A THEORY OF THE FORMATION OF ANIMALS

BY

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WITH 98 ILLUSTRATIONS IN THE TEXT
AND 7 FULL-PAGE PLATES

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PREFACE

It would be impossible to record the names of all the many friends who, either directly or indirectly, have given me help in the production of this book. But there are two names which should be mentioned, namely, those of Dr. Alipow, whom I met at Halle, and Dr. Muller, formerly of Hong Kong, because through their exceptional acts of kindness to me in difficult times the beginnings of the book were made. I am glad to have an opportunity of recording my gratitude to them. In more recent years I have received much help from friends in the Departments of Anatomy and Zoology of the University of Birmingham, and from my co-workers in the Pathological Laboratory of the General Hospital. It is a pleasure to acknowledge their help and the encouragement given me by many other friends too, as well as to praise the care and trouble which the publishers have taken in producing this small volume.

The style of the book is not intended to be dogmatic, even if it may appear to be so. It is necessary to state one's own convictions as clearly as one can in order that the reader may follow the argument. Although the writer may feel convinced of the correctness of his own views, it by no means follows that the reader will agree—in fact, publication is in part a method of ascertaining the views of other people.

A medical training is a most valuable asset for a work of this sort. The course necessitates the careful study of Man (who is one of the most complex animals) in every detail of his structure, development, and physiology; the vast amount of information already acquired in these spheres is being amplified and added to almost daily. Then in the study of Pathology we have the further advantage of meeting experiments of nature and deviations from the usual course of events or of structure. And in Pharmacology and its specialized branch—Anæsthetics—the physical structure of protoplasm itself is brought into view. The advances in all these subjects during recent years have been great, but we are dazzled by the vision of what we persuade ourselves that we know, rather than astounded at the vastness of what we do not know.

It may be a truism to say that the prime mover in any voluntary act is an idea, but nevertheless such a statement implies that the object of a theory is that it should lead to action.

The evidence given in support of the theory is not very uniform; it is like a short row of beads on a thread, with wide gaps between the beads. It is my hope that other beads may be found which when threaded on the cord will make a complete ornament. The method for finding beads is, " Be as imaginative as you please, but control your deductions by facts in Nature observed as accurately as possible." If the beads fit in, and prove to be gems, so much the better for the adornment of Science.

The absence of a bibliography and the entire disregard of contemporary views have no more significance than that they indicate the inability of the writer to deal with such matters.

BIRMINGHAM.
December, 1931.

LIST OF ILLUSTRATIONS

PLATES

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PLATES

ERRATA

Page 13 (line 9).—*Read* " German " *for* " French ".

Page 84 (line 30).—*Read* " urohyal " *for* " hypohyal ".

A THEORY OF THE FORMATION OF ANIMALS

CHAPTER I

INTRODUCTION

THE effect of Life on the Earth has been to transform this planet's rough and barren surface into all manner of picturesque and beautiful scenery, and to people its lands and waters with a multitude of plants and animals. We who live now, have the pleasure of seeing these in what is probably the greatest perfection to which they have attained.

Of the cause of Life nothing is known, but without doubt water has played an important rôle, both in the formation of living material and in the preparation of the Earth's surface for the existence of living things.

For elegance of form, beauty of colouring, and delicious scent, the Flowers must always be held to take the first place. And yet they themselves seem to be incapable of appreciating their own beauty. It is Animals, and of these notably the Insect, the Bird, and Man, which are capable of enjoying the pleasures afforded by plants.

But Animals, too, have a peculiar beauty, and the more carefully and minutely they are studied, the more does our wonder grow, when we realize that even the minutest visible portions have a beauty of structure and function.

The outstanding characteristic of animals which marks them off as so different from plants, is their independence, or, more simply, their power to move from place to place, which, in greater or less degree, has enabled animals to choose their own surroundings.

But Man has found yet other pleasures. The gift of speech brings with it the delights of poetry and song, and the power of abstract thought. The perfection of the senses and of creative intellect have given us the joys of music and art. Independence and originality of mind have supervened on the freedom of the body.

Yet are we still animals. There is, so far as can be told, no essential or peculiar characteristic in the composition of Man's body that makes it different from the body of any other animal, and so it comes to pass that the study of any animal is able to tell us something both about ourselves and about other animals.

When we survey the vast capabilities of living creatures which are the embodiment of living material or protoplasm (First Clay), we cannot but be struck by the wonderful potentialities of this substance; and the study of the Biological Sciences, as they are called, is made all the more fascinating on this account.

The interesting problem of why animals have their own particular form by which we recognize them, seems never to have been well explained.

It might almost be said that this problem, or rather great series of problems, has hardly begun to be solved, although many men have contributed observations and facts concerning animals which have some bearing on the subject.

Aristotle, more than twenty-two centuries ago, attempted that necessary preliminary for scientific investigation—a classification of the various objects (in this case animals) under investigation. The same great man also held the opinion about the development of animals that its progress consisted of a series of changes each of which depended for its correctness on the complete fulfilment of its predecessors. This sequence, termed 'epigenesis,' was regarded as true by such men as William Harvey and Charles Darwin, and has been verified by embryological work.

Another view—viz., that animals exist from the first as miniatures, even within the egg, and gradually unfold —a process which used to be called 'evolution'—is now known to be wholly untenable.

Lamarck, in 1815, gave a definite direction to the inquiry into the problem of animal form by enunciating four 'laws' which may be very briefly summarized thus :—

1. Animals, and their tissues, grow.
2. New organs arise in response to new needs.
3. Organs increase in size according to use.
4. All acquired characteristics are transmitted to offspring.

Of the reason why animals and their tissues grow, nothing is known, although a good deal may be known about how growth takes place.

Lamarck's statement, that new organs arise in response to needs caused by changes in environment, is, in essence, hardly at all different from Darwin's view concerning the origin of species. Some people have translated Lamarck's word 'besoin' as meaning 'desire' and thus have implied that there is a voluntary effort on the part of the animal to modify its form.

Hypertrophy due to use is a well-recognized phenomenon, and in recent years Professor Ariens Kappers has elaborated this principle by showing that brain cells grow in the direction from which they receive most stimuli.

The extent to which acquired characters are inherited is still at the present day a much debated question. Altogether very little is known as to the causes of the diverse forms of animals.

In the first half of the nineteenth century there lived in Germany a man named Lorentz Oken ; he was born in 1799 and died in 1851. He became Professor of Natural Philosophy at Zurich. He seems to have used facts known in his day concerning Zoology, Anatomy, Mathematics, and Astronomy, together with a considerable amount of imaginary matter, to construct a cosmogony. Among his ideas, however, is to be found one, which, it seems to me, really does throw light on the underlying causes of animal form. Oken makes statements to the effect that every animal (and here he probably refers only to vertebrates) consists of two animals, which he terms the 'capital' animal and the 'genital' animal. It is this idea of the dual constitution of animals which forms the theme developed in this book. But from now onwards we part company with Oken, since the arguments he gives can generally be replaced by better ones.

The first question likely to be asked by the reader is, Why should the idea of a dual constitution be reckoned of value ? The answer to this is that there is evidence in the gross anatomy of animals which supports the hypothesis. Yet it has to be sought with a discerning eye. For instance, while it is quite legitimate to regard the fore limbs as belonging to the one constituent of a quadruped and the hind limbs as belonging to the other, and to note the remarkable homologies between them of the bones, muscles, blood-vessels, and nerves, it would be absurd to look for a second head in the middle region of the body. Structures which correspond to some extent with some which are found in the head, may, it is true, be found in that part of the body ; for example, the pancreas has a structure closely resembling that of a salivary gland ; but there is nothing more exact than that, and it falls far short of the resemblances between the fore and hind limbs.

While the anatomist can find some support for the hypothesis of the dual constitution of animals, the zoologist can point to much more conclusive evidence. In 1885 R. Hertwig for the first time watched the fertilization of an ovum by a spermatozoon. Using material obtained from an echinoderm, he saw the spermatozoon, which is the matured sexual cell of the male, penetrate into the ovum (the matured sexual cell of the female), lose its tail, and then within the ovum approach and actually fuse with the nucleus of this cell. The 'head' of the spermatozoon consists almost entirely of nuclear matter, and it is well established that this matter is the bearer of the hereditary qualities which are transmitted to the offspring. The same is also known to be true of the nuclear material in the matured ovum. Moreover, it is known that each mature ovum and each ripe spermatozoon contains only half the usual number of chromosomes or constituent rods of nuclear matter that are to be found in the other cells of the body of an animal. The fusion of the male and female pronuclei, as these matured sexual cell nuclei are called, restores to the fertilized egg-cell the full complement of nuclear material. Thus the nucleus, which is the most important organ in the cell, is seen, in the case of the original cell from which the entire animal is formed, to have a dual constitution.

The egg cell after impregnation wakes into activity. Its nucleus divides and so does its cell-substance, two cells being thus formed. These two cells divide, and division of cells is repeated several times until a mass of cells is produced. In different animals the number of cells constituting this mass varies greatly, but for any particular animal the number is almost constant.

The next feature which shows itself in the developing egg is the appearance of a cavity. This cavity may begin as a chink, or as a vacuole or bubble, or it may begin as several small irregular spaces which fuse together. It may be relatively very small or it may be relatively large, but present it always is at some time in the egg of every animal. In its ideal form the developing egg is now a hollow sphere. Frequently, however, it is very much modified. The presence of a large amount of yolk in an egg may cause the walls of the cavity to be so flattened out that they form a disc lying on the top of the globular mass of yolk, as in the egg of a bird.

The constancy of this hollow mass of cells, which is known as the blastula, is so universally recognized in every phylum of the animal kingdom, that it must be looked upon as the primitive form of every animal. This alludes of course to metazoan animals, and not to protozoa, whose bodies are not divided up into cells.

But now that mention has been made of protozoa, it is well here to note one lesson which their anatomy teaches us. Protozoa have organs. For instance, *Vorticella* (*Fig.* 1) shows a pharynx, a vacuole, a nucleus, a ciliated band, and in its stalk a contractile fibre. From this it is evident that it is not essential for organs that they should be built up of several cells, and organ formation is not restricted to metazoan animals. The theory in this book, however, is applied only to multicellular or metazoan animals, for it takes as its standard unit that very structure, the primitive hollow vesicle or blastula, mentioned above (*Plate I*).

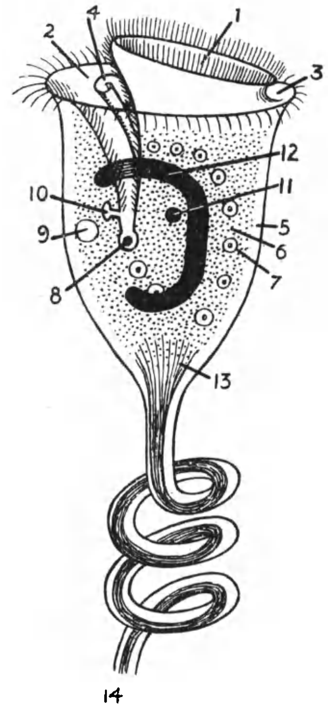


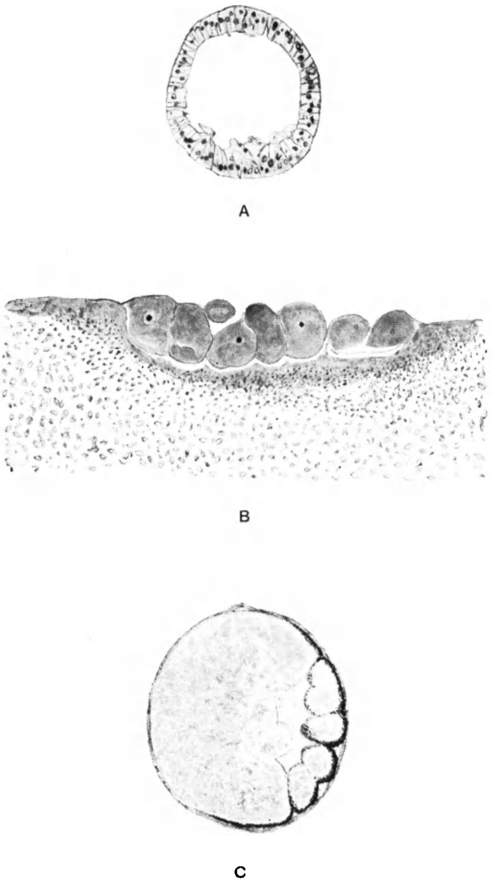
Fig. 1.—Diagram of *Vorticella*. (The cilia at the side of the mouth have been omitted.) 1, Disk; 2, Mouth; 3, Peristomial groove; 4, Vibratile membrane in mouth; 5, Cortical layer; 6, Endoplasm; 7, Food vacuoles (the last of the food vacuoles is nearing the position of the anus); 8, Pharynx, showing formation of food vacuoles; 9, Contractile vacuole; 10, Permanent receptacle into which the contractile vacuole opens; 11, Micronucleus; 12, Meganucleus; 13, Contractile fibrils running into muscle in stalk; 14, Stalk contracted.

(*By kind permission from Sir Arthur Shipley's 'Hunting under the Microscope': Ernest Benn.*)

In the development of all animals the formation of a blastula is followed by another event, by which the single layered organism comes to possess two layers. The resulting animal at this stage is known as a gastrula. The means by which this condition is attained are not alike in all animals. In some animals, most in fact, the process is carried out by part of the wall of the blastula being pushed into the cavity of the blastula—a method known as invagination. Little at first, it increases more and more, until in some cases the inner layer is so close

PLATE I

MICROSCOPICAL SECTIONS OF BLASTULÆ



A, Sea Urchin—*Echinus esculentus*—blastula, 0·27 mm. diameter; B, Dogfish—*Scyllium*—blastula, 1·5 mm. long; C, Frog—*Rana temporaria*—blastula, 1·6 mm. diameter.

to the internal surface of the outer layer that the original cavity of the blastula is almost obliterated. In other animals, however, the inpushing is much less and a large cavity still remains.

Sometimes it is growth and multiplication of cells to form an outer layer burying the other layer beneath it; that is then the means by which the double-layered animal is produced. This process is called epibole; it is well seen in the egg of the primitive arthropod *Peripatus*.

Another way, again, by which the production of two layers is compassed, is by a splitting or delamination of the original single layer of cells into two.

As in the case of the blastula, the method of formation of the gastrula or two-layered animal is modified by the presence of yolk in the egg; but in spite of this, zoologists are able to discern this gastrula stage in the eggs of all animals.

Now it has been said above that in this book the blastula or original hollow vesicle is taken as the unit of animal form for all the metazoa. Moreover it has also been pointed out, in the remarks concerning the fertilization of the egg, that the male pronucleus and the female pronucleus fuse together to form the single nucleus of the fertilized cell. If then the male pronucleus, bearing the hereditary characters of the father, fuses with the female pronucleus which bears the hereditary characters of the mother, and each of these parent animals themselves began life as a blastula, the principle of the dual constitution of animals leads us to expect precisely that occurrence which the formation of the gastrula fulfils, namely, the production of two hollow vesicles as nearly coincident as possible. Furthermore, seeing that the two pronuclei fuse to form one single nucleus in the fertilized egg, it is clear that both constituents are concerned in the formation first of the blastula and then of the gastrula. The gastrula form, like the blastula, is universal throughout the animal kingdom, and, if the hypothesis of dual constitution be true, this follows as a necessity. In the course of development after this, the processes involved become much more difficult of interpretation, and I can give only one example at present. This will occupy some of the next chapters.

In the meantime, however, on the assumption that the hypothesis is true, let us examine some of the results which should be arrived at through its application.

If a very large number of individuals of a species be compared as to the degree in which they possess some one common character, and the results of the comparison be plotted out as a graph, it is found that they give a curve of constant shape, known as the normal variability curve (*Fig.* 2). This curve demonstrates that the vast majority of individuals show the character in moderate degree, and only a small fraction of a percentage of the whole number show a great excess or a great deficiency of the character. All this seems to show that, if every animal has a dual constitution, then the vast majority will naturally inherit what may be termed a more or less normal amount of any one character, since the chance that an animal which possesses a great excess of a character will mate with another which likewise possesses in its make-up an excess of the same character (whether declared or not) must be very small indeed. But other circumstances may, quite likely, make it even more rare, because some lethal quality may be brought about by such a union, or at least some factor of disadvantage to the animal economy.

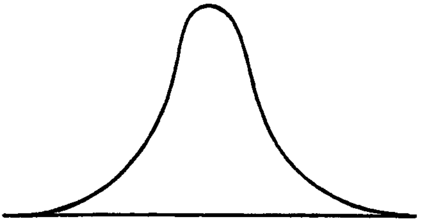


Fig. 2.—Normal variability curve.

Consequently the tendency for animal species to remain constant is very great. Darwin, in fact, observed that species remain constant over a period longer than a geological epoch, so we see that even such great, though perhaps gradual, changes as were involved in the passing away of conditions which for æons had obtained on the surface of the earth, have been insufficient to overthrow the stability of specific reproduction.

As regards the tendency to exhibit variations, which some people appear to have attributed to animals in general, Darwin did not believe that "variability is an inherent and necessary contingency under all circumstances with all organic beings." At the same time, in the case of domesticated animals he did not doubt that "the intercrossing of species aboriginally distinct has played an important part in the origin of our domestic productions." This last statement is noteworthy, because it is very generally held that different species cannot breed together, and that the failure to produce fertile offspring is a criterion of specific difference. Possibly, under natural conditions, in contrast to artificial conditions, the occurrence is so rare as never to have been observed, but this is not saying that it can never happen.

We may conclude, then, that it is not an impossibility for animals of different species to unite and have fertile offspring, but that this, under natural conditions, must be so rare that it has never been actually observed. A rider may be added to the effect that such offspring is only likely to succeed if it differs very markedly from both its parents and if its points of difference confer upon it advantageous qualities; and, in respect of this last point, these qualities are only likely to be possessed in sufficient degree and number by the most abnormal members of a species.

The rarity of the occurrence, and the small chance of survival, of a new type of more than generic difference, is reflected in the extremely small number of the major divisions of the Animal Kingdom. When one considers the enormous progeny of some of the lower animals, and the frequency with which reproduction occurs during one year alone, and the thousands of times by which these must be multiplied during a geological epoch, one can hardly be more amazed at the variety of animal forms than at the fewness of the great classes of animals.

The facts observed so far, then, are in accordance with the theory of dual constitution.

Now let us look at a rather different aspect. If an animal has, by virtue of its production by two parents, a dual constitution, then not only must the animal under discussion have this, but so must its parents, and their parents, and all their ancestors in the same way. Viewing the matter from the phylogenetic aspect, this inherited likeness, so long as a single species is considered, is mere repetition work; but if we look at genera, or more fundamentally different animal-groupings such as families or orders, then, as shown above, the probability of their being brought about by means of mere repetition with variation, even if the effects of these were cumulative, seems less than that the origin of such distinct types is due to the coupling of two exceptionally unlike parents. Each of these parents, however, may be assumed to have come from a definite stock and to have much repetition work in its ancestry, while its exceptional qualities are not new, but due to excess or deficiency of those normal to its species.

It is evident, therefore, that if an animal A unites with a different one B to form a new type C, then C should exhibit in its structure some characters of both A and B. Similarly, an animal E, uniting with one of a different kind F to produce a new type G, should together with F be represented in the anatomy of G. And further, if C united with G to produce a new type H, then H should not only show characters of C and G, but, though in less obvious amount, those of A and B, and of E and F. Nor is this only a matter of probability; it is one of necessity if dual constitution is a fact.

By the operation of this simple rule, it is easy to see that such experiments as the excitation of the process of development by artificial means is only likely to affect the developmental peculiarities which result from the latest phylogenetic union (meaning by this the union of two dissimilar animals which originated the type of animal to which the one under consideration belongs) at the most, and except in so far as it may have caused some physical mutilation, it is powerless to affect the inherent properties in respect of other characters of the species. In the case of H, for instance, characters which appeared for the first time in it might be affected, but not those which had first appeared in A, B, E, or F, or even C or G—these would all remain unaffected. Consequently, when the ovum of a frog, say, is artificially stimulated to undergo development, the changes will of necessity for the most part take place according to the usual routine, and only a small part of them be affected by the experimental interference.

Another aspect of the consideration of the hypothesis of dual constitution leads to the conclusion that if new types of animal arise through the fusion of two animals of dissimilar kind, then we ought to find among the members of the Animal Kingdom some forms which might be called Type Animals—i.e., animals of rather simple structure as regards their several parts, while related to them are many other animals which show modifications of these same parts which obscure their original detail. Two of these Type Animals are dealt with in this book.

The archi-annelid *Polygordius* is one of them. It is of more simple structure than most of the annelids.

The other is the Herring (*Clupea harengus*). This fish, though by no means to be described as simple in structure, yet exhibits a simple and unmodified anatomy as compared with other fishes of the herring tribe. Its bones seem to show in a more or less discrete manner the primitive elements which compose them. There is not the same fusion of several bones into one mass, nor do any bones appear to be missing. Such features as the auditory bullæ do not excavate unduly the bones which they are in, and yet they are amply represented. In fact the bones of the herring may be said to show a more balanced proportion than do the bones in most of the others of its tribe. For instance, Ridewood has described how in *Pellona molius* the auditory bulla hollows out the whole bone, and in *Coilia nasus* the bulla does not occupy a central position ; whereas in the herring the auditory bulla in the prootic bone, and in the squamosal bone too, forms a central body about which the other parts of the bone are evenly grouped.

Modifications of the type form must, of course, arise in the way that species are formed, according to the theory of Darwin and Wallace. And so, with a very successful type form such as the herring, many adjacent species may be expected.

Again, it may be pointed out that, as far as Mendel's theory of heredity is concerned, the conception of dominant and recessive characters, and indeed of the whole principle of the theory, is closely bound up with the view that every animal has a dual constitution, part of its hereditary characteristics coming from the male and the rest from the female parent. This, moreover, is quite independent of the possibility that dominant or recessive characters may be only widely different amounts of one and the same condition or trait.

As in some degree cognate to this, is to be reckoned the fact that the higher an animal is in the scale of life the more complex are its tissues and organs. The increasing complexity of, say, the eye, the heart, or the brain in mammals generally, as compared with the reptiles and fishes, is notable, and the deep fasciæ and aponeuroses which are so evident in mammalian limbs are not to be seen in the limbs of reptiles and amphibians (*Ligaments*, J. Bland-Sutton, 1902, p. 19). The dual constitution of animals could hardly avoid causing an increase of complexity both of tissues and organs, while on the other hand there can be no doubt that complexity is far from being essential for efficient action, for the animals which are of simpler structure are yet well able to hold their own in spite of being of simpler design.

Finally, one may hazard the guess that the vesicular form or blastula, which throughout this book is held to be the universal primitive form of all metazoan animals, is no other than an attempt—and a very successful attempt at that—to reproduce on a larger scale the model of a single cell. Since the model is altogether larger it has greater possibilities, and these have been exploited to their fullest extent.

It was the opinion of the French protozoologist Schaudinn that the minute sporozoon which is the cause of malaria, whose asexual form in its very early stages develops within itself a vesicle, achieves thereby an increase of its surface for absorption and so grows more rapidly. This perhaps may be an early phase in the animal kingdom of the same principle of vesiculation, and it is not unlike the principle enshrined in the story of Dido and the foundation of Carthage.

