodite has two strong spines on its under or sternal surface, while its sharp inner edge presents many strong spines. Its upper surface is marked by a longitudinal depression, and is beset with sharp tubercles. The length of the propodite, from its base to the extremity of the fixed claw of the chela, measures rather more than twice as much as the extreme breadth of its base, the thickness of which is less than a third of this length (fig. 20, p. 93). The external angular process, or fixed claw, is of the same length as the base, or a little shorter. Its inner edge is sharp and spinose, and the outer more rounded and simply tuberculated. The apex of the fixed claw is produced into a slightly incurved spine. Its inner edge has a sinuous curvature, convex posteriorly, concave anteriorly, and bears a series of rounded tubercles, of which one near the summit of the convexity, and one near the apex of the claw, are the most prominent.

The apex of the dactylopodite, like that of the propodite, is formed by a slightly incurved spine (fig. 20), while its outer, sharper, edge presents a curvature, the inverse of that of the edge of the fixed claw against which it is applied. This edge is beset with rounded tubercles, the most prominent of which are one at the beginning, and one at the end of the concave posterior moiety of the edge. When the dactylopodite is brought up to the fixed claw, these tubercles lie, one in front of and one behind the chief tubercle of the convexity of the latter. The whole surface of the propodite and dactylopodite is covered with minute elevations, those of the upper surface being much more prominent than those of the lower surface.

The length of the fully extended forceps generally equals the distance between the posterior margin of the orbit and the base of the telson, in well characterized males; and, in individual examples, they are even longer; while it may not be greater than the distance between the orbit and the hinder edge of the fourth abdominal somite, in females; and, in massiveness and strength, the difference of the forceps in the two sexes is still more remarkable (fig. 2). Moreover there is a good deal of variation in the form and size of the chelæ in individual males. The right and left chelæ present no important differences.

The ischiopodites of the four succeeding thoracic limbs are devoid of any recurved spines in either sex (*Front.*, fig. 46). The first pair are the stoutest, the second the

longest: and when the latter are spread out at right angles to the body, the distance from tip to tip of the dactylopodites is equal to, or rather greater than, the extreme length of the body from the apex of the rostrum to the posterior edge of the telson, in both sexes. In both sexes, the length of the swimmerets hardly exceeds half the transverse diameter of the somites to which they are attached.

The exopodites of the appendages of the sixth abdominal somite (the extreme length of which is rather greater than that of the telson) are divided into a larger proximal, and a smaller distal portion (fig. 37, F, p. 144). The latter is about half as long as the former, and has a rounded free edge, setose like that of the telson. There is a complete flexible hinge between the two portions, and the overlapping free edge of the proximal portion, which is slightly concave, is beset with conical spines, the outermost of which are the longest. The endopodite has a spine at the junction of its outer straight edge with the terminal setose convex edge. A faintly marked longitudinal median ridge, or keel, ends close to the margin in a minute spine. The tergal distal edge of the protopodite is deeply bilobed, and the inner lobe ends in two spines, while the outer, shorter and broader lobe, is minutely serrated.

In addition to the characters distinctive of sex, which have already been fully detailed (pp. 7, 20, and 145), there is a marked difference in the form of the sterna of the three posterior thoracic somites between the males and females.

Comparing a male and a female of the same size, the triangular area between the bases of the penultimate and ante-penultimate thoracic limbs is considerably broader at the base in the female. In both sexes, the hinder part of the penultimate sternum is a rounded transverse ridge separated by a groove from the anterior part; but this ridge is much larger and more prominent in the female than in the male, and it is often obscurely divided into two lobes by a median depression. Moreover, there are but few setæ on this region in the female; while, in the male, the setæ are long and numerous.

The sternum of the last thoracic somite of the female is divided by a transverse groove into two parts, of which the posterior, viewed from the sternal aspect, has the form of a transverse elongated ridge, which narrows to each end, is moderately convex in the middle, and is almost free from setæ. In the male, the corresponding posterior division of the last thoracic sternum is produced downwards and forwards into a rounded eminence which gives attachment to a sort of brush of long setæ (fig. 35, p. 136).