CHAPTER II

POLYGORDIUS

POLYGORDIUS is a marine worm of small size and simple structure. Three inches is about the length of a well-grown adult worm, and the thickness of it would be about a millimetre ($\frac{1}{25}$ in.). Its name implies that the worm exhibits many knots. This of course is an exaggeration, or, shall we say, poetic licence. Several worms are usually found intertwined, and they are much curled up.

The North Sea species, *P. lacteus*, which is obtained between Heligoland and the mainland, is very similar to the kind found in the Mediterranean, but one Mediterranean species, *P. appendiculatus*, is characterized by having two long appendages at the hinder end.

The classical monograph on *Polygordius* is that of Fraipont, No. XIV of the monographs on the Fauna and Flora of the Gulf of Naples, 1887, Berlin. This gives a full account of the appearances and anatomy of the worm.

The embryology has been worked out by Prof. R. Woltereck. His researches on the development and cell-lineage of *Polygordius* are published in *Archiv. für Entwicklungsmechanik*, 1904, Bd. xviii, pp. 379–403. He has also published other papers in connection with the subject.

A delightful account of Woltereck's work has been given by Professor MacBride in English in the *Textbook of Embryology—Invertebrata* (London: Macmillan & Co., 1914, p. 128 et seq.) from which nearly all the account here given is taken.

An account in English of the anatomy of *Polygordius* is to be found in T. J. Parker's *Lessons in Elementary Biology*, 1891.

DESCRIPTION

The worm (*Fig.* 3), externally, shows but feeble evidence of segmentation. The front segment of all is much smaller than the rest and carries two tentacles which

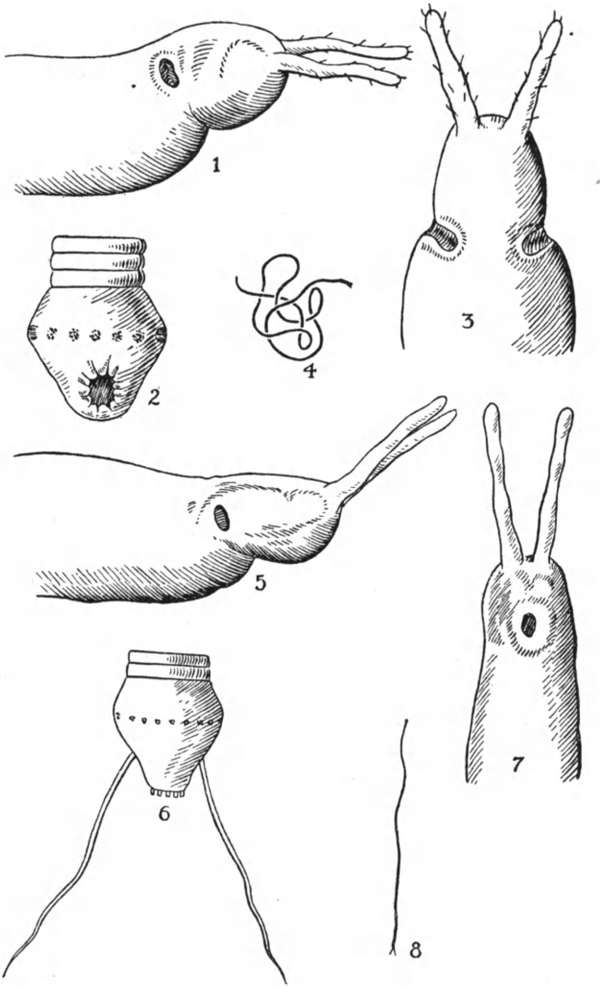


Fig. 3.—*Polygordius*, head end and pygidium. *P. neapolitanus*: 1, Head, side view; 2, Anal segment, ventral view; 3, Head, dorsal view; 4, Worm, natural size. *P. appendiculatus*: 5, Head, side view; 6, Anal segment, ventral view; 7, Head, dorsal view; 8, Worm, natural size. (*After Fraipont.*)

point forwards and upwards and have a few small bristles. The tentacles are moderately stout and have rounded ends, and are only just visible to the unaided eye. The front segment, being situated in front of the mouth, is termed the prostomial segment. On either side of its dorsal aspect where it joins the second segment is an oval pit lined by ciliated cells. A conspicuous groove on the under aspect of the worm marks off the prostomial segment from the second or peristomial segment. The triangular-shaped mouth, with base of triangle in front and apex behind, occupies about three-quarters of the breadth of the under aspect of the worm in this segment at first, but rapidly narrows posteriorly, and leads into a very short protrusible pharynx. Behind the second segment all the remaining segments are of practically uniform size and almost devoid of peculiar features until the last segment or pygidium is reached. This one is of greater diameter than any other part of the worm. It bears round its widest part a zone of clumps of adhesive cells, and behind this zone the segment has the shape of a blunt cone. The opening of the anus is on the under side of this part.

The pharynx passes into the œsophagus, which is confined to the peristomial segment and has thicker walls than the rest of the alimentary canal. After the second segment the œsophagus is continuous with the intestine which runs straight to the anus. The gut is oval in cross-section with its long axis vertical. This is well seen in a transverse section of the worm (*Fig.* 4), which also exhibits the following points. The skin, covered externally by a thin cuticle, shows a number of nuclei, but it does not show any indication of being divided up into cells. In the mid-line ventrally may be seen the ventral nerve-cord cut across. It is not marked off from the skin. Next the skin is seen a broad belt of radiating bands. These are the longitudinal muscles cut in transverse section. They form the greater part of the thickness of the body wall, and can be seen to be divided into an upper group and a lower group by an oblique septum which runs upwards from beside the ventral nerve-cord to the skin half-way up the side of the body. This oblique septum crosses a space which is the cavity of the cœlom, and on the septum in this cavity are situated the genital cells. A single layer of cells separates the radiating bands of the longitudinal muscles from the cœlom, and this cœlomic epithelium is continued over the wall of the gut, and forms a mesentery to support that tube. This it does by running upwards to the muscular wall of the body above, and downwards to it below, as a double layer in each case, instead of being closely applied to the gut all round. The two layers of mesentery above the gut together with part of the gut wall form the wall of the dorsal longitudinal blood-vessel, and the two layers of the mesentery below the gut are parted to form the wall of the ventral longitudinal blood-vessel.

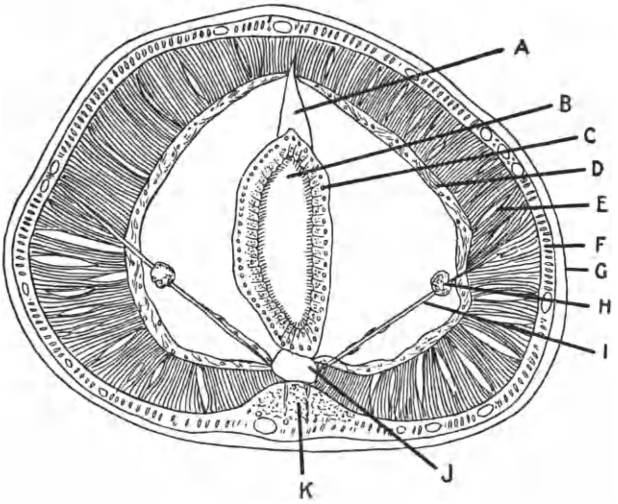


Fig. 4.—Polygordius. Transverse section. A, Dorsal vessel; B, Intestine; C, Visceral layer of cœlom; D, Parietal layer of cœlom; E, Longitudinal muscle; F, Skin; G, Cuticle; H, Genital gland; I, Oblique septum; J, Ventral vessel; K, Ventral nerve-cord. (*After Fraipont.*)

There is no heart. The ventral longitudinal vessel splits anteriorly into two stout trunks which run forwards and upwards in the cavity of the cœlom of the peristomial segment on either side of the œsophagus and reunite above it to form the dorsal vessel. The longitudinal blood-vessels run backwards above and below the intestine to the last segment where they terminate blindly, but the two vessels are connected by many lesser channels known as commissural vessels which come off as branches of the dorsal vessel and run round in the septum which separates one segment from another to join the ventral vessel. In all except the first ten and last two segments each of these commissural vessels gives off half-way along its course a recurrent branch which ends blindly. The fluid contained in the vessels is called the blood and is faintly coloured.

The cœlomic cavity contains fluid. The cavity of one segment is separated from that of the one in front or behind by a septum, so that each segment has a cœlomic cavity. Besides separating one segment from another the septum helps to support the gut, and the lumen of this tube is slightly constricted where it passes through the septum. The wall of the intestine is formed by a single layer of columnar cells.

The nephridia are difficult to detect. Each consists of a small funnel opening forwards in the lower part of one cœlomic sac, and from it a fine tube which passes backwards through the septum into the cœlomic cavity of the next segment behind. After gaining this it turns downwards to open externally. The first five segments, and the last one, do not possess nephridia.

The same segments which carry nephridia also carry genital cells. The sexes are separate. The ova when ripe are shed out through rupture of the body of the worm. The escape of the spermatozoa from the male worm is believed to be by way of the nephridial pore.

The nervous system consists of a supra-œsophageal mass which occupies practically the whole of the prostomial segment and sends extensions into the two tentacles. From this two large nerve cords pass back, one on either side of the œsophagus, and reunite below the alimentary canal to form the ventral nerve-cord. From the nerve-cord fibres pass out to an intermuscular plexus, and to the nerve-cord run sensory nerves from the skin.

The thick muscular layer which forms the bulk of the body wall of the worm consists for the most part of cells having large nuclei, and these cells give rise to fibres which run longitudinally, while internal to these is a delicate layer of circular fibres.

The wall of the intestine consists of but a single layer of cells, and these are columnar in shape and furnished with cilia.

Some varieties of *Polygordius* show an eye spot on the dorsal aspect of the head. It is said to be of little functional use.

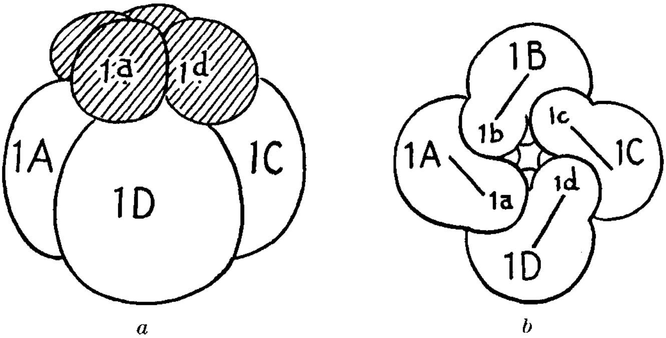
DEVELOPMENT

The egg of *Polygordius*, being devoid of yolk, is very small. It, like the eggs of other annelids and of molluscs, divides first into two cells and then into four by meridional cleavages. Unlike the majority of these eggs it does not show any difference in size between each of the four cells or macromeres as they are called.

For the purpose of tracing the ancestry of every cell during the early stages of the development of an animal, the method devised by American zoologists is employed. Since, in the eggs of most annelids and molluscs, the macromere which gives rise to the posterior part of the animal is of larger size than the others, this cell is designated the 'D' cell. This is done because the egg when viewed from above, with this cell placed posterior, shows
B
A on the left, B in front, and C on the right—A C
D

In the case of *Polygordius* it is not possible to determine which is the D cell until a rather later stage, when the quadrant of the egg formed from B becomes recognizable through one of its cells dividing into two very small ones, before any such cells are to be seen in any of the other three quadrants.

The first two cleavages, then, of the egg have been meridional and pass through the poles of the egg. The third cleavage is of different nature. All the cells, it is true, divide at the same time, but the division is unequal and takes place in a zonal manner, so that four small cells, or micromeres, are cut off from the upper ends of the four large cells or macromeres. This is called the budding off of the first quartette of micromeres. Furthermore, during this cleavage the nuclear spindles which appear, incline to the right, so that the micromeres lie above and to the right of the macromeres. The egg now consists of eight cells. The four macromeres, after they have given off the first quartette of micromeres, are now named 1A, 1B, 1C, 1D, and the four micromeres corresponding to them are named 1a, 1b, 1c, 1d (*Fig.* 5).



a *b*

Fig. 5.—Dexiotropic division, first quartette. *a*, Side view; *b*, View from above.

At the fourth cleavage of the egg the macromeres bud off a second quartette of micromeres and at the same time the first quartette of micromeres also divide; in other words, all the cells of the egg divide simultaneously. In accordance with the scheme of nomenclature used, the macromeres are now 2A, 2B, 2C, 2D, the second quartette of micromeres are of course 2a, 2b, 2c, 2d, while the eight cells of the first quartette are now called $1a^1$, $1b^1$, $1c^1$, $1d^1$, $1a^2$, $1b^2$, $1c^2$, $1d^2$, the index figure '1' meaning that the cells bearing it are situated at a higher level in the egg than the cells numbered '2'. If the relative position of any two cells formed by division is right and left, then the index letters 'r' and 'l' are used, or if one of the cells lies in front of the other the index letter 'a' is used for the anterior one and 'p' for the posterior one.

At the fifth cleavage all the cells again divide simultaneously. The macromeres bud off a third quartette of micromeres. It has been said that at the third cleavage of the egg—the first two having been meridional, and the third one zonal, when the first quartette of micromeres were formed, all the spindles inclined to the right—dexiotropic division. On the occasion of the formation of the second quartette, the nuclear spindles throughout the egg all inclined to the left, and this type of division is termed læotropic. Now when the third quartette of micromeres arises and the cells of the second quartette divide as well as all those derived from the first quartette, the spindles incline once more to the right. This process characterized by alternate right and left inclination of the spindles is called *spiral cleavage.* The egg now consists of thirty-two cells and all four quadrants are alike. The quadrant A may therefore be taken as an example of the nomenclature. It consists of eight cells—the macromere 3A, one micromere of the third quartette 3a, two micromeres of the second quartette $2a^1$, $2a^2$, and four micromeres of the first quartette $1a^{11}$, $1a^{12}$, $1a^{21}$, $1a^{22}$. At this time the egg is of spherical shape and has a central cavity ; it is a blastula.

Once more all the cells of the egg divide at the same time. Sixty-four cells are formed, a fourth quartette of micromeres being budded off. The upper hemisphere of the egg at this stage is formed entirely of first quartette cells. Of these cells, the cells (in quadrant A for example) named $1a^{211}$, $1a^{212}$, $1a^{221}$, $1a^{222}$, are situated at the equator of the egg and become furnished with long powerful cilia, and together with the similar cells in quadrants B, C, and D, they form the prototroch which is the principal organ of locomotion of the creature at this time. By their activity the egg escapes from the vitelline membrane which up to now has enveloped it. A simplified manner of referring to the cells in all four quadrants at once is to use the letter Q as meaning A, B, C, and D, or q for a, b, c, and d. Thus the cells which form the prototroch may be shortly designated $1q^{2--}$, which shows that they are all derived from $1a^2$, $1b^2$, $1c^2$, $1d^2$, four cells coming from each source making a total of sixteen cells.

The four cells $1q^{111}$ are also ciliated and form the apical tuft, while the remaining cells of the first quartette fill up all the rest of the upper surface between the apical plate and the prototroch. They are arranged as two crosses (*Fig.* 6). One cross has its arms placed diagonally, when the egg is viewed from above with the D cell posterior, and is characteristic of annelidan eggs; and in the other, which is known as the molluscan cross, the arms are vertical and horizontal.

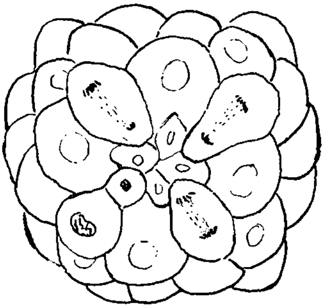


Fig. 6.—Showing annelidan cross. (*After Woltereck.*)

The cells of the other quartettes and the four macromeres are to be seen composing the under surface. The egg at this time is beginning to flatten out, and by the time that the two next cleavages have been completed the embryo is nearly flat and has a squarish outline with very much rounded corners.

At the seventh cleavage, a fifth quartette of micromeres is budded off (*Fig.* 7). With the exception of the cells $1q^{111}$ and $1q^{2--}$ all the cells of the embryo divide.

Lastly there is a cleavage which only concerns the macromeres—by now much reduced in size. 5A divides into $5A^a$, $5A^p$, 5B into $5B^r$, $5B^l$, 5C into $5C^a$, $5C^p$, while

5D divides first into $5D^1$, $5D^2$, and then $5D^1$ divides into $5D^{11}$, $5D^{12}$. But some of the cells also of the second and third quartettes divide, all of the fourth, all of the fifth, and its posterior ones even once again.

Cell division now ceases for a time and the animal consists of 135 cells, or in one species of 137 cells, owing to a division occurring of two fourth quartette cells in this species which in other species do not divide until the changes have taken place which are now to be described.

The numbers of cells making up the total 135 are distributed as follows: first quartette, 40; second quartette, 38; third quartette, 28; fourth quartette, 8; fifth quartette, 12; residual macromeres, 9.

From being nearly flat, the embryo gradually changes to a subconical form, and then the under part of this form begins to bulge also until a complete almost spherical trochophore larva is realized (*Fig.* 8).

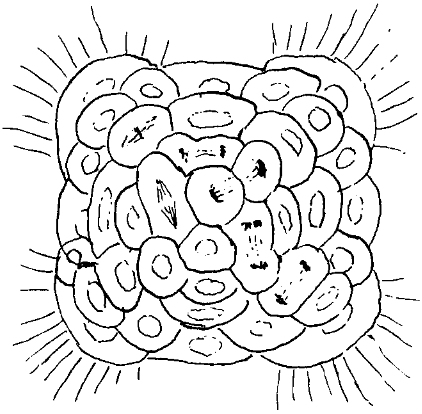


Fig. 7.—Fifth quartette being formed. (*After Woltereck.*)

The first sign of these changes is the sinking inwards of the two central cells of the under surface $5D^2$, $5D^{12}$, and the appearance of ridges bounding the depression on each side. These ridges are made up of cells of the fifth quartette, with two fourth quartette cells at their midpoints. These two cells are of large size, and begin to close together, cutting the oval opening into two. Following this the hinder opening closes, by the fifth quartette cells there coming together, and as this is happening the whole of the oval area becomes still more thrust into the now more conical animal and other lateral boundaries are formed, this time from cells of the second and third quartettes. The first depression is called by some people the primary blastopore, and the later accentuation of it the secondary blastopore. Four cells on each side form the margins of the secondary blastopore, and of these the hinder three on each side come together so that the only persistent part of the original blastopore is the anterior end of it. In the case of the first blastopore the meeting of the two large cells, $4a^a$, $4c^a$, created a very primitive alimentary canal with mouth in front and anus behind. Then the anus was closed, and the hind gut, such as it was, drew away from the ectoderm; and inasmuch as this occurred before the cells of the secondary blastopore had met together, the interior of the blastocœle for a time communicated with outside world.

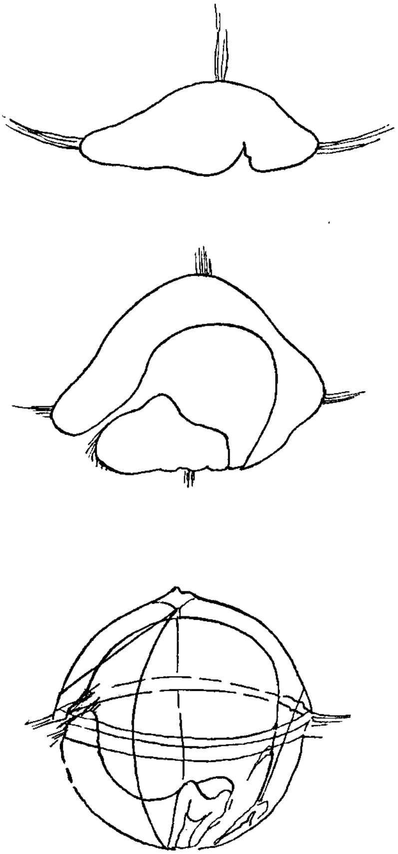


Fig. 8.—Outlines of *Polygordius*. Optical sections, showing changes in shape as embryo develops. (*After Woltereck.*)

The closure of the secondary blastopore is not a mere process of meeting of opposite cells. The two anterior pairs of cells may do so, but the two hindmost cells meet by rotating through half a circle, and some other cells at the same time show remarkable movements. Two cells, namely, $3c^{2ppa}$, $3d^{2ppa}$, wander into the blastocœlic cavity to form part of the primitive excretory organs or archinephridia. Three other cells on each side swing round from their original position to form the lower lip of the large slit-like mouth. One other cell on each side becomes drawn out into a long band and forms much of the lesser ciliated band or metatroch.

But the most surprising sight noted by the observer is the deliberate wandering of the cell named $2d^{222}$ over the surfaces of the cells $4d^r$, $4d^l$, to join company with the cells $3c^{2paa}$, $3d^{2paa}$. The last-named cell ($3d^{2paa}$) develops a tuft of cilia which projects from the lower pole of the trochophore larva, as the apical tuft does from the upper pole.

As the flat blastula is changing into the nearly spherical larva the alimentary canal is also fashioned. The cells which compose it are those of the macromeres and of the fourth and fifth quartettes : that is to say, the mid-gut or stomach and the hind-gut or intestine are formed from these cells, but the fore-gut or stomodæum, as already described, is made of cells from the second and third quartettes.

The stomach is of nearly globular shape and its diameter is about half that of the larva itself. The wide mouth of the trochophore larva situated between the great ciliated band or prototroch above, and the much lesser ciliated band or metatroch below, leads through the stomodæum into the anterior aspect of the stomach. Behind the stomach, and nearly shut off from it by a flat valve, is the hind-gut, which runs nearly vertically down to the newly reopened anus. The position of the new anus is immediately behind the site of the first one, and in front of it is the telotroch or ciliated tuft which springs from the cell $3d^{2paa}$.

While all these changes are going on the animal does not feed, nor is there any evident cause for them. It is only after the larva has reached this degree of elaboration that it begins to feed, and it passes from the subconical shape to a globular shape, and then the body of the future worm begins to show itself, while at the same time many other changes occur which modify its viscera into those of the worm.

With the commencement of feeding, rapid growth takes place of certain cells of the fourth quartette which up to this time have been altogether only eight (in one species ten) in number. The progeny of the two cells $4d^r$, $4d^l$, which are the particular cells in question, and are now known as the teloblasts, form two long bands of cells called the mesodermic bands because it is from these bands that the walls of the cœlomic cavities are formed. The muscular wall both of the body and of the intestine arise from the parietal and visceral layers respectively of the cœlomic lining. The ectoderm of the body of the future worm, as it now begins to project from the globular trochophore, is formed from the three cells, $3c^{paa}$, $3d^{2paa}$, $2d^{222}$. When the larva is of subconical shape the primitive excretory organs are the archinephridia, and these consist of two cells each. The excretory tube on the right side is formed from the cell $3c^{2ppp}$, and runs from the external opening close to the telotroch upwards and forwards because its inner end has been dragged in by the cell $3c^{2ppa}$, which becomes a 'flame-cell', a hollow cell with cilia inside it. On the left side, the tube is formed from the cell $3d^{2ppp}$ and the solenocyte or flame-cell from the cell $3d^{2ppa}$. Now that the larva has begun to feed and the body of the worm is springing forth, the archinephridia become modified to form the protonephridia. Descendants of cells of the third quartette join company with the archinephridia and furnish them with many more solenocytes, while the excretory duct is elaborated out of cells budded from a pore cell in the ectoderm of the first segment of the worm.