The importance of this long enumeration of minute details* will appear by and by. It is simply a statement of the more obvious external characters in which all the full-grown English crayfishes which have come under my

* The student of systematic zoology will find the comparison of a lobster with a crayfish in all the points mentioned to be an excellent training of the faculty of observation.

notice agree. No one of these individual crayfishes was exactly like the other; and to give an account of any single crayfish as it existed in nature, its special peculiarities must be added to the list of characters given above; which, considered together with the facts of structure discussed in previous chapters, constitutes a definition, or diagnosis, of the English kind, or *species*, of crayfish. It follows that the species, regarded as the sum of the morphological characters in question and nothing else, does not exist in nature; but that it is an abstraction, obtained by separating the structural characters in which the actual existences—the individual crayfishes—agree, from those in which they differ, and neglecting the latter.

A diagram, embodying the totality of the structural characters thus determined by observation to be common to all our crayfishes, might be constructed; and it would be a picture of nothing which ever existed in nature; though it would serve as a very complete plan of the structure of all the crayfishes which are to be found in this country. The morphological definition of a species is, in fact, nothing but a description of the plan of structure which characterises all the individuals of that species.

California is separated from these islands by a third of the circumference of the globe, one-half of the interval being occupied by the broad North Atlantic ocean. The fresh waters of California, however, contain crayfishes which are

so like our own, that it is necessary to compare the two in every point mentioned in the foregoing description in order to estimate the value of the differences which they present. Thus, to take one of the kinds of crayfishes found in California, which has been called *Astacus nigrescens*; the general structure of the animal may be described in precisely the same terms as those used for the English crayfish. Even the branchiæ present no important difference, except that the rudimentary pleurobranchiæ are rather more conspicuous; and that there is a third small one, in front of the two which correspond with those possessed by the English crayfish.

The Californian crayfish is larger and somewhat differently coloured, the undersides of the forceps particularly presenting a red hue. The limbs, and especially the forceps of the males, are relatively longer; the chelæ of the forceps have more slender proportions; the areola is narrower relatively to the transverse diameter of the carapace (fig. 61, C). More definite distinctions are to be found in the rostrum, which is almost parallel-sided for two-thirds of its length, then gives off two strong lateral spines and suddenly narrows to its apex. Behind these spines, the raised lateral edges of the rostrum present five or six other spines which diminish in size from before backwards. The postorbital spine is very prominent, but the ridge is represented, in front, by the base of this spine, which is slightly grooved; and behind, by a distinct spine which is not so strong as the postorbital spine.

There are no cervical spines, and the middle part of the cervical groove is angulated backwards instead of being transverse.

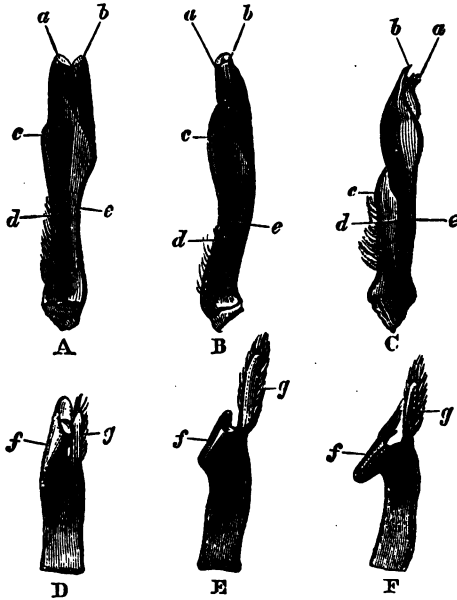


FIG. 62. A & D, *Astacus torrentium*; B & E, *A. nooilis*; C & F, *A. nigrescens*. A—C, 1st abdominal appendage of the male; D—F, endopodite of second appendage ($\times 3$). *a*, anterior, and *b*, posterior rolled edge; *c*, *d*, *e*, corresponding parts of the appendages in each species; *f*, rolled plate of endopodite; *g*, terminal division of endopodite.