The anus of the globular trochophore is carried out on the extremity of the growing body of the worm, and the teloblasts are in this growing end, so that the mesodermic bands to which they give rise are formed of cells budded from their anterior sides. The bands increase in thickness by longitudinal divisions of the cells which form them, and within these masses there appears on each side a cœlomic space, a pair of spaces in each segment. These two spaces rapidly enlarge and meet and open into one another above and underneath the gut. In doing this they have almost obliterated the original cavity that existed within the outgrowing body of the worm and was continuous with the blastocœlic cavity of the trochophore, but the lengthy chinks that remain at a later stage, namely, after the metamorphosis, are given a lining of cells and form the longitudinal blood-vessels and their connections.

Immediately beneath the apical plate, cell multiplication occurs and is the first sign of a cerebral ganglion, and now also mesenchyme cells grow out across the blastocœle as muscle-strands to the fore-gut and skin.

At the same time the muscular walls of the body and the intestine of the worm are forming, the already modified excretory organs are beginning to be superseded by the formation of the permanent organs of the adult, and the nervous system, too, is being elaborated. The two head tentacles begin to appear, and close to their bases arises the double mass of nervous tissue which becomes the supra-œsophageal ganglion of the worm and forms a large part of the brain. From it run the two large strands to the ventral nerve-cord which, together with the ganglion above and their junction with the cord below, form a ring of nervous tissue round the œsophagus. Six other nerves pass out radially from the supra-œsophageal ganglion, and there are rings of nerve strands associated with both the prototroch and metatroch. Besides these there is a diffuse network of nerves immediately under the skin. This curious feature of the systems of nerves is noted by Woltereck as reminiscent of the condition of affairs in ctenophores. The six lesser nerve strands, the two rings, and the diffuse network, have counterparts in the form of muscular fibres, which, like the nerves, belong to the larval life only and are cast off at the metamorphosis. Eye-spots are formed at the edge of the head region in which the tentacles are situated, and by this time the apical tuft of cilia has been shed. The beginning of the ciliated pits is seen close to the base of each tentacle.

The internal structure of the organism has also been changing. A new lining to the œsophagus, coming from an area like an imaginal disc on each side, replaces the original lining. In the intestine there has been a great multiplication of the lining cells, certain special cells being detailed off for this purpose. In the North Sea species, the body of the worm, instead of protruding as it grows, is held puckered up within an 'amniotic' cavity, and while thus kept in confinement, the multiplying cells of the intestine are very closely packed and lie obliquely on one another. When at the metamorphosis the body of the worm is extended, then these cells accommodate themselves to cover a larger area.

Besides the two stout lateral nerve-strands which run from the apical region of the globular trochophore in a radial manner round to the beginning of the ventral nerve-cord in the body of the worm, there are also two large muscular strands lying beneath them, and a third muscular strand placed mid-dorsally, which also connects the apical region with the outgrowing body of the worm.

By the time that all these structures have come into existence the trochophoral part of the animal is beginning to show signs of decay. The stomach, demarcated from the œsophagus by a ring of ciliated cells, and from the intestine by a flat valve which also is ciliated, decreases in size by the shedding of its cells, and unlike the œsophagus it is not renewed from any source. The cells of the ectoderm situated between the apical region and the prototrochal ring begin to degenerate, and so do the cells between the prototroch and the commencement of the worm-body. In consequence of this the apical region comes down upon the prototroch and the prototroch comes down upon the beginning of the worm. Then a sudden violent contraction of the ring muscles tears the skin of the trochophore right through until the whole prototrochal region is set free as a belt, out of which the worm wriggles, while at the same time the reconstituted apical region is pulled down and fixed to the worm-body and forms part of its head (*Fig.* 9).

Woltereck remarks that the worm sometimes swallows the cast-off prototroch.

Although the worm is now in existence it undergoes some minor changes in structure. During the rapid changes of the metamorphosis a very remarkable contraction of the lateral nerves and of the lateral muscles took place. The nerves now form a small ring encircling the œsophagus, and the muscles have shortened to an extent which is some six or seven times the amount of an ordinary muscular contraction, and also differs from it in not being followed by a relaxation.

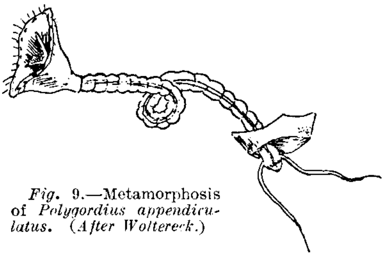


Fig. 9.—Metamorphosis of *Polygordius appendiculatus.* (*After Woltereck.*)

Other changes are the development of a space between the pharynx and the brain, the disappearance of the primitive kidneys or protonephridia, and the formation of a ridge in the floor of the pharynx, somewhat resembling the ridge known as the typhlosole in the mid-dorsal line of the intestine of the earth-worm.

It is to be noted that practically every part of the original trochophore vanishes. The apical region which is pulled down on to the end of the body of the worm to form part of its head is newly produced and has replaced the apical region formed at first. Similarly the œsophagus which becomes part of the worm is re-formed. Those parts of the protonephridia which existed within the trochosphere disappear just before the metamorphosis occurs. The large stomach of the trochophore entirely goes to pieces, never to be reconstituted. The intestine, it is true, is continuous with that of the worm, but the actual cells have been renewed. The skin of the trochosphere in part withers away and the rest of it is cast off with the prototroch. The only strands of muscle and nerve which persist and form part of the worm were not formed as part of the original larva but appeared at a late stage of its existence, and at the metamorphosis they become profoundly altered in bulk and extent.

But although all these parts of the trochophore larva have gone, they have served as prototypes for the parts in the fully formed worm. The skin of the worm is derived from the descendants of the cells $2d^{222}$, $3c^{2paa}$, $3d^{2paa}$. The supra-œsophageal ganglion which has become the brain appeared before the trochophore disintegrated, and the two lateral nerves which sprang from the ganglion end beneath the œsophagus by becoming the ventral nerve-cord. So, too, the intestine began within the trochosphere and was continuous with that in the worm. The blood-vessels are the continuation into the worm of the cavity of the blastocœle. The permanent kidneys are copies within the worm of the protonephridia of the trochophore.

The ciliated bands of the trochophore are not represented in the worm, while in the worm are to be found the cœlomic cavities which did not exist in the trochophore. The two head-tentacles are also new.

In these brief accounts of the anatomy and development of *Polygordius* a host of minor details have been omitted. If the reader should wish to know about them, the works of Woltereck and Fraipont and others should be consulted.

CHAPTER III

THEORY OF DEVELOPMENTAL HISTORY OF POLYGORDIUS

IT is necessary from the first to make quite clear to the reader the manner of application of the theory of dual constitution in explaining the developmental history of *Polygordius.*

Imagine for a moment that this worm, instead of being a wonderful machine in which the fuel and machinery are indistinguishable, yet both remarkably efficient, and repairs are done to the machine by itself as they are required—in a word, an animal—were a piece of mechanism made by man. It would have to be made in some engineering works. Let the reader come as a visitor to these works and be shown round them. He would visit the erecting shop and see there the finished thing and the main details of how it is constructed. In the case of *Polygordius* he has seen this in the account which has been given of its anatomy. Then the visitor would go to the various machine shops and see how the parts were built up. This corresponds to the developmental history, which has been given. Now I wish to take him to the drawing office to see the designs by which these various operations are guided. These designs, be it remembered, are abstract things—not concrete—but they govern the other phenomena. On the other hand, the animal is a very concrete thing as far as the material composing it is concerned, so that the living animal may be looked upon as a compromise between the characters of the theoretical design and of the substances in which the design is carried out.

For the most part, however, in this section, the reader is to be shown the designs and how they are drawn, and only an occasional visit will be paid to other parts of the factory.

The unit of design, from which, according to this theory, all metazoan animals are built up, is the blastula. The blastula is recognized by zoologists as the original form of all animals which are built up of cells.

I hope to demonstrate that *Polygordius* is built up by the interaction of four such blastulæ—phantom blastulæ, if you like, since they are purely abstract, but none the less they are as real as any pedigree. After all a pedigree is a purely abstract thing, though a record of it in writing may be kept. This written record would, in ordinary everyday affairs, be spoken of as the pedigree, whereas in reality the pedigree is the abstract history, and the record of it is the summarized picture of the pedigree.

It is part of the hypothesis of the dual constitution of animals that each animal preserves its pedigree, and the individuality of each parent probably contributes to it as a rule, in equal degree.

The way in which I hope to show that the design of this worm has been made from four blastulæ and no more, is by explaining the chief events recorded in the foregoing account of the development of the worm, in terms of this hypothesis ; that is to say, giving a reason for the different movements of cells to form organs, on the assumption that they have had to follow out a definite design. At the same time I wish to show how the design has come about.

Let us start with an idealized conception of a blastula as a hollow sphere of living matter. In actual fact such a thing does not exist. There is at least one spot upon the sphere which differs from the rest by being the site of active growth. This spot is the lip of the blastopore, and the existence of this site marks the occurrence of a definite arrangement and determines the axis about which the animal will be built up. The animal then from the very first has a definite polarity. The anterior pole of a quadruped is the head end and the posterior pole is the tail end, in ordinary parlance. The point which I want to make clear is that the blastula is not an indiscriminate sphere, but it always has a definite polarity and a definite axis. This is a fact recognized by every zoologist. It is also well known that the blastula is capable of great modifications of shape while yet it preserves its essential properties; in other words, it is highly plastic. There is reason to assume then that the blastulæ we are about to consider are endowed with a definite axis and are highly plastic. The main axis therefore remains unaltered or very nearly so, but any other diameter of the blastula may be shortened or lengthened as the case may require provided that the integrity of the blastula is not imperilled.

Now the egg of *Polygordius* consists at first of but one cell. This divides into two, then four cells are formed, then eight, and then sixteen, and now the animal is seen as a blastula.

The reason why four blastulæ are postulated as entering into the composition of *Polygordius* will become apparent later. At present I must ask the reader to bear with me while I refer to other points.

If, instead of having abstract ideas of blastulæ to deal with, we had four spheres of plastic material which could be moulded just as one might wish so long as one did not shorten one particular diameter or tear any of the surfaces at all, and we wished to pack them all four into a single spherical shape, there can be little doubt but that we should mould each one of the four into the shape of one quadrant of a sphere, and put them together with their long axes parallel. They would be arranged like the four quarters of an orange. It is precisely thus that I assume the design for *Polygordius* to be begun.

But we have already got on too fast, and there are things which the reader will want to have explained.

First of all, if the hypothesis states that every animal is built up of two animals, how can it be that *Polygordius* begins with four?

The answer to this is that the four are in reality two successive pairs, and do not correspond to four simultaneously existing animals. There is, however, ground for thinking that the union of the one pair with the other pair of blastulæ, to make up the four, reflects a very early union in the life history of these ancestors, taking place, probably, while the animals were yet in a larval stage. Union during a larval stage is a thing which actually does happen sometimes, for it is well known that the axolotl (*Siredon*), which is the larval form of the lizard *Amblystoma*, is capable of laying eggs from which young axolotls hatch out. The claim then that the four blastulæ required for *Polygordius* are two pairs, nearly, but not quite, cœval, has evidence to support it.

Secondly, although four blastulæ, or rather phantom blastulæ, have been mentioned, nothing has been said of how the design for these has been made.

If we wish to draw a circle, we do it with a pair of compasses, but to describe a sphere, we should probably use a circle or semicircle of wire, and twirl it round on an axis which would be its diameter. In this way the path of the curved wire describes a sphere in space. It is necessary to assume that the design of the phantom blastulæ is actually made in some way not very different from this.

In the first chapter mention was made of the fact that every animal after attaining to a blastula stage goes on to become a two-layered animal or gastrula. The process by which this is accomplished may be one of invagination of the wall of the blastula, or it may be done by an overfolding or epibole, or the blastula wall may be duplicated by splitting or delamination. But none of these phenomena necessarily represent the way in which the design was imagined by the living system which is the live animal. From the consideration of the later stages in the development of *Polygordius*, it seems probable that the gastrula is designed by the rolling of one sphere towards the other until they become coincident. If one sphere approached the other directly, the exactly opposed movements would, it seems to me, only lead to mutual destruction of the two spheres. By rolling together, the two spheres have part at any rate of their motion in common and therefore each maintains its entity. In the case of *Polygordius*, where the two pairs of spheres are involved, we may believe that what applies to one pair holds also for the other. Like every other multicellular animal *Polygordius* begins as a blastula, which it actually realizes when it consists of sixteen cells. But if four hypothetical blastulæ are postulated, we must assume that the animal, even though at present it shows only one of them, is yet under commission to construct the other three. Nevertheless we can hardly expect but that they would be considerably modified. They will have to be pointed out at a much later stage than the present; in fact, they have only been mentioned here in order to emphasize the principle that in theory they already exist, and, as suggested, are packed into the globular form of the embryo at this stage like the four quadrants obtained by bisecting two hemispheres. The phantom blastulæ, however, even if no more than abstract designs, would not have sharp edges, but would tend to an ovoid form, with two flattened surfaces where they were in contact with their neighbours (*Fig.* 10). Each phantom, moreover, is regarded as having a main axis round which it is turning.* This axis is at first set almost vertically and passes through the mid-point of the cross-sectional area, or close to it, at the level of the equator. A line drawn, in each quadrant,

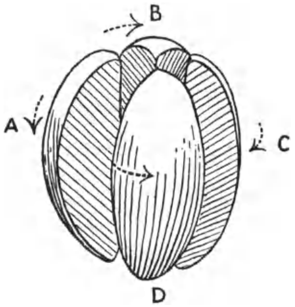


Fig. 10.—Diagram of four phantom blastulæ, early stage.

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* *Note.*—This axis which here is postulated is not to be thought of as an axis of symmetry such as Gegenbaur employs in describing body form.

from the upper pole of its axis over the surface of the embryo to the lower pole, cutting the equator where one quadrant is in contact with another, marks a meridian, and each quadrant is considered to have one meridian which is the agent concerned in designing its phantom blastula. There is reason to think that this 'active meridian' in the case of the two anterior phantoms runs at first along the middle line of the embryo in front, and that the active meridians of the two posterior phantoms start from a point on the equator half way between the anterior and posterior middle lines (*Fig.* 11). It is evident that it is necessary for each active meridian to turn through a little more than a quarter of a circle in order that a globular form may be described. The two anterior active meridians diverge until they reach the points from which the two posterior ones start, and the two posterior ones move round towards one another until they meet.

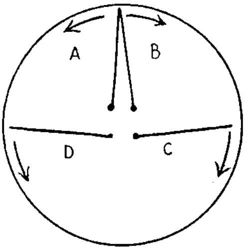

Fig. 11.—Diagram to show position of active meridians.

In order to give these phantoms non-committal names so that they may not be confounded with actual structures, let us call the anterior pair Phantom Blue and Phantom Green, and the posterior pair Phantom Red and Phantom Yellow.

Consider now their behaviour. Blue rotates on its axis, say, to the left (counter-clockwise) to fuse with Green which rotates to the right (clockwise). Similarly Red, which lies behind Blue, rotates to the left to meet Yellow, which is turning in the opposite direction to meet it (*Fig.* 12). It is in this manner that all the four

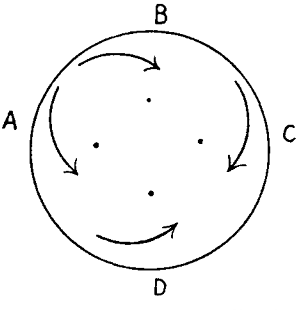

Fig. 12.—Diagram to show directions of rotation.

phantom blastulæ take part in designing the blastula which is seen in the flesh.

Each phantom has not had to do much more than turn through one-quarter of a circle for the whole sphere to be delineated. The reader will have perceived that the axis of each of these phantoms is considered to be situated near the axis of the whole blastula which they design, so that diagrammatically they would be shown as four upright parallel lines rather close together, almost in the innermost corner of their respective quadrants (*Fig.* 13).

If we leave the drawing office and go into the works to see whether the design is being properly carried out, we find that it is not being done quite in the way that we might have expected.

The single cell which is the fertilized egg divides into two by a meridionally placed line of fission, and the two cells which result from this divide meridionally and so become four, the second line of division being at right angles to the first. It might have been expected that in further divisions the lines of division would continue to be meridional and to bisect the four cells in this way. But this is not the case. The third cleavage, instead of being meridional is horizontal or zonal; moreover it is not equatorial, that is, it does not divide the four cells which have been formed into two groups of four equal-sized cells in each, but it cuts off a group of four small cells from the top ends of the four large cells and leaves the lower parts still of large size. At the next cleavage a horizontal division again occurs. Another set of four small cells is cut off from the upper ends of the macromeres and at the same time the first set of four little cells also divide. This sort of thing is repeated some four or five times.

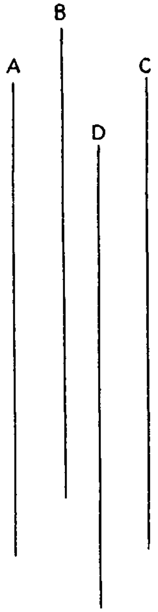

Fig. 13.—The four main axes described in the text.

There is nothing in the drawing office to show why this peculiar method of going to work should have been adopted. It might at first be thought that the principle being followed was that each plane of fission should be at right angles to the one preceding it, but when we find that the fourth cleavage is not only in the same plane as the third one, but like it is also unequal, this idea becomes untenable.

The explanation is given when the development of some other animals is observed, or rather, when their life cycle is traced.

It is well known that among some animals reproduction takes place sometimes asexually and sometimes through sexual means; they show in fact an alternation of generations. The best known instance of this phenomenon is the case of the Aphidæ among the Insects, but it is also seen in other groups, such as the Scyphozoa among the cœlenterates, and it occurs among the Protozoa. The parasite which causes malaria is a sporozoon which commonly multiplies asexually, but after it has lived for some time in a man then sexual forms of the sporozoon begin to appear, and it has been thought that the occurrence of these sexual forms is due to the reaction on the part of the host to the presence of the increasing numbers of parasites (Schaudinn).

In the usual course of affairs the members of the asexual generation are separate individuals, but among the cœlenterates the sexually produced planula larva of Scyphozoa sometimes shows a scyphistoma stage which is attached to a rock by a narrow base while its upper end has a set of tentacles round its rim. A little below this rim a constriction occurs and eventually cuts off this upper layer, which swims away as a new scyphozoon. The part left behind forms tentacles round its edge again and then it too becomes constricted off like the first one did, and so the process is repeated several times. The asexually produced individuals are separated off eventually, but at first they are seen in course of formation as part of the scyphistoma.

Among the tapeworms this kind of thing is seen in a more advanced stage. The scolex or so-called head of the tapeworm is little more than an organ of attachment, and it is the direct successor or modification of the sexually produced embryo. From the scolex there grows out the long series of segments or proglottides which constitute the 'worm'. These segments close to the scolex are scarcely discernible, but as they get pushed further and further away they become more and more developed and half way along the length of the chain they are sexually mature. By the time the segments reach the end whence they become detached the eggs inside the uterus of each proglottis are fertilized and ripe. The 'worm', then, may be regarded as an asexual phase of which the members remain connected for a longer time than is generally the case.

Having observed these things, it is now easy for us to see that the successive quartettes of micromeres which are budded off from the four macromeres of *Polygordius* represent an asexual phase following upon the sexual union of the members of the two pairs of macromeres.

It is the fact that the four cells of each quartette are budded off simultaneously, which makes it seem probable that the anterior and the posterior pair of original blastulæ were in a larval stage when they united to produce the anneïid.

Before returning to the drawing office there is another structural detail which ought to be pointed out.

After the fifth quartette of micromeres has been given off and the residual macromeres have divided so as to form nine cells, no more cells are formed for a time. This, then, marks a very definite stage in the history of the embryo, and it is interesting to note the number of cells which have been formed from each quartette. If we make a graph as shown in the figure (*Fig.* 14) by drawing the ordinates of a length proportional to the number of cells formed from their respective quartettes and then draw a curve through their extremities, this curve is seen to be regular except that the ordinate of the fourth quartette fails to meet it, as does also that of the first, even though the ordinate of the first quartette is considerably longer than any other. Seeing that the first quartette is at one end of the curve, the failure of its ordinate to meet it might, it would seem, be due to some temporary lapse of activity, and be made good later on. But the fourth quartette seems to have no such excuse for its inactivity, and this prompts us to look for some inhibitory cause. At a later stage in the history of the embryo when growth starts again, it is the cells of the fourth quartette which show the greatest energy of growth. The delay for a time is followed by a proportionally greater outburst.

But why should there have been the delay ? And what has caused it ? The answer to these questions will be found soon after we have gone back to the drawing office.

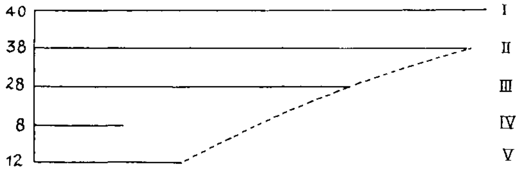

Fig. 14.—Graph, showing number of cells of quartettes.

Before leaving the workshops, one last look at the embryo under construction shows us that it is flattened out into an almost discoidal shape.

We left the design as that of a sphere which had been outlined by the concerted movements of an active meridian of each of the four phantom blastulæ. The visit to the works has shown that the carrying out of this design is being done in part by the original macromeres, and in part by the cells or micromeres of the asexual phase which follows upon the sexual union of the members of the two pairs of phantom blastulæ. To these four hypothetical blastulæ let us assign the names Blue, Green, Red, and Yellow respectively.

Perhaps a short pedantic dissertation may help to make the position of affairs more clear. It is a common saying that " two and two make four ", and, used colloquially, the saying is quite true, because we mean that by adding the numbers two and two we obtain the number four. But if we would be pedantic, then the saying is not true, because two and two do not necessarily make anything at all. The right thing to say is, " Two and two *are* four."

Now it is precisely at the stage when " two and two are four " that the design of *Polygordius* is at present, and the next stages are those in which it goes on to the " two and two *make* four " condition.

The reader may be inclined to think that this is an unnecessary point to pay attention to, but it seems to me that such an experiment as the destruction of half of an early embryo would be followed by complete reconstruction of the animal so long as the embryo had not gone beyond the " two and two *are* four " stage, whereas if it had passed that stage then some parts would fail to be properly designed and deformity would result.

Of the four phantoms, Phantom Blue has united with Phantom Green and Phantom Red has united with Phantom Yellow, to some extent at least, but up to this time there has been only a kind of adhesion between the Blue-Green pair and the Red-Yellow pair.

The manner of union of Blue and Green has been for one to roll towards the other, and the same is true for Phantoms Red and Yellow.

If, therefore, these two pairs are to unite by a similar process of rolling one towards the other, they will have to turn round axes so placed that the new movement does not interfere with rotation round the main axis. There is nothing in the history of this period of the development of *Polygordius* to show that " the even tenor of its way " is disturbed, whereas if the secondary movement interfered with the primary one some irregularity would be bound to follow. As it is, the developing embryo steadily flattens itself out into a regular discoid form and then later on regains its globular shape.