The abdominal pleura are narrow, equal-sided, and acutely pointed in the males (fig. 61, F)—slightly broader, more obtuse, and with the anterior edges

rather more convex than the posterior, in the females. The tergal surface of the telson is not divided into two parts by a suture (fig. 61, I). The anterior process of the epistoma is of a broad rhomboidal shape, and there are no distinct lateral spines.

The squame of the antenna is not so broad relatively to its length; its inner edge is less convex, and its outer edge is slightly concave; the outer basal angle is sharp but not produced into a spine. The opposed edges of the fixed and movable claws of the chelæ of the forceps are almost straight and present no conspicuous tubercles. In the males, the forceps are vastly larger than in the females, and the two claws of the chelæ are bowed out, so that a wide interval is left when their apices are applied together; in the females, the claws are straight and the edges fit together, leaving no interval. Both the upper and the under surfaces of the claws are almost smooth. The median ridge of the endopodite of the sixth abdominal appendage is more marked, and ends close to the margin in a small prominent spine.

In the females, the posterior division of the sternum of the penultimate thoracic somite is prominent and deeply bilobed; and there are some small differences in form in the abdominal appendages of the males. More especially, the rolled inner process of the endopodite of the second appendage (fig. 62 F, *f*) is disposed very obliquely, and its open mouth is on a level with the base of the jointed part of the endopodite (*g*) instead of reaching almost to

the free end of the latter and being nearly parallel with it. In the first appendage (C), the anterior rolled edge (*a*) more closely embraces the posterior (*b*), and the groove is more completely converted into a tube.

It will be observed that the differences between the English and the Californian crayfishes amount to exceedingly little; but, on the assumption that these differences are constant, and that no transitional forms between the English and the Californian crayfishes are to be met with, the individuals which present the characteristic peculiarities of the latter are said to form a distinct species, *Astacus nigrescens*; and the definition of that species is, like that of the English species, a morphological abstraction, embodying an account of the plan of that species, so far as it is distinct from that of other crayfishes.

We shall see by and by that there are sundry other kinds of crayfishes, which differ no more from the English or the Californian kinds, than these do from one another; and, therefore, they are all grouped as species of the one genus, *Astacus*.

If, leaving California, we cross the Rocky Mountains and enter the eastern States of the North American Union, many sorts of crayfishes, which would at once be recognised as such by any English visitor, will be found to be abundant. But on careful examination it will be discovered that all of these differ, both from the English crayfish, and from *Astacus nigrescens*, to a much greater

extent than those do from one another. The gills are, in fact, reduced to seventeen on each side, in consequence

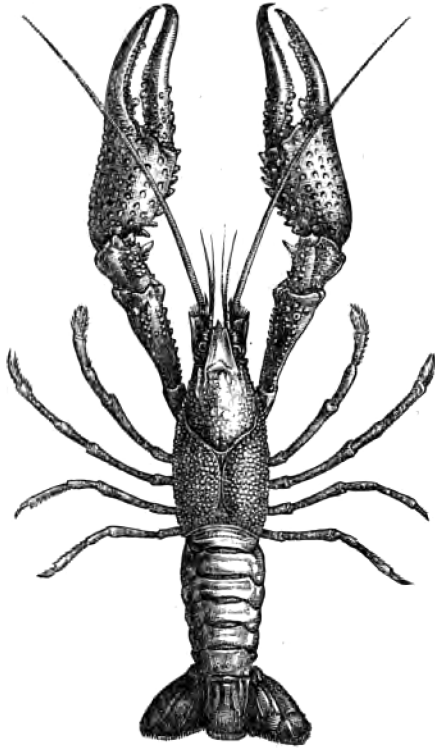


FIG. 63. *Cambarus Clarkii*, male ($\frac{1}{2}$ nat. size), after Hagen.

of the absence of the pleuro-branchia of the last thoracic somite; and there are some other differences to which it is not needful to refer at present. It is convenient to