These changes of shape can be easily accounted for by imagining that the four main axes are themselves turning round four secondary axes which are regularly placed like the four sides of a square all in one plane. For, if this were not the case, then the embryo would not have that regular and symmetrical outline which it has.

While the embryo is of globular shape, before it begins to flatten out, the design of it is made by the four phantom blastulæ Blue, Green, Red, and Yellow, each of these having a main axis which, when the embryo first becomes a blastula, is set upright and parallel to its fellows. The secondary axis about which this main axis turns is at right angles to the main axis and lies in the same plane as the other three secondary axes do. These four secondary axes can be graphically represented as the four sides of a square drawn upon a sheet of cardboard, while the main axes could be likened to four needles thrust through the mid-point of the sides and at first all standing vertically. But no mention has yet been made of the level at which this plane of the secondary axes is placed. It seems obvious that it is not at the half-way point of the length of the main axes that this plane is situated, for if it were there, then there would be no reason for the flattening out. This phenomenon shows that there is some distortion of the original dimensions, while the re-attainment of the globular shape at a later time shows that the distortion is only temporary.

A simple idea suggests itself, viz., that the inhibition of cell division of the cells of the fourth quartette is due to this being the particular region where the four main axes are most firmly tethered together, so that other activities are hindered, but as compensation for this, the necessarily more intimate union of the four components of the animal at this locality results, later on, in an enhanced outburst of active growth. If these things be so, it is necessary to find out, approximately at least, at what level along the length of the main axes, when these are set vertically, the fourth quartette cells are to be found.

So many data which would be required for an accurate determination of it are impossible of being ascertained, that a rough method was employed. Masses of plasticine were weighed out proportional to the number of cells formed from each quartette of micromeres, a different colour being used for each quartette. There were thus six masses of plasticine, one for each quartette and one for the residual macromeres. These masses were then moulded in as even a thickness as possible in the form of an upper and lower circular cap and four intermediate zones over the surface of an india-rubber ball, so as to cover it in entirely. This of course was done on the assumption that the ideal form of the embryo at this stage is a sphere, and that the ideal arrangement of the quartettes of micromeres is in successive belts. By this device the position of the narrow belt which the cells of the fourth quartette form is found to be at a level above the lower end of the main axis of one-fifth of its length. Consequently in a diagrammatic model with the four secondary axes represented as the four sides of a square and the four main axes represented by four needles thrust vertically through the middle points of the sides of the square, four-fifths of the needles would be above the level of the card and one-fifth below it, as shown in *Fig.* 15.

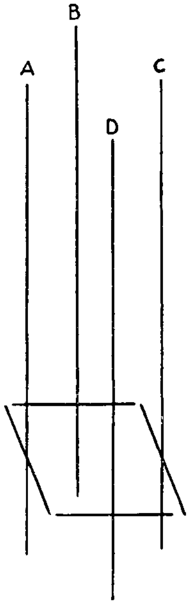

Fig. 15.—The four main and four secondary axes.

For the union of the Blue-Green phantom with the Red-Yellow phantom the long main axes have to turn round the secondary axes, and owing to the low level of the plane of these secondary axes the design flattens out and does so to an extreme degree. In fact the distortion of the design is so excessive that in order to preserve the integrity of the animal and yet fulfil the design, the cells round the edge have to become vacuolated and in this way occupy an unwonted amount of space. The greatest flattening, of course, occurs when the four main axes are all as near the horizontal position as possible. Later events go to show that the Blue-Green axes reach the horizontal position before those of the Red-Yellow phantom, so that at no time can all four be in the exactly horizontal position at once.

Thus far, the interpretation of the phenomena of the development of *Polygordius* has been fairly easy. The next stages are much more difficult to follow, and the account about to be given is tentative only.

There are certain cells which undergo much transposition. While the majority of cells show either a steady invagination or gradual regular movement, these other cells are translated in various directions in a different manner.

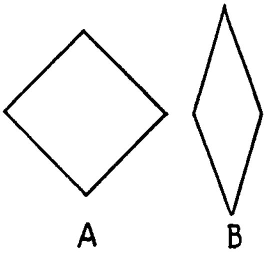

Fig. 16.—Diagram showing change in the relative position of the four secondary axes from A to B.

During the time that the embryo is flattening out, and cell division still going on, the shape is that of a nearly round disc, and this can hardly be the result of anything but symmetrical designing movements in all four quadrants. It is precisely what would occur if the main axes of the four phantoms as they turn were placed like the four arms of a cross.

But when cell-division has ceased for the time being, and the embryo begins to return towards a globular form again, the invagination of the under surface, though it begins in the centre, soon shows a depression longer anteriorly than from side to side, indicating that some change in the design has occurred—either an actual alteration in the position of the secondary axes from being like the sides of a square to becoming the sides of a rhomb or diamond (*Fig.* 16), or, if the secondary axes remain unchanged in position, then the alteration is due to the active meridians.

Seeing that the embryo later on regains its globular form, there is no reason to think that any change has occurred in the relative positions of the secondary axes; moreover, the oval shape of the primary blastopore and its subsequent constriction and division into two are but the natural consequence of a design sketched by four phantom blastulæ when the two members of the anterior pair roll towards one another and the two members of the posterior roll towards one another, especially, if as already stated, one of the pairs is a little in advance of the other in the degree of the rotation of its main axes round the secondary axes.

An active meridian has already been postulated as the phantom agent which designs the phantom blastulæ, and it is not difficult to realise that when the main axis of a blastula is in the horizontal position, if the active meridian is at that moment hanging vertically down from it, any turning of it round the main axis in either direction is bound to make it begin to rise. This then is the cause of the invagination.

It is necessary to remember, however, that while the active meridian is turning round the main axis, that axis itself is turning round its secondary axis, and the effect of this is eventually to bring it from a position at right angles to its fellow to one in which the main axis is parallel to that of its fellow. This is probably one of the factors concerned in causing the mouth to have the form of a broad slit.

Hitherto no mention has been made that the path followed by the active meridian may be other than a circular one as it turns round the main axis; but if this path be circular, it is difficult if not impossible to account for the formation of the organs as described by Woltereck. By supposing a spiral path, however, for the active meridians instead of a circular one, we can see that the viscera may be designed by them, and then the cells which are the material part of the animal are constrained to carry out the design.

Woltereck in his paper (*Arch. für Entwick.-mech.*, vol. 18, 1903) gives figures of the under aspect of the embryo *Polygordius* at various stages, beginning with the time when the 135 (or 137) cells have been formed, and ending with the trochophore larva furnished with stomadæum, stomach, valve, intestine, archinephridia, ciliated bands and tufts. These figures are capable of being superposed, and then they give an idea of the relative positions of the cells and of their migrations.

The cells which are specially notable for their movement are: $3c^{1a}$, $3c^{2a1}$, $3c^{2a2}$, $3c^{1p}$, $3c^{2paa}$, $3c^{2pap}$, $3c^{2ppa}$, $3c^{2ppp}$, $3d^{1a}$, $3d^{2a1}$, $3d^{2a2}$, $3d^{1p}$, $3d^{2paa}$, $3d^{2pap}$, $3d^{2ppa}$, $3d^{2ppp}$; in other words, all the descendants of the cells 3c and 3d, together with the cell $2d^{222}$.

By superposing one figure on another, bringing the outlines of them into as close correspondence as possible, and keeping the middle part of the mass of entomeres (residual macromeres) central, it is possible by marking the position of the centre of each cell by a dot to get some idea of the path which these cells take.

Fig. 17 was drawn in this way, and two things come out very clearly from the study of it. One of these is, that the cells of the right and left sides do not cross, although Woltereck's figures show that they meet; the other is, that all these cells move forwards.

The approach then of the main axis of quadrant Red to that of quadrant Yellow as they pass from being at right angles in the horizontal position to being parallel in the vertical position, is counteracted by the diverging paths of their active meridians as they turn round their respective main axes, and so the designs of the phantom blastulæ at present do not cross. The second finding, viz., the general forward movement of the cells, is accounted for if the rotation of the main axes of quadrants Red and Yellow is somewhat later than that of the main axes of Blue and Green as they turn about their secondary axes. The design made by phantoms Red and Yellow, then, covers in that made by phantoms Blue and Green.

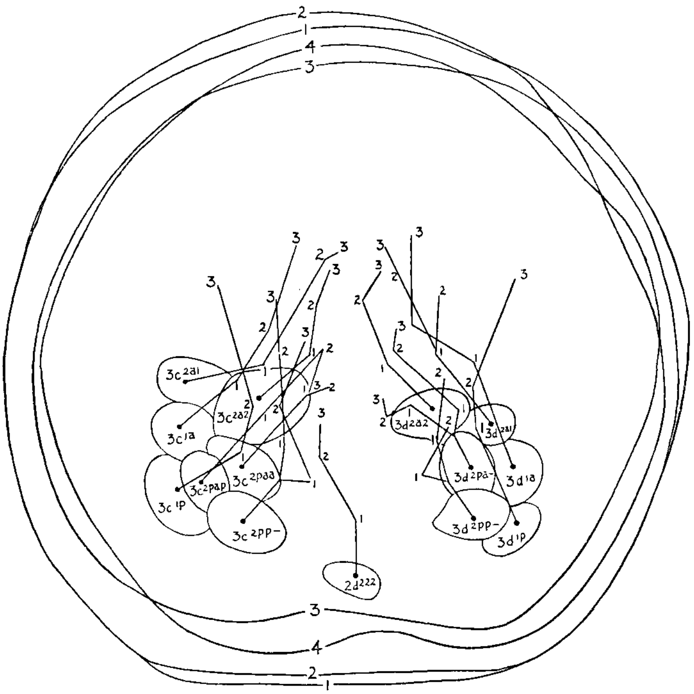

Fig. 17.—Composite diagram from Woltereck's figures, showing drift of cells of c and d quadrants. The successive outlines are numbered 1, 2, 3, 4. The original positions of the cells are shown, and the three subsequent positions 1, 2, 3.

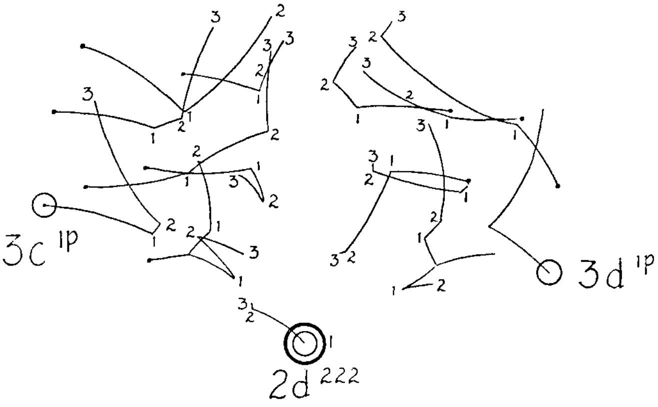

Fig. 18.—Constructed from the same source as *Fig.* 17, but the cells $3c^{1p}$ $3d^{1p}$, and $2d^{222}$ are kept as fixed as possible.

Having now dealt with the general forward movement of the cells we are specially considering, we can turn our attention to other factors dominating the paths of the cells. Using the same figures given by Woltereck, but keeping the three cells $3c^{1p}$, $3d^{1p}$, and $2d^{222}$ in as constant a position as possible, *Fig.* 18 is obtained, and this may be modified by drawing the paths as curves, giving *Fig.* 19. Finally the obvious drift to the left may be eliminated and the whole conventionalized into a symmetrical form as shown in *Fig.* 20, and with this before us it may be possible to see the design of the animal in the making.

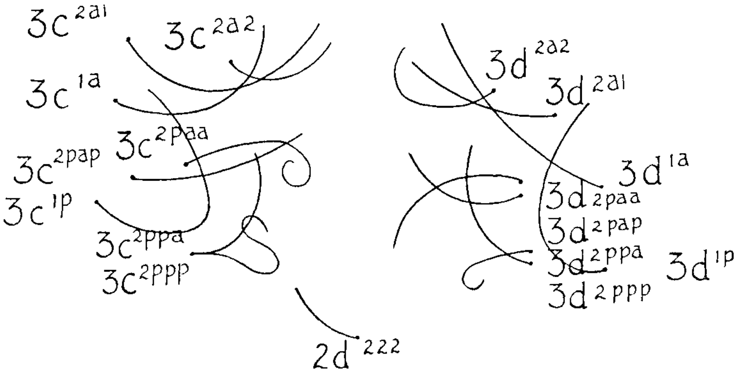

Fig. 19.—The same as *Fig.* 18, but with curves substituted for straight lines.

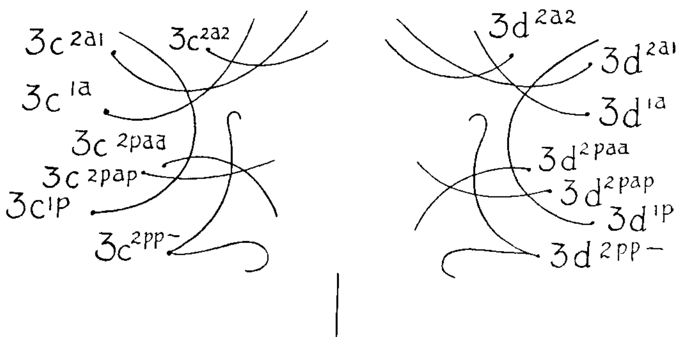

Fig. 20.—Conventionalized final result.

Seven cells on either side are under consideration, but they soon become eight in number by the division of one of them into two.

The general impression conveyed by the diagram is that the cells $3c^{2ppa}$, $3d^{2ppa}$ lie almost along some axis of rotation, and $3c^{2ppp}$, $3d^{2ppp}$ are in very nearly a similar position. At a greater distance from the axis but moving in the same direction are the paths for $3c^{2paa}$, $3d^{2paa}$. The paths of all the other cells except $2d^{222}$ curve in the opposite direction; $3c^{2pap}$, $3d^{2pap}$ have slightly curved paths, so have $3c^{1a}$, $3d^{1a}$; more curved are the paths of $3c^{2a1}$, $3d^{2a1}$, $3c^{2a2}$, $3d^{2a2}$, while $3c^{1p}$, $3d^{1p}$ have the most curved paths of all.

It will be observed that the cells $3c^{2a2}$, $3c^{2a1}$, $3c^{1a}$, $3c^{1p}$, are at first placed in that order from front to back. Their movements bring them into the same order, but in a line almost at right angles to their original one. The same thing, of course, is true of the cells of the other side which correspond to them, viz., $3d^{2a2}$, $3d^{2a1}$, $3d^{1a}$, $3d^{1p}$. Except cells $3c^{1p}$, $3d^{1p}$ they move, like all the other cells under consideration, inwards towards the middle line, but during their journey their alignment becomes turned through about a quarter of a circle.

The paths of $3c^{1p}$, $3d^{1p}$ do not seem to be under the same influence; they move quite as much away from the middle line as they do towards it, and form the greater part of the metatroch on the surface of the animal and do not enter into the composition of the viscera.

Woltereck's figures of the early stages of invagination show first of all an oval impression, the edges of which then become pinched in to form a figure-of-eight. Next they meet, and divide the opening into two—an anterior one the mouth, which never closes up, but widens out transversely, and a posterior one, the anus, which before long closes up.

It is to this and the immediately following stages that the movements of the descendants of the cells 3c, 3d belong. As far as the hollow organs are concerned there are two groups of these cells. One group turns forwards and inwards, and the other group turns backwards and inwards. That at least is the brief summary of the results arrived at from the foregoing study of the diagrams, or, keeping to the metaphor used before, that is what has been learnt during the tour of the erecting shops.

On returning to the drawing office we find that there are required for drawing the designs the same instruments as before—namely, the active meridians with their main and secondary axes.

At first, when the embryo is in the form of a sphere, the main axes are all set nearly vertically. From this time they begin to diverge, and when the main axes are all as nearly horizontal as possible the embryo has attained to its most discoidal shape.

When the original upper ends of the main axes (which for convenience may be called their north poles) are below, so that the main axes slope downwards while still pointing outwards, the middle of the under surface begins to be tucked in because the active meridians are now rolling together, those of phantoms Blue and Green towards one another, and those of phantoms Red and Yellow towards one another. But the active meridians of phantoms Blue and Green are more advanced along their course than are those of phantoms Red and Yellow, so that while the main axes (of phantoms Blue and Green), as they turn round their secondary axes, gradually approach one another as they become more vertical in position again, the active meridians are turning away from one another and so the mouth opening is never closed.

In phantoms Red and Yellow the active meridians are still approaching one another when the main axes are also coming nearer together.

It is to be remembered that at the level of the secondary axes the main axes are stationary as regards approaching or receding from one another, and the nearer a point on the main axis is to the level of the secondary axis the less will be its movement from this cause, and in consequence the greater will be the effect of the turning of the active meridian round the main axis. This, then, is an adequate cause for the narrowing and subsequent cutting into two of the primary blastopore, which is the name given to the oval depression which first is seen when invagination begins. Following on this is the closure of the hinder of the two openings (or primitive anus) according to the design, the manner of making which has just been given.

After this, the continued turning of the main axes round their secondary axes causes the embryo to become of conical shape, and invaginates still more of the under surface, deepening the stomadæum, burying the site of the primitive anus under a layer of cells, and defining a more complex alimentary canal as the design of the body grows more bulky to house it.

For showing the manner in which the design of the viscera is sketched out, the reader will, I think, learn more from considering the diagrams given in ***Fig.*** 21 than by trying to follow a long wordy description. Let it suffice to say that while a meridian in turning round the axis of a sphere describes the entire surface contour of the sphere, the same meridian if transported along a straight line (perpendicular to the plane in which the meridian lies) would describe a trough or gutter. The active meridians of the phantoms designing *Polygordius*, being under the influence of two simultaneous turning movements, describe contorted gutters, as shown in the diagrams, and these when associated together are found to complete the designs of the hollow organs.

In the next chapter suggestions are made as to the nature of these supposed active meridians and main axes. They are abstract things, and regarded as modified parts of one and the same cycle, as shown in ***Fig.*** 22. In ***Fig.*** 21 the main axes are not shown. Each contorted gutter consists of an enormous number of successive positions of the active meridian, and might have been drawn as shown in ***Fig.*** 23, if such a method of depicting them would not have spoilt the clearness of the diagram as a whole. The curvature of the meridians is probably to some extent variable and capable of adaptation to circumstances; but such variations could not be shown in the diagram, because it is not certain either whether they do really occur, or (if they occur) what their nature and extent may be.

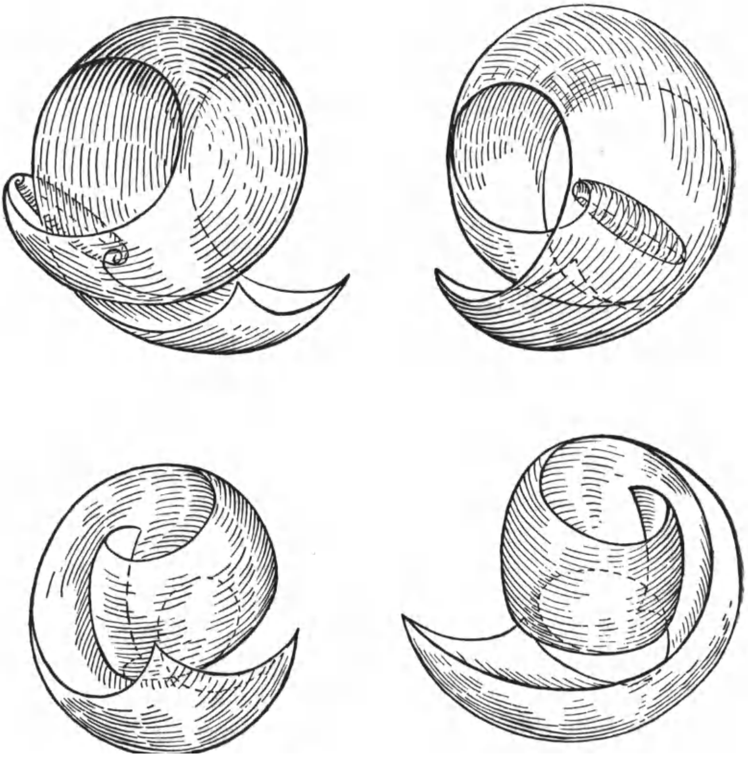

Fig. 21.—Diagrams showing part of the paths of the active meridians of the phantom blastulæ. Above are the paths of phantoms Blue (right) and Green (left), and below those of phantoms Red (right) and Yellow (left). All four are shown begun at the time when the main axes of the phantoms are practically horizontal. The curvature of the meridians is only slightly marked, in order that their paths may be more easily discerned.

Actually, the phantoms Blue and Green can be held responsible for designing the stomadæum, the posterior part of the stomach, and the two archinephridia, while the phantoms Red and Yellow can be credited with the anterior part of the stomach and the intestine.

If, instead of representing the paths of these meridians as following their proper paths in three dimensions of space, we take the paths in two dimensions only, and consider their tracks round the main axes, we see that these paths are not circular, but are spirals. It has been found necessary to represent them in this way if they are to be successful in designing the viscera. Precisely why these courses should be in the form of spirals I cannot say, although it is not difficult to imagine several possible causes. But it is well to remember that the difference between a circular and a spiral course is one of angular acceleration only, and that a meridian does not travel through any greater or less distance in a given time; its rate of travel is not altered, but only its direction.

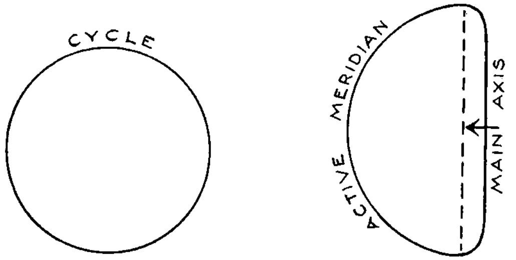

Fig. 22.—Showing the relationship between the cycle and the active meridian and main axis.

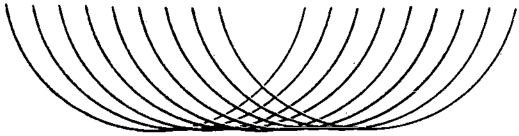

Fig. 23.—Illustrating the formation of the gutter by successive positions of the active meridian.

The steepness of the pitch of the spiral course of phantoms Blue and Green is probably twice as great as the steepness of the spirals of phantoms Red and Yellow. A reference to *Fig.* 24 will show that, while at first there is but little difference in the course of the two spirals, there is in the later stages a great difference.

Phantoms Blue and Green design narrow tubes, which are separate from one another, while phantoms Red and Yellow together make the design of a single wide structure —the intestine.

The spiral courses, like the active meridians, are not material in the sense of being formed of visible particles, but having been described they determine the form of the structures which the cells of the embryo perforce have to build.

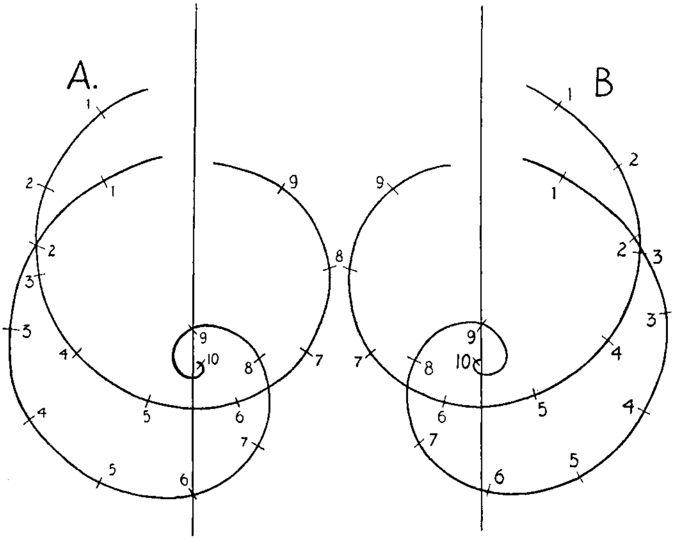

Fig. 24.—Spiral paths of rotation of phantom blastulæ round main axes.

There are some interesting points which the reader may take note of now. The stomach, inasmuch as it represents one blastular cavity stowed within another (which is the trochophore larva), is built up by all the four phantoms that enter into the composition of *Polygordius*. This is as it should be, for all metazoan animals exhibit a gastrular stage. The other points of interest concern the spiral curves.

In order to find the course which a spiral curve takes, provided it is a perfectly regular one, a very simple way is to draw a large circle with a large number of evenly-spaced radii. Then, selecting one radius as a starting point, mark the point where it cuts the circle. Make a mark on the next radius at a given (small) distance along it nearer the centre. The mark on the next radius is put at twice this distance from the circumference, that on the fourth radius at three times the distance, and so on. An evenly-curved line through all the points marked in this way will give a regular spiral, and this spiral comes to an end at the centre. This is the most regular type of spiral. Many other types of spiral may be drawn by other methods, but this simple type seems to be all that is necessary for explaining the formation of the organs of *Polygordius.*

It is evident that although the spiral comes to an end at the centre, yet, by continuing the same process of marking the radii past the centre, a similar spiral will be drawn, which, however, opens out instead of closing in as the former one did.

There is evidence that this actually happens in the case of *Polygordius.* The archinephridium which has been modified to form the first protonephridium, breaks up and disappears at the metamorphosis. The cells forming the wall of the trochosphere on either edge of the prototrochal belt begin to wilt shortly before the violent changes of the metamorphosis set in. The stomach too at this time becomes reduced in size and is ultimately got rid of.

Now the re-describing of a spiral design, opening out instead of closing in, but still going on in the same direction, would but design fresh structures or reinforce those already existing. But this is not what happens in the *Polygordius* embryo, because the turning of the main axes on their secondary axes has the effect of causing the later spiral paths to run in the opposite direction to the earlier ones. This reversal begins when the main axes have turned through a quarter of a circle, and reaches its maximum when they have turned another ninety degrees, after which it fades away again.

The supposition that the main axes of phantoms Blue and Green are relatively more advanced in their rotation round their secondary axes than are the main axes of phantoms Red and Yellow, accounts for certain of the phenomena which have been recorded by Woltereck.

In the first place the closure of the primitive anus may be attributed to convergence of the backward moving designs of phantoms Blue and Green. Then, as the 'north poles' of the main axes of these begin to lift, those of phantoms Red and Yellow will be nearing their lowest position, so that a space is left between the two designs. Moreover, when phantoms Blue and Green are in this position, they both point inwards so much that their cavities must coalesce. In this way is explained the appearance of the space which Woltereck calls the Neocœle. It opens on the one hand into the blastocœle of the embryo, and on the other to the exterior, but this latter opening is very transient.

Again, the forward movement of the cells of quadrants C and D must be put down to the sweeping forwards of the Red and Yellow phantoms, although in part it may be accounted for by rotation of the active meridians. But the remarkable travel of the cell $2d^{222}$ over the ventral aspect of the cells $4d^{r}$, $4d^{l}$ seems entirely to depend upon the forward movement of the main axes, and not at all upon any rotation of the active meridians. In a later chapter some remarks will be made concerning the supposed nature of such hypothetical things as the phantom blastulæ, their main axes, and the active meridians, with a view to endorsing their reality, but at present I can only ask the reader to admit their utility for the purposes of explanation.

The cell $2d^{222}$ is, almost certainly, the cell from which the ventral nerve-cord of the adult worm is derived, and here it is being carried over those cells of the fourth quartette which are the mother cells of the adult mesoderm and intestine. In the trochophore larva, two stout nerve-strands connect the cell $2d^{222}$ with the nerve-cells situated beneath the apical plate which constitute the supra-œsophageal ganglion, and so we see that in this way a large loop of nervous tissue is made and carried like a skipping rope over the rudiment of the alimentary canal. In the trochosphere larva these two large strands of nerve tissue run round the periphery of the embryo practically from the upper to the lower pole, and are at some distance from the alimentary canal which they encircle. At the metamorphosis, the stomach of the embryo undergoes dissolution, and the alimentary canal is completed by the fusion of the newly re-formed œsophagus with the anterior end of the intestine. It is therefore much smaller in diameter. But while so much of the embryo is destroyed the nerve loop is not. Instead, it becomes shortened and thickened to an extraordinary degree and forms the nerve collar. Thus the camel has passed through the eye of the needle, and Nature has accomplished it by allowing the camel to go through as an embryo, and making the eye of the needle of extra large size until the passage is effected. Theoretically, it is the eye of the needle which is passed over the diminutive camel. The present theory does not seem capable of explaining why it should be a loop of nerve tissue which is carried in this way over the gut rudiment, but only why, granted the presence of nerve material in this situation, it follows this path.

The allusions to the metamorphosis are in some respects rather premature, but they are so bound up with the rotation of the phantoms that it seemed a pity to interrupt the story of them.

On referring to *Fig.* 25 the reader will observe the shortness of the length of the archinephridia and the obliquity of their position. The design of them, it will be remembered, was attributed to the rapid angular velocity of the active meridians of phantoms Blue and Green which are responsible for them. While the next portions of these meridians would lie in the substance of the body wall and so at this stage do no more than outline a fine channel through it, their terminal parts may reach the outer surface of the trochosphere and be the cause of the elongation of the cells $3c^{1p}$, $3d^{1p}$ to form the metatroch. This, however, is very conjectural.

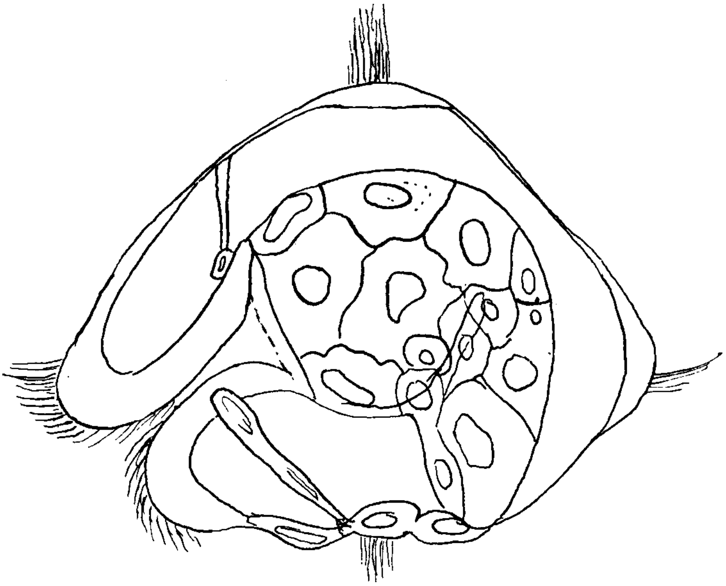

Fig. 25.—Optical section of early trochophore larva of *Polygordius*. (*After Woltereck.*)

All the time that the organs have been taking shape in the trochophore larva no food has been taken. But when the changes are completed then the larva begins to feed again. Following upon this the animal starts to grow. It seems to be impossible, however, to ascribe the character of the growth which takes place either to the food itself or to the habits of the animal.

The parts which now grow form the body of the worm itself. The actual manner of growth is rather different in the two species described by Woltereck, but the ultimate result is the same.

Hypothesis can point to a reason for this growth as well as for its nature.

In an earlier part of this chapter the budding off of quartettes of micromeres from the macromeres was shown to represent an asexual phase in succession to the phase of sexual union when phantoms Blue and Green united, and phantoms Red and Yellow united. Then cell-division came to an end, and the formation of the viscera took place. During this process, as we have seen, the union of the Blue-Green animal with the Red-Yellow phantom animal occurs. This, then, is a second sexual union in the phylogeny of *Polygordius*, and therefore it is followed by a second period of asexual production. The characteristics of asexual production are repetitions without the appearance of new structures. The body of the worm as it now grows, presents an alimentary canal which is made up of a continuous chain of miniature replicas of the intestine of the trochosphere. In the same way the permanent nephridia are repetitions of the protonephridia, and the nerve-cord and skin are continuations of structures present in the trochosphere. For a second time, then, we find that growth in size is due to the asexual phase, while structural innovations only come in during the sexual phase.

In *Polygordius* there is some overlapping in point of time of the two phases, for as the worm develops, a new structure appears, which is not only explicable on the present hypothesis but is actually demanded by it. This structure is the cœlom.

The embryo of *Polygordius*, although it exhibits a gastrula stage, yet differs from a cœlenterate in possessing a blastocœlic cavity between the alimentary canal and the body wall. The cavity of the blastula of both the Blue-Green moiety and of the Red-Yellow moiety is evidently in existence in the embryo when it is in its most flattened condition, for at this time there has been very little fusion of them, and yet the blastula cavity extends into all parts except the extreme edge.

The initiation of such an important structure as the cœlom, however, might be expected to be marked in some way in the embryology of the animal, and indeed this is the case. The actual irruption of the body cavity of the one cœlenterate ancestor into that of the other is seen in the formation of the Neocœle as mentioned above.

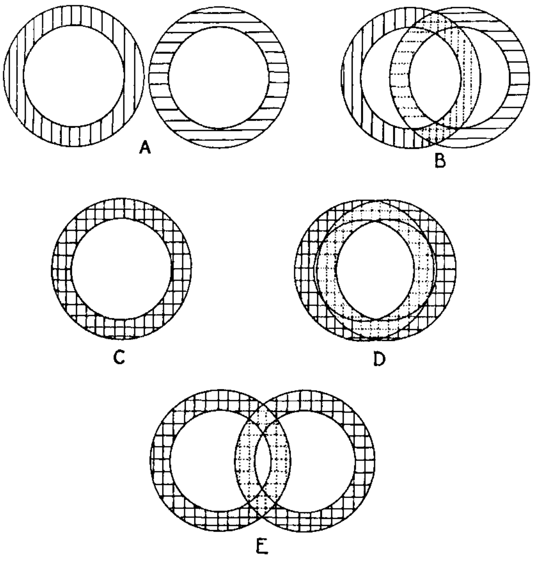

Fig. 26.—Diagram illustrating crossing of blastulæ. A, Two blastulæ, separate; B, The two have met—the portions dotted are not seen in real life; C, The two coincide as nearly as possible—gastrula stage; D, The two, having coincided and mutually exchanged properties, begin under constraining influences to draw apart—the original blastular cavity is enclosed by the dotted part, and the new cavities just beginning on either side will be the cœlom; E, Later stage as in *Polygordius.*

In the case of two blastulæ fusing to form a gastrula there is no cause for one cavity to do more than become as nearly coincident as possible with the other, as in cœlenterates. But when two cœlenterate-like animals fuse, the process of the second fusion may constrain the cavities in another manner, and cause them to meet, fuse, become coincident, cross over, and reappear again as two cavities. These new cavities should possess all the potentialities of the body cavities from which they have originated, and be representative of the whole interior economy of the animal. It may be on this account that the genital cells are found in the cœlomic space.

As the cœlomic cavities increase in size, so the blastocœle diminishes in size, as can be seen from the diagram (*Fig.* 26) that it may be expected to do.

The fact that in the adult worm there are no nephridial tubes in some of the anterior segments is easily explained on the assumption that the rudiments of these anterior segments were begun before the design of the archinephridia had been completed.

The anal extremity of the worm is formed by what was formerly the lower pole of the trochosphere, and the body segments have been formed between the upper and lower pole of the trochosphere.

Judging from Woltereck's description of the embryo, it is highly probable that the Red-Yellow phantom ancestor was inverted when it fused with the Blue-Green phantom. This possibility does not, so far as I can see, affect the theory.

A large number of anatomical minutiæ have not been considered, but the main features of the development of *Polygordius* have now been dealt with.

CHAPTER IV

FURTHER CONSIDERATIONS

FOR most people, I suppose, the subject of disinfection is associated with ideas of illness and general inconvenience. But from a biological standpoint it is seen in a very different light.

In the *Journal of Hygiene*, 1908, Dr. Harriette Chick contributed a paper on " An Investigation of the Laws of Disinfection," and among other conclusions which she arrived at concerning disinfection by chemical reagents are to be found these :—

" It is a gradual process, without any sudden effects, and if the disinfectant is sufficiently dilute to admit of a reasonable time being taken for the process, the reaction velocity can be studied by enumerating the surviving bacteria at successive intervals of time."

" In the case of disinfection of anthrax spores the reaction proceeds according to the well-known equation for a unimolecular reaction embodying Guldberg and Waage's law."

And in another part of the paper she says :—

" We may employ one of the well-known interpretations as to why these reactions should be gradual and not sudden, viz., that at a particular time only a proportion of the . . . bacteria are temporarily in such a state as to permit of the combination " with the disinfectant. Dr. Chick was here referring to the idea of a cycle of changes occurring in what is practically an isolated system, and the time of its susceptibility to external influences lasting for only part of that cycle.

In her experiments with living bacilli clear-cut results could not be obtained, for, because of the rapidity with which the bacilli multiply in culture, they are of all different ages. But when dealing with the spores of *Bacillus anthracis* the results are much more exact.

It should be remarked that the 'spore' of the anthrax bacillus is a nearly round body with a thick protective covering. One bacillus gives rise to one spore, and the spore is considered to be a more resistant form of the organism. When placed again in favourable conditions, the spore becomes a bacillus—but only one, and no more—although this bacillus can then grow and multiply as usual. The point to note is, that spore-formation is not a method of multiplication. By virtue of its capsule each spore is isolated and becomes almost a little world of its own, and the protected life of the spore is slow-going compared with that of the bacillus; consequently a collection of spores is like a population of nearly uniform age.

The nearly-round form of the spore, and its protective coat, seem to make it actually like a diagrammatic illustration of the theory of the process of disinfection put forward by Dr. Chick, in depicting her view of what takes place.

The spores of anthrax bacilli are but single modified vegetable cells of rounded form, but it is not difficult to imagine for the many-celled blastula of an animal, which also (when free and unencumbered by yolk) is of nearly globular form, that its life, too, may consist of a series of chemical reactions of a cyclic character, very much in the same way as the life of the spores of bacilli is held to consist of a cycle, or cycles, of changes. These reactions in an animal would not be violent ones, but only of the nature of an exchange of a small organic grouping or molecule between two cells or parts of a cell. These exchanges then can be supposed to lead to similar small exchanges in their immediate neighbours.

If we assume that, for the blastula to live, some changes of this sort must be going on every moment, it gives us the conception of a rapid current of minute particles travelling at a high speed round the circuit of the system and having to go by a route which, though capable of modification in many ways, yet can, in one direction at least, not be shortened at all; that is to say, not one of the really essential reactions can be left out. The current does not consist always of the same particles, but the arrival of one particle at a point necessitates the departure at once of another from that point to the next, and so on. And these changes probably occur hundreds of times in a second of time.

It has been said (by the late Sir William Crookes) that if a drop of water could be magnified to the size of the earth, the atoms in it would appear about the size of a football. If even as many as a thousand million blastulæ could be packed into a drop of water, and the moving particles, on an average, consisted of ten atoms each, there would yet be almost incredible numbers of particles to be moved, if they all took it in turn, before it came to the same one's turn again.

An example of a very short cycle of chemical changes is seen in the continuous method of the manufacture of ether. It is not unreasonable to suppose that many cycles of changes occur in natural chemical processes, some of them entirely outside living cells, but some of them almost entirely within them, especially in such isolated units as free-moving animals are. It seems highly probable that the hollow ball of cells which we call a blastula maintains its integrity by reason of rapid cycles of changes occurring in its cells, by which very minute particles—far smaller than can be rendered visible—are in constant exchange. But these rapid cyclic movements, since they have to follow a particular route which may not be short-circuited without damage to the organism, would confer a rigidity upon the animal's structure, in the same way as a ring of chain can be made to have rigidity if it is given a rapid rotation.

By this time the reader will have guessed the drift of the foregoing remarks. It is to show that by regarding life as, in part at least, a cyclic succession of changes going on in a cell, or in a system of cells which has an existence independent of others (as a blastula has), we obtain the instruments needed for our designs—namely, a *main axis*, i.e., the diameter of the path which cannot be shortened although any of those about it may be shortened ; and the *active meridian*, which is the path of the rapid current of particles.

Since the same particles probably never complete a whole cycle of the life-activity of the blastula, the cycle itself may be regarded as an abstract entity, and in any case be considered to have those properties which have been claimed for it in the theory of the developmental history of *Polygordius.*

Presuming that these claims are admitted, it is worth while to make comments on some points which herein seem to be established.

It is not likely to have escaped the reader's notice that to postulate an abstract design as the controlling influence of developmental changes is practically tantamount to postulating a psychological quality. That is why it has been necessary to make it clear that, although the design may be abstract, yet the basis for it is attributable to the behaviour of material particles. Anyone who has read Professor Eddington's book, *The Nature of the Physical World,* will realize that, although at first sight this physical explanation of a psychological phenomenon seems to explain things, because we are so familiar with material objects, yet in reality it does not go far in that way, because the nature of matter itself is not rendered thereby one whit less mysterious.

But if indeed we behold in the control of an animal's development a simple psychological phenomenon, as seems to be the case, we can also easily perceive that such a thing can only happen in a complicated system, and that the more complicated an animal is in structure, the more psychological phenomena is it likely to exhibit.

If the design of an animal is an abstract idea, yet the animal body is a very concrete thing. The living animal is therefore a compromise between the ideal and the concrete, between the process and the substance. This is readily seen at some moments in the development of *Polygordius*, as for instance when the rapid turning of an active meridian passes through 360 degrees of angularity within the compass of a single cell, and the latter in consequence forms a narrow tube; for, although the spiral curve cannot form a circle, yet the thick cell can form a tube (*Fig.* 27).

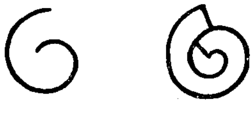

Fig. 27.—Showing how a spiral can form a tube.

In the course of the explanation of the embryological history of *Polygordius*, the assumption has been made that twice it exhibits a complete alternation of generations, and that while the asexual phases provide material, the sexual phases provide new structures. These suppositions seem to be confirmed and established by the precise and satisfactory way in which they have fitted into the scheme, and consequently a strict alternation of sexual and asexual phases bids fair to become an axiom of embryonic phylogeny. As a rider to this may be added the probability that long tubular structures represent asexually formed repetitions of hollow structures which for the most part originally had a globose form, and that serial structures in general have resulted during asexual phases.

The original hypothesis, then, of the dual constitution of all metazoan animals has dragged with it in its course other hypotheses which seem to agree with it in giving a true picture of affairs.

The period of an animal's existence when the design chiefly operates is during embryonic life—a period when either the animal is sheltered from the dangers of Natural Selection, or runs the gauntlet of immediate extinction. In the latter case Nature provides such enormous numbers that a few almost always survive.

If we regard the product of each fusion of two sufficiently unlike animals, in giving rise to a new type, as a kind of husk outside the previous ancestral stage, we can see that the workings of Natural Selection will affect immediately only the outermost husk, and hardly touch even the one next beneath; in fact, the deeper the other husks are, the less they will be affected. Also, the higher up that an animal is in the scale of complexity, the more husks will there be in its make-up, and the less, on this account, will be the amount of it which can be susceptible to modification by outside influences, though other happenings may come in here to mitigate this effect.

Up to the present the synthesis of *Polygordius* alone has been attempted in detail, though in a general way that of cœlenterates has been touched upon. It is easily possible that if the development of other cœlomate animals were studied in a similar way, further light would be thrown on obscure points, such as the formation of the protonephridia from the archinephridia, or the different method exhibited by *Polygordius lacteus* in its later larval stage, when the body of the worm, instead of growing out as in *P. appendiculatus,* is retained within a kind of amniotic fold of the lower part of the trochosphere.

Incidentally it may be remarked that since the ultimate result of the method of development of *P. lacteus* is the same as that of *P. appendiculatus,* the compressed and pleated condition of the worm-body in the one is the equivalent of the form in the other which grows out directly. The two are potentially alike. It will be remembered that the worm-body is put theoretically to the credit of the asexual phase when no fresh design is made, so that here we see the freedom of behaviour which nature grants to living things to enable them to adapt themselves to circumstances. A similar state of affairs is recognized in the case of ova. In eggs with much yolk the blastula is extremely flattened, while in eggs with little or no yolk the blastula may be almost globular. Ova, be it remembered, represent an asexual phase, and their development into animals only begins after the initiation of the sexual phase which is known as fertilization.

The more widely distinct the parents are which by their union give rise to a different type of offspring, the more pronounced is the diversity of the offspring from its predecessors likely to be. Also, the more often in an animal's ancestry a new type has arisen, the more complicated in structure must it be too.

It has already been mentioned that serial structures are indicative of an asexual phase; it may therefore be pointed out that the segmentation of the body is due to a process of this nature. This indeed was seen in the case of *Polygordius*.

In higher animals—e.g., fishes—the body may be definitely segmented, but if the meaning of 'segmentation' is really that the parts are produced in response to an asexual phase in the animal's phylogeny, then it would be absurd to expect that all the sets of serially repeated structures found in an animal—as, for instance, the gill arches, the fin-rays, the ribs, the vertebræ—are the outcome of one and the same asexual phase and therefore ought to show precise correspondence. It is far more probable that some of them might show exact agreement, but that not all of them would.

The theory of developmental history as given in the preceding chapter is to a large extent based on the tacit assumption that the rolling of one blastula towards the other is a process which takes place at a uniform speed—an assumption which is evidently made also for the life-processes going on in the bacterial spores. The mental picture presented of a cycle of changes constantly occurring within a cell or system of cells does not preclude the possibility of the cyclic route being a little inexact and the cycles being more like the form delineated by the thread in a ball of wool always passing along practically the largest circle possible but never quite meeting perfectly. The ancient Greek conception of the thread of life may, like so many of their thoughts, prove to be a wonderfully exact view.

In the development of *Polygordius* it was necessary to assume that each phantom blastula preserves its individuality unimpaired, which is equivalent to saying that the cycle of changes within the blastula continues incessantly. But while regularity of movement and individuality of existence continue, there may be compulsory motions impressed upon the phantoms owing to complicated conditions. The rolling of one blastula towards another seems to be due to a simple attraction acting from a single central point in each blastula—like a centre of gravity—and for this reason two blastulæ alone, when coincident, do not tend to go further; but when two pairs of blastulæ (at least) are concerned—as in cœlomate animals—then the movements of the larger phylogenetic components—e.g., the cœlenterate animals in the case of *Polygordius*—compel modifications of the movements of the smaller ones, and so the phantom blastulæ not only meet but cross over.

This, or compulsion due to a similar cause, may so displace the course of a design that it takes a longer time than it otherwise would to attain a certain point or to constitute a certain feature. In this way it may be that the phenomenon of heterochrony can occur.

If indeed the attraction of one blastula for another takes place from a centre—in the same way as we think of a centre of gravity—then the attraction will be greatest along the shortest line joining the two centres. This state of affairs is what has been claimed for *Polygordius*, and these centres for the four blastulæ were located in the plane of the fourth quartette.

Whether the intensity of the attractive force can be due to the diversion of other forces from their usual function at this region, or not, is open to question, but whatever the immediate cause may be, the cells of the fourth quartette remain for a long time almost inactive, until the fusion of the phantoms is well advanced and new energy is supplied by the resumption of feeding. The conditions remind us of the resting stage of protozoa previous to division, or, in the case of higher animals, of the immaturity of the ovaries until puberty and then of the almost complete inactivity of the ovum until it is fertilized. In the higher animals this inactivity of the ovum seems to point to all the activities of the animal being centred in this one place so that they are incapable of expression in action until there is sufficient material provided to give them scope for their performance.

Although the life of an animal only proceeds in one direction, yet hypothesis shows that design is not subject to this condition and may be reversed. There is no difficulty about this. The design is but the path of the active meridian; the active meridian itself is, however, held to be the path of actual particles. The path of these particles cannot be reversed.

Thus we see that a path in one plane—the path of the particles in the plane of the active meridian—is uniform and irreversible; while the other qualities are introduced through the abstract part of the system, and an additional dimension, so to say—the path of the meridian and not the path of the particles—is directly concerned.

Metamorphosis is put down to causes of this sort of reversibility in design, and is regarded as not an accidental occurrence but a deliberate act, in so far as it follows a definite plan (*see* page 55).

Of a different nature from either the concentration of potentialities in the genital cells, or from the time changes of heterochrony, or from the changes of metamorphosis, is the reduction of detail and shortening of developmental time seen when serial structures are produced in an asexual phase. In part it may be due to rapidity of production in order to satisfy the more urgent demands of design without fulfilling every detail, possibly because there may be a recrudescence of the stimulus to produce before each product attains to full size, or it may be that, as in *Polygordius*, the design tends to diminish in volume at the period when the preceding sexual phase is taking place.

The study of the synthesis of *Polygordius* opens up many possibilities, and these have been presented to the reader in a rather dogmatic form from the point of view of the hypothesis of the dual constitution of animals, and no attempt has been made to weigh up their relationship to any other hypothesis.

Vertebrated animals are far too complex for the method of synthesis to be used to explain their anatomy and development; for the study of the Herring, therefore, analysis must be used, and for this purpose some account of the fish's anatomy will be needed.

CHAPTER V

THE HERRING

(*Clupea harengus*)

DESCRIPTION

A good-sized adult herring is about a foot long, 2½ in. deep and 1½ in. broad.

When the mouth is closed the lower jaw projects further in front than any part of the face, and the black lower lip slopes forwards and downwards from the mouth opening to the point of the lower jaw. The lower lip is formed by a turned-down fold of skin which covers the bone beneath.

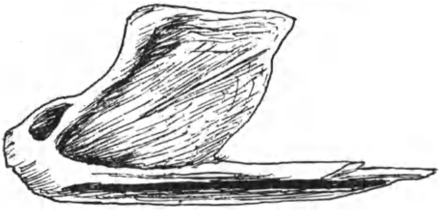

Fig. 28.—Dentary, left.

If the lower jaw is pushed down so as to open the mouth widely, the jaw looks as if it consists of a semicircular plate of bone on each side, hinged to the head at its hinder end. Actually each right and left half of the jaw consists of two bones, the dentary (***Fig.*** 28) in front, which is joined to its fellow by fibrous tissue at the tip of the jaw, and the angular (***Fig.*** 29) behind. The angular bone forms a hinge with the quadrate bone (***Fig.*** 30).

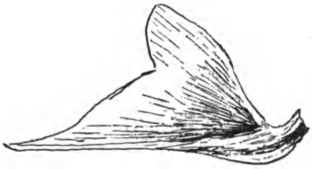

Fig. 29.—Angular, left.

When the mouth is closed the lower jaw fits into the deep groove formed by the upper jaw with its attendant bones and the premaxillæ (***Fig.*** 31).

The two little premaxillæ form the arch of the upper lip and are covered by black skin. They are curved bones, and their wider end, which is next the middle line, rests on the head of the maxilla. By their outer narrow end they are also anchored to the maxilla again. The maxilla (*Fig.* 32) itself is for the most part a flattened scale-like bone, but its anterior end is made of yellow bone and curves inwards in the upper lip, and the skin over this part of it is black.

Fig. 30.—Quadrate, left.

Fig. 31.—Premaxilla, left.

Fig. 32.—Maxilla, left.

Before dissection the outline of the maxilla on the side of the face appears with straight upper and lower edges and a rounded posterior end when the mouth is closed. But when the mouth is widely opened, the bone turns round into a nearly vertical position, and its upper edge—now become posterior—is seen to be supplemented by a thin bone, in shape like a fly's wing, lying over the rounded end—the buccal bone (*Fig.* 33); while a lesser narrow scale of bone, the supramaxillary (*Fig.* 34), lies along the border. The lower edge of the maxilla, now anterior, bounds the opening of the mouth, and is finely serrated.

Fig. 33.—Buccal, left.

Fig. 34.—Supramaxillary, left.

Fig. 35.—Nasal, left.

The upper edge of the lower jaw, when the mouth is being closed, passes up inside the maxilla and beneath the nasal bone (*Fig.* 35)—a thin leaf-like scale with a flat canal running along it. The outline of this bone cannot be very well made out, as it is imbedded in the skin. The bone is the most anterior of a series of bones of similar composition which partially encircle the orbit. The one next behind the nasal is of smaller size; it is called the lachrymal (*Fig.* 36). Then come three bones, of which the lowest is large in area but very thin, the middle one is much smaller, and the top one the smallest of all, the suborbital or circumorbital bones (*Fig.* 37). The flat canal seen on the nasal and lachrymal is continued on these other three bones round the margin of the orbit. In some herrings there may be five of these suborbital or circumorbital bones instead of three. The skin over the side of the face where the circumorbital bones are, shows fine lines issuing from the flat canal and running downwards. These lines are due to channels in which are found the organs of the acoustico-lateral-line or neuromast system, the function of which appears to be the detection of slow vibratory movements in the water or of streaming movements (*see Fig.* 52).

Fig. 36.—Lachrymal, left.

Fig. 37.—Suborbitals or circumorbitals, left.

On the side of the face below and behind the circumorbital bones is the large crescentic preopercular bone (*Fig.* 38). The skin over this also shows some channels of the neuromast system.

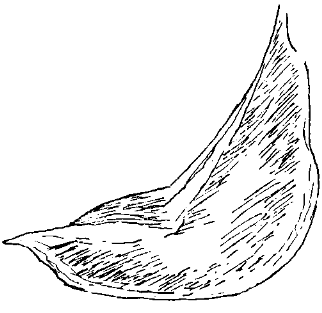

Fig 38.—Preopercular, left.

The lower and anterior point of the preopercular bone is at the hinge of the lower jaw. The upper horn of the crescent lies in the gelatinous tissue which covers up all the irregularities of that part of the head which is formed by the side of the skull and the bones in relation to it.

Behind the preopercular are the opercular and subopercular bones (*Fig.* 39). Their hinder edge forms the anterior boundary of the opening of the gill-chamber, and it fits accurately against the outer surface of the bone which forms the posterior margin.

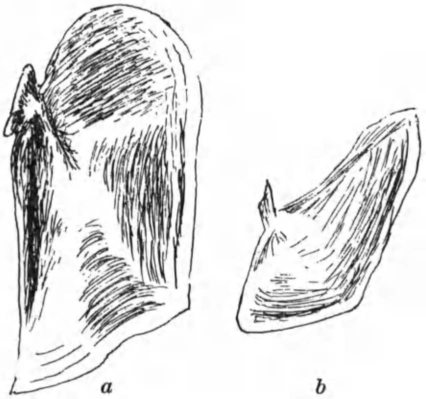

Fig. 39.—*a*, Opercular, left; *b*, Subopercular, left.

All the bones which have been mentioned by name—dentary, angular, premaxilla, maxilla (and its two attendant bones which might be called buccal and supramaxilla respectively), nasal, lachrymal, circumorbitals, preopercular, opercular, and subopercular bones, form a compact system of which the lower border can be swung outwards, owing to the movable joints between the opercular and subjacent hyomandibular bone, maxilla and palatine, and the limited freedom permitted by the tissue which unites the two dentaries.

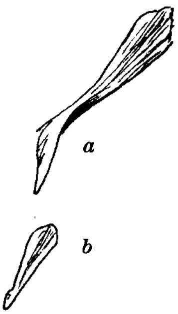

Fig. 40.—*a*, Supra-orbital, left; *b*, Ad-nasal, left.

A narrow bony scale is found in the skin along the snout. Its upper end is exactly above the middle of the eye, and from here the bone reaches downwards and forwards till it meets a much smaller bone of similar nature at the level of a small opening which leads directly into the cavity lodging the organ of smell. The smaller bone, shaped like a narrow triangle, has its apex at the tip of the nasal bone. The upper of the two bones is called the supra-orbital, and the smaller lower one is the adnasal (*Fig.* 40).

The eye shows a bright silvery ring about $\frac{1}{8}$th in. wide surrounding a nearly black pupil in which is placed the nearly globular lens. The lens is transparent, but if it is boiled it becomes opaque white like the white of an egg.

The sharp edge of the silvery frame of the eye round its periphery is formed by the outer edges of two curved bony plates of bone—the sclerotic plates (*Fig.* 41). They are curved to fit the circumference of the eye, and are more sharply curved across their length because the depth of the eye from without inwards is small. The anterior sclera is placed rather in the lower and front part of the eye, and it is a little smaller than the posterior sclera which lies in the upper and back part of the eye. With the mention of the sclerotic plates the enumeration of the bones which form the facial armour is complete. Other bony surfaces, points, and ridges visible externally belong either to the skull or to bones more deeply placed than those described above, with the exception of parts of some of the gular bones and the interopercular.

Fig. 41.—Scleræ, left.

The lower edges and hinder ends of these bones are all that can be seen of them at present as they show beyond the edge of the gill-cover. The skin over them is bright and silvery.

By turning the fish on its back, and pulling apart the gill-covers of the two sides, a view is obtained of the structures which underlie the floor of the mouth. From in front, where the two dentary bones are held together, a tapered ridge runs backwards in the middle line, and on each side of it a transparent membrane connects it with the lower jaw in front. Further back the clear membrane is narrowed through the median ridge being replaced by a thick membrane on each side, and in these are seen curved bones which look like the ribs of an umbrella. The skin over the median ridge is rather silvery, and it ends behind as a thin edge shaped like a wide V; here it is succeeded by the brighter thick membranes with the bones in them. These two membranes are attached laterally to the lower borders of parts of the hyoid arch, which run outwards and backwards as thin vertically placed bony plates from the middle line to the hinge of the lower jaw, but they are not visible without dissection.


Fig. 42.—Branchiostegal rays, left (5).

The mesial edges of the silvery membranes are free and lightly scalloped. The anterior end of the left membrane overlaps that of the right one as seen when the fish is placed, as now, belly upwards.

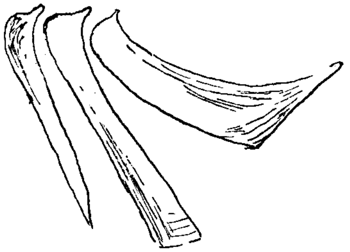
Fig. 43.—Gulars, left (3).

The little curved bones which occur in these membranes are the branchiostegal rays (*Fig.* 42). They are five in number; they are all curved, but the hindermost one least so. Behind them come three broader bones to whose lower edges the silvery membranes are also attached. These are the gular bones (*Fig.* 43), and, as noted before, they are partly visible on the surface of the fish.

Behind these again, but overlapped by them to a great extent, is the large oblong scale known as the interopercular bone (*Fig.* 44).


Fig. 44.—Interopercular, left.

The gular bones by their hinder edges form a nearly straight transverse line which cuts the middle line of the ventral edge of the body at right angles almost immediately in front of a minute black spot. Here can be felt the foremost point of a sharp bony ridge. Actually the ridge is formed by the lower edges of the two coracoid bones (*Fig.* 45), which lie flat against one another. A knife blade can be inserted between them, and if passed vertically upwards for about $\frac{3}{4}$ in. it would enter the heart. The outer surface of each coracoid bone gives attachment to the muscles which work one of the front pair of fins, and the fin is hinged to a thickened part of the upper edge of the bone.

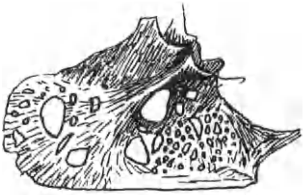
Fig. 45.—Coracoid, left.

The coracoid bone is a much fenestrated plate, for the most part remarkably flat, but its upper edge is thick and provides an articular surface for the basal bones of the fin, minute nodules, and interarticular cartilage.


Fig. 46.—Cleithrum, left.

Other bones which enter into the composition of the 'fin-girdle' are: the large curved bone known as the cleithrum (or clavicle) (*Fig.* 46), to the mesial aspect of which the coracoid bone is applied; the mesocoracoid (*Fig.* 47), a slender bone which sits on the top of the coracoid and is attached above to the deep aspect of the cleithrum, thereby completing the outline of a large triangular opening; in the lumen of this opening is another bone of peculiar shape—the scapula (*Fig.* 48); there is nothing in the appearance of this bone to suggest any resemblance in shape to the mammalian scapula.


Fig. 47.—Mesocoracoid, left.


Fig. 48.—Scapula, left.

The bone of which the cleithrum is made is thin, and generally transparent. Very little of the bone can be seen from the exterior. The flat upper plate which forms the curved hinder boundary of the opening of the gill-chamber is close to the surface, but on it lie some scale-like bones which partly obscure it. The lowest of these epicleithral bones (*Fig.* 49) is a narrow strip gently curved like an S; sometimes there are two such bones close together. Next above this is a small very thin bone which might be described as leaf-shaped. Above this is a larger and stronger bone in outline a little like a bird's wing. Two other bones continue the series upwards, the post-temporal and supratemporal bones (*Fig.* 50), but these are so buried in the gelatinous tissue of the head that their form cannot be made out yet.

Fig. 49.—Epicleithrals, left.

The upper end of the cleithrum ends in a spine which points nearly vertically. A strong ligament binds the base of this spine against the underlying muscles, and runs inwards to the first vertebra.

While the upper extremity of the cleithrum reaches up to above the uppermost part of the gill-opening, its lowest point is on the midventral line and consists of a blunt hook. Most of the lower part of the bone gives attachment to muscles which go to the gill-arches and anterior paired fin, while to the upper part of the bone some of the body-muscles are attached.

Fig. 50.—*a*, Post-temporal, left; *b*, Supra-temporal, left.

Half-way along the whole length of the anterior border of the bone from the tip of the spine above to the end of the curved process below is a thin hatchet-shaped plate of bone which, in the body, protects the heart.

The basal bones and the bony rays complete the skeleton of these anterior paired fins. The rays of these fins vary in number from sixteen to nineteen. The largest ray is on the dorsal border of the fin, and below this the rays diminish in size.

If the edge of the gill-cover is raised, it will be seen to fit very snugly against the outer surface of the cleithrum and its epicleithral bones, but lower down is found a curious ridge of dense tissue over which the skin is bright and silvery, which seems only to exist for the sake of making the gill-opening perfectly watertight.

Behind the anterior paired fins the lower edge of the herring is characterized by a series of some eighteen large U-shaped scales (*Fig.* 51) which have a median low ridge and on each side are prolonged upwards into a narrow horn. The last one of the series is close up against the posterior pair of fins, and has the appearance of being made up of two or more of these scales fused together.

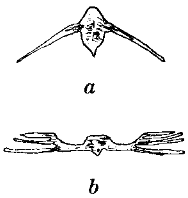

Fig. 51.—*a*, U-shaped scale; *b*, The last U-shaped scale.

The posterior pair of fins, much smaller than the anterior, are placed close together at the lower edge of the body, and, like the anterior pair, their rays point backwards. The largest ray, too, is on the outside edge. Nothing can be seen of the bone which provides the articular surface for the rays and site for attachment of muscles, until dissection is made. It lies deeply above the posterior U-shaped scales.

Immediately behind the posterior pair of fins the lower edge of the fish is formed by a set of about fourteen small scales which have a definite ridge along the middle of them.

Between the last of the small keeled scales and the anal fin is the cloaca. This is an oval depression about $\frac{1}{4}$ in. long; its long axis is antero-posterior.

In the female the posterior third of the depression has a smooth membranous floor, against which lies the large posterior lip of the opening of the alimentary canal. The anterior lip of the anus is less prominent, so that the tube opens obliquely backwards and downwards, and the posterior part of its margin forms a kind of hood. Behind the anus is the opening of the genital gland, and between the anus and genital gland is the minute opening of the fine terminal canal of the swim-bladder.

In the male fish the anus has a less prominent posterior lip, but, as in the female, the openings of the swim-bladder and of the genital glands lie behind it.

The anal fin begins immediately behind the anus. It consists of seventeen rays as a rule. The longer ones—about $\frac{3}{4}$ in. long—are in front, and the shorter ones—about $\frac{1}{2}$ in. long—are behind.

A short length of rounded border covered by ordinary scales intervenes between the anal fin and the root of the tail where the fulcra or supporting ray-like scales begin which support the long great outermost ray.

The tail-fin is symmetrically built. The fulcra at the dorsal border are like those at the ventral border and they support the great uppermost ray. From above and from below the rays diminish in size towards the mid-point, and there are usually nine rays in each half, upper and lower.

The whole of the dorsal margin of the fish is rounded and covered with scales except the part occupied by the dorsal fin, which, like an island, forms a median projection a little behind the middle of the length of the fish. The dorsal fin has about seventeen rays.

Immediately behind the skull the skin of the dorsal border is marked by some faint branching lines of the same nature as those which run over some of the bones of the face, such as the suborbital and preopercular.

The body of the fish is practically everywhere covered by scales, but shows hardly any other anatomical features than the fins and peculiar scales along the ventral border.

Many kinds of fish possess a well-marked 'lateral line', but a 'lateral line' is not seen in the herring. The canals which lodge neuromast organs on the surface of the head are of the same nature as those of the lateral line of other fishes. Along the course of them are special sense-organs in connection with some of the cranial nerves, and their function is believed to be the detection of vibrations of low frequency such as might be produced by a current of water.

The back of the fish down to the level of the upper edge of the gill-cover is very dark, while the sides from a little below this level are silvery grey, and in their lower parts almost white.

The darkness of the upper part is due to two things. One of these is the presence of pigment-bearing cells, or chromatophores, which appear as innumerable little black points situated especially round the edges of the scales, and the other thing is the absence of the brilliantly white material which lies on the skin of the lower parts and gives rise to the silvery look. The white material is said to be of the nature of an excretory product allied to uric acid.

It is worth while to note that the lower limit of the black edging of the scales extends in a nearly straight line backwards towards the middle of the tail fin, but that opposite the hinder end of the anal fin it turns downwards and so includes the whole of the root of the tail.

The silvery deposit can be seen to have an upper limit about the width of one of the fish's scales above the lower limit of the black outlines. It ends posteriorly, however, in a blunt point opposite the middle of the root of the tail and level with the roots of the supporting rays or fulcra.

The black pigmentation and the silvery deposit are then not bounded by one another, but the difference between their boundaries is not a wide one.

Turning our attention now to the head, we find that in the fresh state clear jelly forms a smooth covering over the top of the head and over the eye. When moist it looks continuous over the whole eye, but as it dries there can be seen an oval opening in it, with the longer axis running downwards and backwards. The edges of the membrane round the opening are very thin, and the transparent fold forms the outer wall of the orbit. The cavity of the orbit is only separated from that of the olfactory space in front of it by the same kind of thin membranous wall. The entrance to the olfactory space is a small hole in the skin between the supra-orbital and adnasal bones on the outer side, and the rounded median ridge on the inner side which runs down to the premaxillæ. This ridge is due to the mesethmoid bone and the cartilage of the snout which underlies it.

On the top of the head behind this median ridge is a smooth, more flattened, leaf-shaped area occupying the lower and front part of a larger oval field which everywhere else is finely stippled. The stippling is due to fine whitish points scattered through the transparent skin, which is like clear jelly.

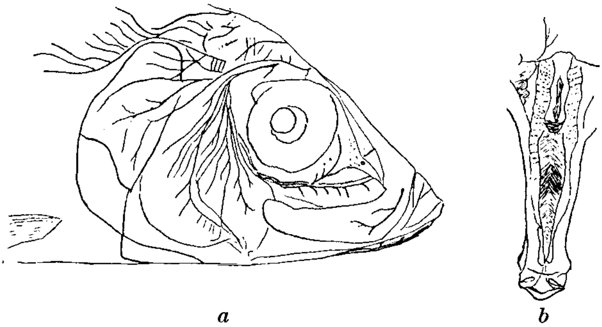
a b

Fig. 52.—Canals of neuromast system. *a*, Side view. *b*, View of head from above; the only canals seen are those behind the head, and the right side only is shown. The stippled areas referred to in the text are shown in this figure.

Over the bones of the gill-cover the skin is bright and silvery, but above the level of the gill-cover it is dark and has an iridescent greenish tint which may extend on to the body region close by.

In addition to the lines already mentioned as running over the surface of the suborbital and preopercular bones there are others which can be made out in a good light as shown in the drawing (*Fig.* 52). The line which runs above the top of the gill-cover is in the position of the 'lateral line'.

A transverse crest on the supra-occipital bone marks the posterior boundary of the roof of the skull. On a line joining this crest and the top of the pupil of the eye is a point level with the hindmost end of the smooth leaf-like area where the stippled border turns round it, and at this point a needle thrust horizontally inwards enters the skull through a crescentic opening and passes out at the corresponding spot on the other side without having encountered any marked resistance. The skull, then, is defective here. The opening is enclosed between parts of the frontal and parietal bones. The gap in the skull does not seem to correspond to any particular sense organ, and yet it is difficult to believe that it has no special use. It is deeply placed, and well concealed by thick gelatinous tissue.

The only part now remaining for inspection, without resorting to dissection, is the interior of the mouth and gill-chamber.

When the mouth is forced open, the most prominent object in view is the so-called ‘ tongue ’. It is of pyramidal shape with an edging of black mucous membrane. The main mass of it is formed by a block of hyaline cartilage, which, however, cannot be seen at present. The apex of the block is at the tip of the ‘tongue’ and the base is behind. A rounded ridge runs along the middle line of the upper surface of the ‘ tongue ’, and from this the sides slope away on either side like a roof. At the back part of the ridge is a small strip of bone which carries teeth.

Below the ‘tongue’ the floor of the mouth is formed by a ridge under which is situated the hypohyal bone and the ligaments which connect it to the middle line of the lower jaw. A deep groove intervenes between this median ridge and the inner aspect of the lower jaw. The floor of the groove is formed by transparent membrane and has already been mentioned (p. 76) in connection with the description of the under aspect of the head.

The rounded ridge on the ‘tongue’, if traced backwards, is seen to be continuous with the median ridge of the gills which forms the floor of this part of the mouth. On either side are to be seen gill-arches converging upon it as they curve forwards in the lower part of their extent. The edges of these arches are furnished with a close palisade of flat blades which point forwards horizontally. These structures are the gill-rakers. Those on the foremost arches are large, but on the less well-developed arches, which cannot be seen from in front and are much smaller, the gill-rakers are also much less in size.

The entrance to the throat as seen from the front is funnel-shaped, the walls of the funnel being made up of the gill-arches with their bristly armament below and at the sides, while the roof is almost smooth.

Far back the gill-arches do actually curve over to take part in the roof, but in the parts now visible the roof is formed in the middle line by the vomer and a small part of the parasphenoid. The front end of the vomer is seen as a triangular block, and behind it is a ridge on the bone which is toothed. On either side of the middle line the roof of the mouth bulges downwards slightly. This is because it is formed by the entopterygoid bone which is hollowed on its upper surface where the eye rests on it. The lateral boundary of this part of the roof of the mouth is formed by the small palatine bone. The edge is sharp and in front it runs into a triangular knob, which provides an articular surface for the maxilla. The deep recess to the outer side of the palatine bone receives the upper edge of the lower jaw when the mouth is closed.

The gill-slits between the arches permit water going in at the mouth to pass out over the gills, and the gill-rakers, being very closely arranged, make a very efficient strainer to prevent any but the smallest objects from passing on to the gills. The gills themselves cannot be seen from the mouth, but are seen at once if one raises the edge of the operculum or gill-cover. They consist of a crimson fringe of regularly arranged rods which stand out like rays from the bones of the arch and from the hinge of gristle which joins the upper and lower bones together.

Only the first arch and its fringe of gills can be seen as yet, with perhaps just the edges of the second and third, which are parallel with it and close to it like the leaves of a book. The inner wall, or floor, of the gill-chamber, where it is not formed by the gill-arches and gill-slits, is smooth.

In order to pursue the study of the Herring further, resort must be had to dissection, or to other means, which are to be spoken of later.

The internal organs of an animal are so often considered to be of such great anatomical importance, that it is necessary now to give some account of those of the Herring, although this part of its anatomy has perhaps less to do with the theory under discussion than any of the other anatomical details.

A line drawn from the upper edge of the gill-cover to the middle of the root of the anal fin, lies, for practically the whole of its length, close above the level of the upper boundary of the cœlom, so that all the principal viscera, except the brain and spinal cord, lie below it (*Figs.* 53–55). These organs are the stomach and intestine, the liver and the mass of large simple tubular glands known as the pyloric cæca which open into the first part of the intestine, the spleen, and the two large genital glands commonly known as the 'roe', and finally close beneath the spinal column are to be found the swim-bladder and with it the kidney tissue. These are the organs found in the body cavity of the fish. In the head region are the gills, and between the head and the body is the heart.

To open up the body cavity a cut is made through the skin along the line from the top of the gill-cover to the middle of the root of the anal fin, and the cut is deepened to nearly half the thickness of the body so that the ribs are also cut through. Another cut is made along the middle line of the lower margin of the fish, beginning at the black spot which marks the foremost point of the coracoid bones and passing backwards between these two bones and then through the median ridges of the U-shaped scales to between the hinder pair of fins, and on through the keel of the scales behind them to the anus. This cut needs only to be about a quarter of an inch deep in most places to open into the body-cavity.

A vertical cut from immediately behind the anus to the upper incision allows the flank of the fish to be taken away with very little more cutting of tissue, and the whole side of the lower part of the body is pulled forwards until the girdle of the front pair of fins is reached, when it is necessary to divide a strong ligament connecting the upper end of the cleithrum with the backbone. By freeing the cleithrum and taking it away as well as the coracoid and the rest of the fin structures of that side of the animal, the heart is exposed as it lies in its triangular pericardial cavity, with the gill-chamber in front of it, the cœlom behind it, and the coracoid bone below it.

According to the season of the year at which the fish was caught, so will the contents of the body-cavity be mainly filled, or not, by the 'roe' or genital glands. The other organs lie between the two genital glands, and in consequence the one which is exposed must be taken away before the deeper structures can be seen. A thin band of tissue connects the milt ('soft roe') (10)* or the ovary ('hard roe'), as the case may be, with the roof of the body cavity, and can be easily cut or torn through. If the 'roe' is small then the organs are packed round with fat, which being very soft can be gently scraped away until the form of the organs can be properly seen.

At the front end of the body cavity the appearances met with will depend upon whether the right or the left side has been opened up. On the left side, the large mass of the liver (6) occupies the front end, and lies both over and in front of, and to a less extent deep to, the beginning of the intestine. The length of the liver horizontally is about one-third that of the body cavity; it extends backwards nearly to the fifteenth rib.

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* The numbers in the text correspond to those in *Figs*. 53–55.

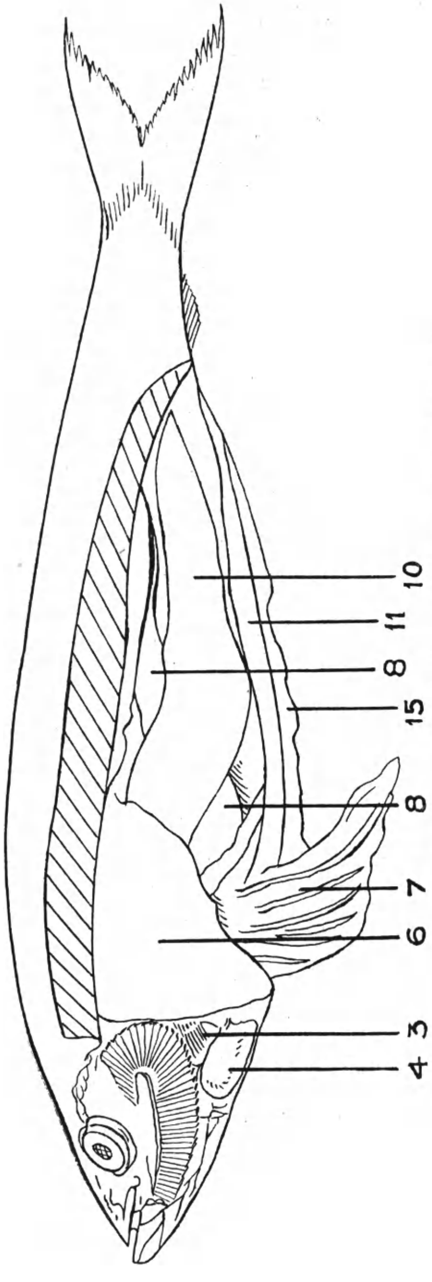

Fig. 53.—Outline sketch of viscera from left side. For details, *see Fig.* 55.

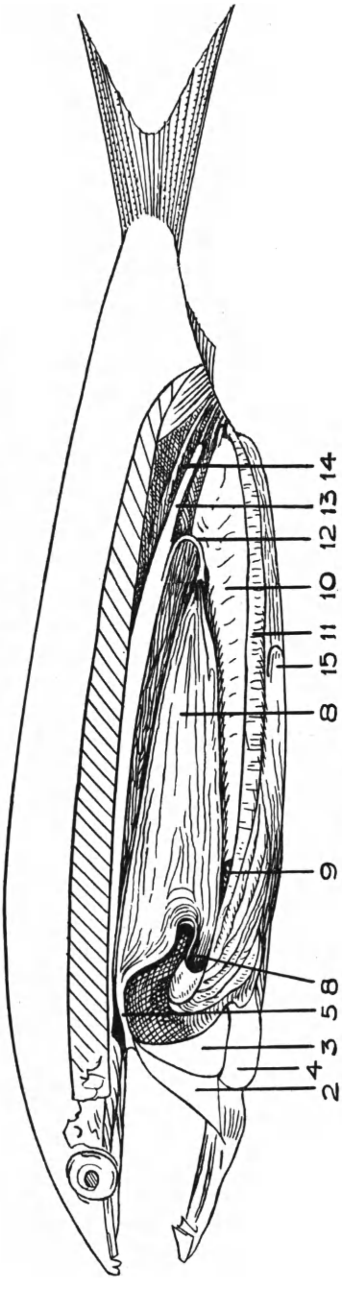

Fig. 54.—Stomach laid open. For details, *see Fig.* 55.

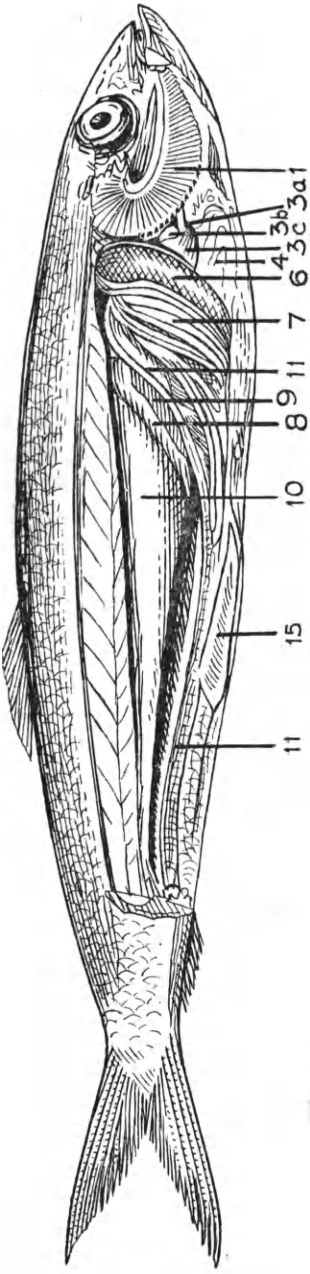

Fig. 55.—Viscera of herring seen from right side. 1, Gills; 2, Floor of gill-chamber; 3, Pericardium; 3*a*, Aortic bulb; 3*b*, Sinus venosus; 3*c*, Ventricle (3*a*, 3*b*, and 3*c* constitute the heart); 4, Coracoid; 5, Pharynx; 6, Liver; 7, Pyloric tubes; 8, Stomach; 9, Spleen; 10, Genital gland (roe); 11, Intestine; 12, Duct from stomach to swim-bladder; 13, Swim-bladder; 14, Kidney; 15, Root bone of posterior paired fin.

When the liver, or as much of it as is on the left side, has been cut away, the shape and dimensions of the stomach (8) can be made out. Several large blood-vessels encircle the pharynx exactly above the heart, and here the pharynx becomes continuous with the short and narrow gullet (5). After a length of about a quarter of an inch the gullet or œsophagus opens out into the stomach. The stomach is a large cavity, and opposite the level of the tip of the front paired fin is quite half as deep as the body-cavity. It tapers as it extends backwards, and at the level of the tip of the hinder fin it is like a string (12), which turns upwards and then runs forwards above the main part and is attached to the swim-bladder. (The many kinds of teleostean fishes which show this feature of the stomach being connected with the swim-bladder are classed together as Physostomi.) Below and in front, the stomach sends forwards a tubular branch or limb, which becomes the first part of the intestine. At first it runs forwards and inclines to the left, then it slopes a little upwards and turns sharply round to the right, then it turns tailwards as it inclines downwards, and finally it gains a median position and runs as a straight tube (11) to the anus.

The part of the tube which curves so much carries a number of long simple glandular tubes—the pyloric cæca (7)—which with the fat which surrounds them form a mass that almost encircles this part and is nearly as bulky as the liver.

The spleen (9) is seen as a narrow reddish-brown smooth organ lying along the upper border of the intestine where the mass of the pyloric cæca is beginning to taper off to a point. The pointed tip of the mass of pyloric glands which reaches farthest back inside the body-cavity is level with the pointed end of the bone of the hinder pair of fins, which is in the thickness of the belly wall and is in front of the fin which it carries. From this level backwards to the anus the comparatively narrow tube of the intestine runs along the lowest part of the cavity, while just above it is the mesentery which slings it up. The tube, usually collapsed, is about $\frac{1}{6}$ in. wide and shows transverse markings.

Between the upper border of the cœlomic wall and the under aspect of the backbone lies the swim-bladder (13) —a long sac which tapers almost to a point at each end, and is of a bright silvery appearance. Its hinder end is at the anus. It opens to the exterior through a narrow tube surrounded by a thick sphincter muscle. The front end will require more detailed inspection when it can be seen better after the gills have been taken out of the way. The kidney is a mass of soft red tissue which runs with the swim-bladder for the whole of its length from skull to anus. The large genito-urinary opening is immediately behind the anus and opening of the swim-bladder.

The first or outermost gill-arch (1) is the only one to be seen at present; the second arch is directly beneath it and very similar to it in shape and size. The third and the fourth gills are of lesser size, and of course lie nearer the middle line. All four arches are placed side by side like the leaves of a book, but their attachment is not like the binding, because the first arch is attached well in front of the second, the second in front of the third, and the third in front of the fourth, along the chain of basi-branchial bones.

Behind each arch is a gill-cleft leading out of the pharynx into the gill-chamber. The cleft behind the fourth arch is about $\frac{3}{4}$ in. long. All the clefts are guarded by gill-rakers which project forwards from the anterior aspect of the arch behind.

Each arch consists of an upper part and a lower part joined by a hinge of gristle. The upper part has for its skeleton a forked bone which points forwards and is connected with its neighbours by a smaller bone which has a side branch. But the hinder end of the upper bone is continuous with the cartilage of the hinge. The lower part of the arch consists of two bones, a long one running from the hinge downwards and forwards towards the median chain of basi-branchial bones, and connected with it through the lower smaller intervening bone. In the case of the fourth arch this second bone is usually absent, and at most is a mere nodule. Behind the fourth cleft is a rather long bone which obviously represents the upper of the two lower bones of a fifth arch.

The gills themselves, owing to the blood in them, are seen as a red even fringe standing out from the convex posterior aspect of each bony arch, and made up of a large number of little stiff rods about half a millimetre thick. The depth of the fringe, which is the same as the length of the individual rods, is generally about three-eighths of an inch.

The muscles which act on the upper gill-bones arise from the skull—chiefly from the proötic bone. The muscles which act on the lower gill-bones take origin from the cleithrum. Some lesser muscles pass lengthwise from one bone of an arch to another.

The gill-rakers look like a brush of whitish bristles clamped between the lower and upper parts of the gill-arch.

The heart is enclosed in a pericardial cavity (3) of triangular outline when seen from the side. By opening the pericardium the heart is exposed lying in the lower part. The ventricle (3c), which forms the greater part of the organ, is of pyramidal shape, having three sides which meet at an apex posteriorly and a somewhat hollowed base facing forwards and upwards, against which are placed the thin-walled sinus venosus above (3b), and the very thick-walled muscular aortic bulb (3a) below.

The outer surface of the ventricular part is made up of three triangular nearly flat sides, a dorsal shorter one which looks upwards and backwards against the anterior wall of the cœlom, and two larger ventrolateral ones which meet below to form a ridge.

The aortic bulb is nearly circular in cross-section and is rather barrel-shaped but tapers more in front. Out of it projects the thick-walled aorta as a stiff pipe.

The sinus venosus has very thin walls, is placed above and a little behind the aortic bulb, and communicates with the ventricle through a valve, or rather through two valves, for the sinus is divided in two by a thin septum and each half has its own valve; but these two valves are so close together that there is practically but one opening into the ventricle.

The sinus receives most of its blood from the body through the great vessel on each side which emerges from the kidney tissue (14) and enters the tapering horn of that side. At a lower level a large vein enters at the outer side bringing blood from the regions anterior.

All the principal viscera have now been noticed, but it may be possible by careful dissection to demonstrate the minute but remarkable communication which exists between the anterior tip of the swim-bladder and the interior of the skull. It takes the form of a tube of cartilage shaped like a hairpin. The end of each leg runs into the exoccipital bone of that side. The straight part of each leg lies against the outer surface of the flat wing of the parasphenoid bone and runs downwards and backwards; the bend of the hairpin is above and in contact with the very tip of the swim-bladder.

Beyond the organs which have been spoken of there are no more in the body of the fish, save the spinal cord and nerves coming from it, and the blood-vessels, unless there be some which can only be found microscopically. All the rest of the body and the fins projecting from it are made up of bones, muscles, ligaments, fascia, and skin.

The spinal cord runs along a canal formed by the arches which spring from the dorsal aspect of the vertebræ; the bodies of the vertebræ form the floor of the canal. Nerves come off from the cord to supply all parts of the body.

A good way to obtain a view of the spine as a whole is to wrap up a fish in a piece of rag to prevent it from falling to pieces, then boil it for a minute or so, and then allow it to cool so that the altered gristle sets like glue, after which the loosened muscles (flesh) can be carefully pushed off the vertebræ, ribs, and skull under a gentle stream of water, and the axial skeleton got almost entirely clean. A strong, very elastic ligament of brownish colour runs along from beneath the skull under all the vertebræ. It can be cut across in places and removed piecemeal. Then the soft red tissue beneath the posterior vertebræ can be got rid of by using a stiff brush under a stream of water.

But as soon as the elastic ligament under the spine is cut, the spine will begin to curl up dorsally owing to there being a dorsal elastic ligament which is much more difficult to get away. It is white in colour and is a vertically placed band running through the vertebral arches. At the anterior end of the spinal column it is widest, and it appears to spring from the little cartilaginous hood which roofs over the spinal cord as it passes from the skull to the spinal canal. The ligament diminishes in depth as it passes backwards, and half way along the spine it has become relatively insignificant. With care the tail fin and its connection with the spine may also be preserved.

By reckoning as a vertebra the last element of the spine, which has a minute cone-shaped body and both a dorsal and ventral process, the total number of vertebræ is usually fifty-eight. Even behind the last bony element there is a fibrous structure which might be reckoned as another, though it is not ossified.

Of the fifty-eight vertebræ the first two do not carry ribs. Next to them come twenty-two vertebræ which carry ribs. These ribs are long slender bones which form a framework for the walls of the cœlom. Besides the main stem which lies in the wall of the cœlom each rib has a side branch running nearly horizontally backwards and outwards, and where the branch joins the stem at its upper end there is a squarish block of bone through the medium of which the rib is attached to the vertebra by the block being lodged in a recess on the under surface of the vertebral body. The side branches of the ribs form a horizontal palisade, and parallel with and above it is a nearly similar palisade formed of the side branches of the 'spinous processes' of the vertebræ. The width of the space between the two palisades is the depth of a vertebral body.

Behind the twenty-two pairs of ribs there are fourteen pairs of long slender bones occupying a similar relationship to the wall of the cœlom but only having a ligamentous connection to the vertebræ and not possessing a side branch. These bones may be termed 'false ribs'.

The true and the false ribs correspond exactly in extent with the cœlomic cavity, but it is interesting to find that behind the fourteenth pair of false ribs there are three pairs of shorter slender bones running parallel with their direction, but not nearly reaching up to the spine. These look as if they may be the lower ends of members of the same series as the ribs on the one part, while on the other they form a transition between the false ribs and the 'radials' of the anal fin.

The vertebræ which correspond to the false ribs and the three bones behind them are furnished with an arch of bone hanging down below their body. The first nine of these arches are wide, and the pillars which form their sides are prolonged downwards as two small spines, but behind the ninth of the series the spines tend to become fused into one, and the arches are narrower and V-shaped. V-shaped hæmal arches hanging from the bodies of the vertebræ occur on all the remaining bones of the spine to the tail.

The muscular tissue of the body of the Herring is difficult to describe satisfactorily. It is, of course, segmented as it is in most fish. If the body be cut across in places an idea can be gained of the arrangement of the principal masses of muscle.

The muscles which connect the head with the body can be divided into a median mass and a lateral group on either side of it.

The median mass is bilaterally symmetrical and consists of a sheaf of muscles which are for the most part small, and which, more posteriorly, become continuous with the system that may be designated ‘the dorsal longitudinal muscle’.

The lateral group is a complex one. Some of its members spring from the side wall of the skull, and on their deep aspect have a tendinous surface which plays over the rounded upper part of a ridge forming the outer edge of the back of the skull. The lower surface of this lateral set of muscles is striped with lines of tendinous fibres, and forms part of the roof of the gill-chamber.

The muscles of the body proper are arranged more or less as a series of hollow cones with their apices directed forwards (*Fig.* 56). They ought rather, perhaps, to be called segments of cones, since in no case do they form a complete conical structure. The apices or most pointed regions of these cones, at the back of the skull, are three in number on each side. Each apex or focus is characterized by an osseous feature.

The most internal focus is where a delicate 'tendon-bone' springs from the back of the exoccipital close to the margin of the arch through which the spinal cord

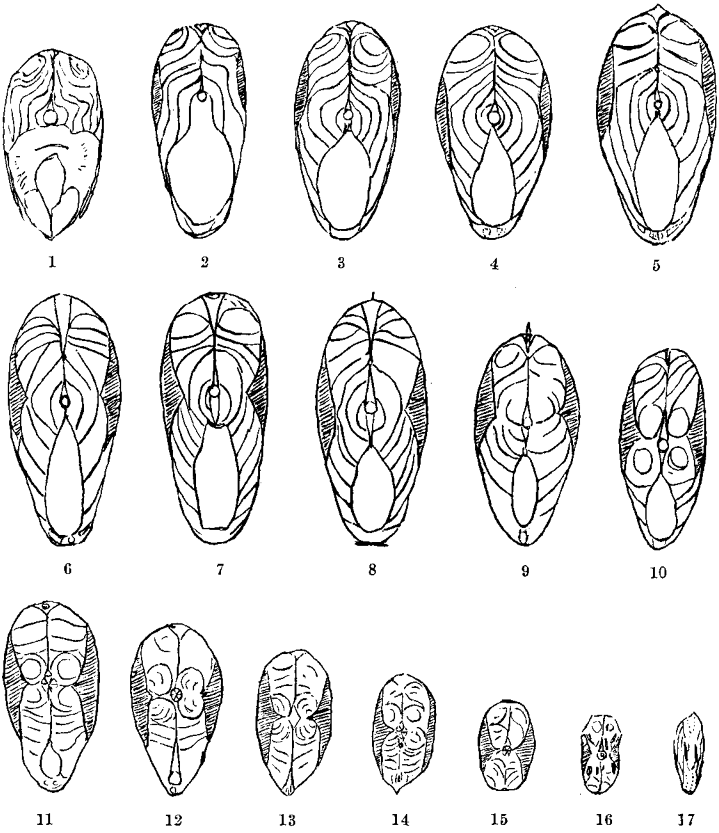

Fig. 56.—Transverse sections across the body of an adult herring at successive levels, with their approximate positions and their distances from the skull. Viewed from in front. 1, Anterior end of coracoid. Disc between vertebræ 4 and 5. 22 mm. 2, Middle of coracoid. Disc between vertebræ 8 and 9. 34 mm. 3, Posterior end of coracoid. Vertebra 12. 48 mm. 4, Tip of front paired fin. Vertebra 15. 63 mm. 5, 1 cm. behind tip of anterior paired fin. Vertebra 19. 78 mm. 6, 2 cm. behind tip of anterior paired fin. Vertebra 23. 92 mm. 7, Front of dorsal fin 3 cm. behind tip of anterior paired fin. Vertebra 27. 108 mm. 8, 1 cm. behind 1st dorsal fin ray, 1 mm. behind root of posterior paired fin. Vertebra 30. 122 mm. 9, 2 cm. behind 1st dorsal fin ray. Vertebra 34. 136 mm. 10, 2 mm. behind dorsal fin. Disc between vertebræ 37 and 38. 149 mm. 11, 1 cm. behind tip of posterior paired fins. Vertebra 41. 161 mm. 12, Posterior edge of cloaca. Vertebra 44. 172 mm. 13, 1 cm. behind cloaca, ⅓ along anal fin. Vertebra 47. 185 mm. 14, 2 cm. behind cloaca, ⅔ along anal fin. Vertebra 50. 195 mm. 15, Posterior limit of anal fin. Vertebra 53. 207 mm. 16, Between anal fin and root of tail. Disc between vertebræ 55 and 56. 217 mm. 17, Root of tail.
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issues from the skull. As a rule this ‘tendon-bone’ consists of two or three fine gently curved rods joined at the end where they are fixed to the skull but diverging slightly at their free ends (*see Plate VI*). Above and external to this focus is another formed by the finely bifid point of the epiotic bone. Lastly, below and externally is the sharp spine of the squamosal or pterotic bone.

From the last-mentioned sharp spine a very superficial band of dark muscle starts, which runs horizontally backwards, right to the root of the tail. As it runs over the anterior ribs, the septa in it show dense crescentic thickenings, but further back these become quite feeble. These crescents are connected deeply with the lateral processes of the ribs. These cease at about the thirty-sixth vertebra, and here the horizontal muscle is best marked as regards thickness and depth. It forms a band which, although beginning in a very feeble and inconspicuous manner, becomes greater as it runs back towards the tail; about the middle of its length it covers practically the middle two-fourths of the width of the flank. Further back it is relatively wider because the body is tapering at the tail end. The insertion of the muscle is, in conjunction with the insertion of other muscles lying deeply to it, into the larger of the upper and lower tail-fin rays.

The deeper body-muscles are of whiter colour. The dorso-lateral mass, which starts from the point of the epiotic bone as focus, is seen on section as a somewhat lens-shaped mass placed on either side of the median septum. These muscles can be traced throughout the length of the fish, until they are replaced by tendons close to the tail.

In the front region of the body, below the dorso-lateral mass of muscles, are the concentric layers of the main mass, which is centred on the exoccipital bone and has the cœlom below it. In general it may be described as formed of layers arching round the vertebræ, and ending abruptly at the margin of the body-cavity. Behind the level of the dorsal fin, transverse sections of the body show that this single mass is becoming supplanted by two masses on each side of the spine, and in the sections near the end of the cœlom these muscles appear as four circles regularly arranged, two above and two below, with the vertebral column in the centre. These also end in tendons to the tail, and they are, in this region, scarcely distinguishable from the other muscular masses. By dissecting inwards from the side it becomes evident that these four round muscles are really separate muscles which begin at about the thirty-fourth vertebra.

It is usual to speak of the muscles as being segmented in the fish, but this gives rather an erroneous view. The fibrous septa which, when a fish is boiled, seem so feeble and soft, are in the living fish very strong. They are not gaps in the continuity of the muscles, but are partitions for the attachment of muscular fibres, transmitting the power of the contractile tissues throughout the whole length of the body if necessary, and permitting of the distribution and modification of power over a much wider range than the muscle fibres alone would allow of.

So much for the sketch of the general body-muscles. Now let us look at the muscles of the middle line, beginning at the back of the skull and passing via the tail to the anterior paired fins.

The mid-dorsal line between the back of the skull and the most anterior of the root-bones of the dorsal fin is found on dissection to be the site of a fairly dense fibrous septum or partition in which are a number of little bones standing upright. These little bones, usually seventeen in number, are mere rods without any flanges or thickenings. They have the appearance of being root-bones of a fin rather than anything else, and there can be little doubt that they are the vestiges of a fin now submerged.

The median muscles which connect the head with the body converge upon the septum in which the submerged fin is, and some reach to its hindmost end. At its rear end the septum is fixed to the prominent anterior keel of the first root-bone of the dorsal fin. On either side of the middle line the median muscle fades out to a thin edge formed by fascia through which the muscle gains origin from the septa of the body-muscles. A more lateral strip of muscle lies against the upper ends of the root-bones of the dorsal fin.

The dorsal fin has about seventeen rays, which are connected by a double layer of transparent skin. The first two rays are short, the third ray is the longest of all, and behind it the rays diminish in size. The rays are jointed on to the upper ends of the root-bones through intermediary nodules of gristle, and they are moved by four muscles. These muscles arise entirely from the root-bones. The anterior root-bones have side flanges which increase the area of muscular attachment, but the hinder bones have not got these. The front root-bone of all has a very large keel which projects straight forwards. Of the four muscles to each ray, the anterior pair are erectors; the posterior pair, if they act together, depress the ray, but if they act singly they draw the ray to their own side. The dorsal fin is remarkably independent of the muscles and bones of the body among which it is placed.

Behind the dorsal fin, along the middle line of the back, is a curious muscle which takes origin from the hindmost root-bone of the dorsal fin, and gives off long delicate tendons which are inserted into the tips of the spines of the posterior vertebræ. Some of the tendons split into finer ones, so that in all there are about eighteen of these tendons, and the last one of them goes to the most anterior of the small horny rays or fulcra which abut against the tail. Generally the muscular tissue is an inch or two in length, but sometimes it is only half an inch or so long.

The tail fin is a complicated structure, and part of its skeleton is formed by the terminal vertebræ (*Fig.* 57).

The fifty-sixth vertebra differs from all those in front of it by its lower or hæmal arch ending in a square-cut quill-like process instead of in a sharp spine. The fifty-seventh vertebra has the same feature, and a narrow bony flange may spring from its lower border. This vertebra, moreover, sometimes carries two dorsal spines. The fifty-eighth vertebra has a small conical body or centrum which is only about one-eighth of the size of an ordinary one. It has no ventral process sometimes. Its dorsal spine is broad, being formed of two spines joined side to side with a groove between them. A fibrous process projects backwards from the small end of the fifty-eighth vertebra and doubtless represents part of a fifty-ninth vertebra. Both above and below the fibrous process there is a triangular, nearly flat, bony plate. The apex of each triangle is anterior, and the base, which is relatively narrow, is posterior. These bones, called hypurals, are held vertically in the middle line. Although flat, or nearly so, they too have a quill-like appearance, and their straight bases are almost in line with the square-cut ends of the hæmal arches of the fifty-seventh and fifty-eighth vertebræ. Above the upper hypural are two or three much smaller bones of similar shape. Between the fibrous process representing the fifty-ninth vertebra and the hypural bone above it is a triangular membrane which is pigmented.

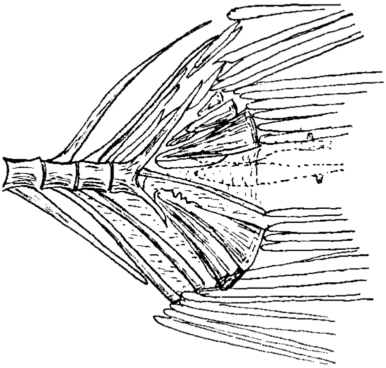


Fig. 57.—Semidiagrammatic sketch of skeleton of tail.

The two middle fin-rays of the tail are short ones, and each is continuous at its anterior end with a narrow leaf-shaped scale-like bone having a minute side process (*Fig.* 58, *a*). There are in all four of these peculiar ray-bones, an upper and a lower pair, and the pigmented membrane mentioned above lies between the bones of the right and left sides.

Above the two middle rays come two other rather longer ones, which are connected by soft cartilage with the upper hypural. Below, two similar rays are connected with the lower hypural in like manner (*Fig.* 58, *b* and *c*).

Above the two upper rays again are four or five longer ones, which near the edge of the tail split up into finer rays. At their anterior ends, in the root of the tail, these rays are jointed to a short tapering bone. In precisely the same way, there are four or five similar rays in the lower part of the tail next the two connected with the lower hypural bone.

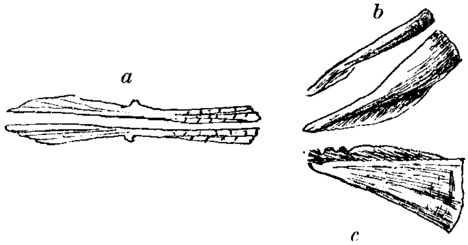


Fig. 58.—*a*, Leaf-shaped scales; *b* and *c*, Hypural bones.

The upper and the lower limit of the tail-fin proper is formed in each case by a large entire ray, against the proximal part of which lie a diminishing series of about seven lesser structures called fulcra, which have some resemblance to rays on the one hand, and to scales on the other.

The muscles which operate the tail-fin are numerous, and their arrangement is difficult to unravel because they are not quite alike on each side of the body, and because they are very much interconnected.

Those muscles of the body which begin about the level of the thirty-sixth vertebra and lie close to the spine for the whole of their length, send some fibres to the upper and some fibres to the lower half of the tail-fin, so that their fibres, in part, are crossed. The same is true of some of the small muscles which arise from the hypural bones and terminal vertebræ. All these muscles go to the large rays at the upper and lower edges of the tail and to the four or five rays next to them. Very small muscles arise from the little blade-like bones of the middle rays and act on the skin over the root of the more central jointed rays. The more superficial muscles of the body and the dark lateral median muscle end in two powerful tendons, one going to the upper, and one to the lower, largest ray. It is between the widely diverging strands of these muscles that the small deep muscles, which have their origin in the tail-region, make their appearance on the surface.

The last tendon of the longitudinal muscle which springs from the root of the dorsal fin is inserted into the anterior fulcrum of the upper edge of the root of the tail.

At the lower margin of the root of the tail the second and third largest fulcra grasp between their two prongs a small plate of gristle which caps the ventral process of the fifty-seventh vertebra. Into this cartilaginous plate the ventral longitudinal muscle gains a fibro-tendinous insertion. The other fulcra afford attachment to the longitudinal strands of muscle which run from the back and sides of the cloaca and pass one on either side of the root of the anal fin. These two muscles also end in a number of fibrous bands which are continuous with the septa of the body-muscles. The anal fin lies between these muscles and is independent of them.

The dense fibrous band which runs between the anal fin and the tips of the ventral spines of the penultimate vertebræ is found, as it is traced forwards, to form a sheath which encloses the basal bones of the anal fin and their muscles.

The anal fin has seventeen or eighteen rays. As in the dorsal fin, these rays consist of two separate halves enclosed in a double layer of skin. The muscles which elevate or depress the rays arise from the basal bones and are unconnected with any other bones than those of the fin. The basal bones are like those of the dorsal fin in having a lateral flange.

In front of the anal fin is the cloacal depression, its front part occupied by the anus; behind this is the genital opening; and, in the partition between, the fine tube of the swim-bladder.

Along the deep aspect of the fourteen keeled scales which border the fish between the cloaca and the hinder pair of fins runs a double strand of muscle arising from a stout tendon which passes beneath the root of the posterior paired fins. These two muscles enclose the sides of the cloaca between them and are inserted into the root of the anal fin.

The posterior paired fins have, generally, nine rays each. The line of the root of each fin is directed outwards and forwards, and the two fins are only about a sixth of an inch apart. The outermost ray is the longest and strongest of all. The rays are actuated by a well-defined group of long muscles, all of which arise from a triangular plate of thin bone which has a thick mass of yellow bone at its posterior edge, over which the tendons of the muscles play and on which the bases of the rays move. The muscles which raise the fin away from the body arise from the under surface of the triangular bone; those which open out the rays, and those which close them against the body-wall, arise from the upper aspect of the triangular bone. The pair of triangular bones with their muscles lie horizontally in a compartment shut off from the cœlom above by peritoneum and enclosed at the sides and below by the body-wall. This pair of fins differs from all the other fins in that its root bones lie practically parallel with the outline of the fish instead of at right angles to it. A very thin, almost horny, septum extends down from the roof to the floor of the compartment which lodges the fin-root between the two triangular bones (*Fig.* 59).

Fig. 59.—Root-bone of left posterior paired fin.

The stout tendon which runs underneath the fin-root between it and the skin is the direct connection between the double-stranded longitudinal muscle extending from the coracoid bones to the neighbourhood of the root-bones of the posterior paired fins, and the very similar double-stranded muscle beginning at the root of the posterior paired fins and reaching to the anus.

The most anterior of the keeled scales is a small one which is situated between the two fins at their root, and immediately in front of it is the wide straggling scale fixed to the fin-root that looks as if it were formed out of parts of two or more scales of the sort found in front of it. These U-shaped scales are seventeen in number.

The skin at the root of the posterior pair of fins, under cover of the outermost ray, is protected by a long narrow triangular scale, and under this is a narrow soft gelatinous process about half an inch long.

The large U-shaped scales have long side processes, which extend upwards on the body-wall, and at about half their length the lower ends of the ribs are found in a subcutaneous position.

The anterior pair of fins has already been noticed (*see Figs.* 45–50), but no reference has been made to their muscles.

The lower part of the deep aspect of the coracoid bone is flat, and is only separated by loose tissue from its fellow of the opposite side. But the upper part of the mesial surface diverges from that of its fellow. At the boundary between these two parts the mesocoracoid bone is attached to the coracoid, and sometimes it is ossified to it. The upper end of this little bone meets the cleithrum, and in the archway thus formed lies the scapula, while through the arch passes the powerful muscle which pulls up the great first ray against the body. The origin of this muscle is from the outwardly diverging part of the mesial surface of the coracoid in front of the mesocoracoid bone. The second ray is raised by a second muscle arising near the other and likewise passing through the arch. The other rays are lifted by two muscles arising also from the upper part of the mesial aspect of the coracoid, but behind the mesocoracoid. They form two broad sheets with numerous short fine tendinous insertions. The muscles which pull the fin-rays away from the body have their origin from the outer surface of the coracoid, and they consist of a superficial and a deep set. Each set is composed of three muscles. One superficial and one deep muscle go to the first and second rays, another two go to the third to the sixth rays, and the third two go to the remaining rays.

The basal bones of the anterior paired fins include, besides the scapula, two little nodules, one of them being rounded at one end and like a claw at the other, while the other nodule is roughly rounded.

In addition to the muscles which raise and depress the fin-rays, there are others connected with the coracoid bone which adjust its position in the body. One of these is the ventral longitudinal muscle, which is attached by tendon to the lower edge of the coracoid. A continuation of the tendon runs along between the coracoid and the skin and gives origin to a muscle which, along with others springing from the coracoid, is inserted into the urohyal bone that lies in front: since this bone is securely held from being drawn backwards, by stout ligaments connecting it with the lower jaw, the muscles between it and the coracoid steady the fin-girdle and may be able to advance it a little. Another muscle steadying the coracoid is that which encloses the first rib. It is inserted into the posterior end of the coracoid.

Further fixation is brought about through the connection of the cleithrum with the coracoid. The deep aspect of the basal part of the spine which marks the upper end of the cleithrum is strongly connected by muscle with the back of the skull, as well as being held in by the strong ligament that pierces the layers of muscle to reach the side of the first vertebra.

From the surface of the cleithrum which forms part of the inner wall of the gill-chamber, there arise some rather feeble muscles which go to some of the posterior gill-arches.

The internal anatomy of the head-end of the fish can be begun by dissecting off the postcleithral bones which border the opening of the gill-chamber. The tip of the lowest one is found half-way between the root of the front paired fin and the foremost U-shaped scale. The upper end of this bone lies under another narrow bone, and the upper end of the second narrow bone is overlapped by a thin, more or less semicircular bone having a little point at each end of the arc. The point at the upper end lies beneath the lower end of a flat bone with an outline like a bird's wing. All the bones so far mentioned are entirely in the skin, and firmly applied to the upper part of the cleithrum. The imbricated arrangement is carried further. The upper end of the wing-shaped supracleithral bone is overlain by the lower end of the post-temporal bone, which is a bone of peculiar shape and connections, in that it has a long sharp spine which curves over the top of the head and is attached to the crest on the supra-occipital bone, and a stalk or process which penetrates deeply into the muscles connecting the head and body. The inner end of this stalk is attached by ligament to a blunt process of bone. This process belongs to the opisthotic bone, which is one of the smallest elements in the composition of the skull, and is wedged in between the edges of the squamosal and exoccipital bones and also touches the proötic, but is excluded from forming part of the cranial wall.

On the outer surface of the post-temporal bone is a low tunnel which is in continuity with one of the tunnels on the supratemporal bone—a triangular thin scale situated in front of the post-temporal immediately above the opercular bone on the side of the head. The tunnel on the supratemporal bone which comes from the post-temporal, runs along near the lower edge of the bone ; it is joined by another tunnel which descends from the apex of the triangle, and it then runs forward.

The supratemporal bone is covered up by a thick layer of jelly, in which is also embedded the upper extremity of the large preopercular bone. More deeply situated still is the movable joint between the hyomandibular bone and the skull and the muscles which work it, and yet more deeply placed are the muscles which close the operculum against the head.

The preopercular bone is firmly bound to the outer surface of the hyomandibular, in part ; while, to the inner or deep aspect of both these bones a piece of the gill-fringe is attached. This piece is the turned-back end of the fringe or ribbon after it has left the upper extremity of the first gill-arch. The posterior limit of this turned-back piece is a free border, and is straight cut.

In front of the preopercular is the thin series of circumorbital bones, which are all superficial. A tunnel runs along them near the orbital margin. These bones and the preopercular bone cover in some flat sheets of muscle going from the hyomandibular bone to the lower jaw.

In order to remove the gill-cover it is necessary first to cut the muscles which run to its upper part from the skull, then detach the opercular bone from the process of the hyomandibular with which it articulates. Next, pass the blade of the knife carefully under the preopercular and circumorbital bones, separating the preopercular bone from the crest of the hyomandibular to which it is firmly bound, and the circumorbitals from the entopterygoid—a thin horizontally placed bone which supports the eye. The knife is then made to cut the skin above the lachrymal and nasal bones, and by turning down the loosened gill-cover and dividing the sheet of muscle to the lower jaw, the joint between the angular and quadrate bones, i.e., the hinge-joint of the lower jaw, can be opened. By passing the knife from before backwards below the jaw, the branchiostegal rays can be separated from it and left connected with the hyoid arch which forms the bony layer inside the jaw. The gular bones and the interopercular will come away with the gill-cover eventually. The interopercular bone is peculiar in not showing at all on the outer surface of the fish in spite of its large size. It lies behind the hinge of the lower jaw. By pulling the lower jaw away from the face, the membranous floor of the mouth between it and the hyoid arch can be seen and divided. After this the strong fibrous union of the two halves of the jaw in front is to be severed. The transparent skin between the lower jaw and the maxilla contains the two thin bones which accompany the latter.

This skin has to be cut through. The disarticulation of the 'head' of the maxilla at its joints with the palatine and mesethmoid bones and vomer requires some care. By division of the upper lip so that the premaxillary bone is separated from its fellow, and cutting through the remaining soft structures of the lip, the whole operculum and all the movable bones of the face connected with it can be taken away.


Fig. 60.—Hyomandibular, left.


Fig. 61.—Palatine, left.

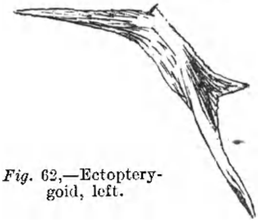


Fig. 62,—Ectopterygoid, left.

The parts exposed by the removal of the gill-cover and jaws are the gills, the hyomandibular bone (***Fig.*** 60) and the hyoid arch, with the branchiostegal rays, and the structures developed in the pterygo-quadrate bar: that is to say, the palatine (***Fig.*** 61), ectopterygoid (***Fig.*** 62), metapterygoid (***Fig.*** 63), and quadrate bones (***Fig.*** 64), and the cartilage which cements them together. Except the palatine bone, these bones are not well seen until the muscles passing from the hyomandibular to the lower jaw are taken out of the way. The ectopterygoid bone is a narrow curved plate which fits against the front border of the quadrate and metapterygoid bones, and the line of its curve is continued forwards by cartilage into the palatine bone. The metapterygoid bone, besides articulating with the ectopterygoid and quadrate, also touches the entopterygoid (***Fig.*** 65) and hyomandibular, and the little symplectic bone (***Fig.*** 66), the lower part


Fig. 63,—Metapterygoid, left.


Fig. 64.—Quadrate, left.

of which is lodged in a groove at the back of the quadrate.

The silvery fold of skin containing the branchiostegal rays and the thin layer of muscle between them is attached to the outer surfaces of the epihyal (*Fig.* 67) and ceratohyal (*Fig.* 68) bones, and it may be stripped downwards by dividing it along the upper edge of these two flat bones. The very small interhyal bone (*Fig.* 69) connects the epihyal with the lower end of the hyomandibular. There is a block of cartilage at the lower end of the hyomandibular bone, and the symplectic and interhyal bones are fixed in this at their upper ends, while their lower ends diverge at an angle of about 90 degrees. The joint between the epihyal and ceratohyal bones follows a nearly straight line, and the joint is almost a hinge. The branchiostegal rays have minute knobs at their attached end, which are held in membrane filling small spaces along the ceratohyal bone or are attached to the outer aspect of the epihyal. At its front end, the ceratohyal articulates with two irregular blocks, the hypohyal bones (*Fig.* 70)—one placed above the other—and these in turn enter into connection with their fellows of the opposite side and with the pyramidal block of gristle called the ‘tongue’.

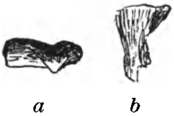

Fig. 65.—Entopterygoid, left.


Fig. 66.—Symplectic, left.


Fig. 67.—Epihyal, left.


Fig. 68.—Ceratohyal, left.


Fig. 69.—Interhyal, left.


a *b*
Fig. 70. — Hypohyals, left. *a*, Upper; *b*, Lower.

The hyoid arch is removed by disarticulating the hyomandibular bone at its joint with the skull, dividing the muscles which run from the skull to it, and dissecting off the piece of gill-ribbon from its deep surface. Nearly the whole arch can then be turned forwards at the joint between the hypohyal and the ‘tongue’, and on dividing the structures of this joint and the foremost attachment of the fold containing the branchiostegal rays, the whole arch can be taken away. The gills then are fully exposed.

The strip of gill-fringe which was attached to the operculum lies over the hinge of the first arch.

Below the gills the chamber in which they lie is bounded by the urohyal bone and the muscles and skin clothing it. The ‘tongue’ is situated in front of the lower part of the gills, and below it are seen the ligaments and muscles passing from the urohyal bone (*Fig.* 71) to the lower jaw. These structures are to some extent overlapped from below by the fold of skin containing the branchiostegal rays. Only the fold of one side now remains, the other having been taken away with the hyoid arch.

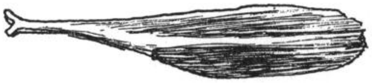


Fig. 71.—Urohyal.

The strong ligaments which tether the urohyal to the mid-point of the lower jaw make the urohyal bone secure as a site for the origin of muscles going to the girdle of the front pair of fins. The coracoid bones are placed below the hinder limit of the gill-chamber. The cleithrum forms part of its back wall, and muscles arise from the upper surface of its lower part and go to bones of the gill-arches (*Fig.* 72) below the hinges.

As now exposed, the outermost gill-arch is seen to run nearly horizontally backwards, from the gristly ‘tongue’ in front to the level of the front edge of the coracoid behind; then it makes a hairpin bend at its cartilaginous hinge-joint, so that its upper part runs forwards almost parallel with the lower gill-bones, but this upper part runs more steeply in towards the middle line and in consequence the upper parts of the gill-arches come to a point underneath the back margin of the eyes, and thus are only about half the length of the lower parts. The closely packed gill-rakers occupy the narrow space between the

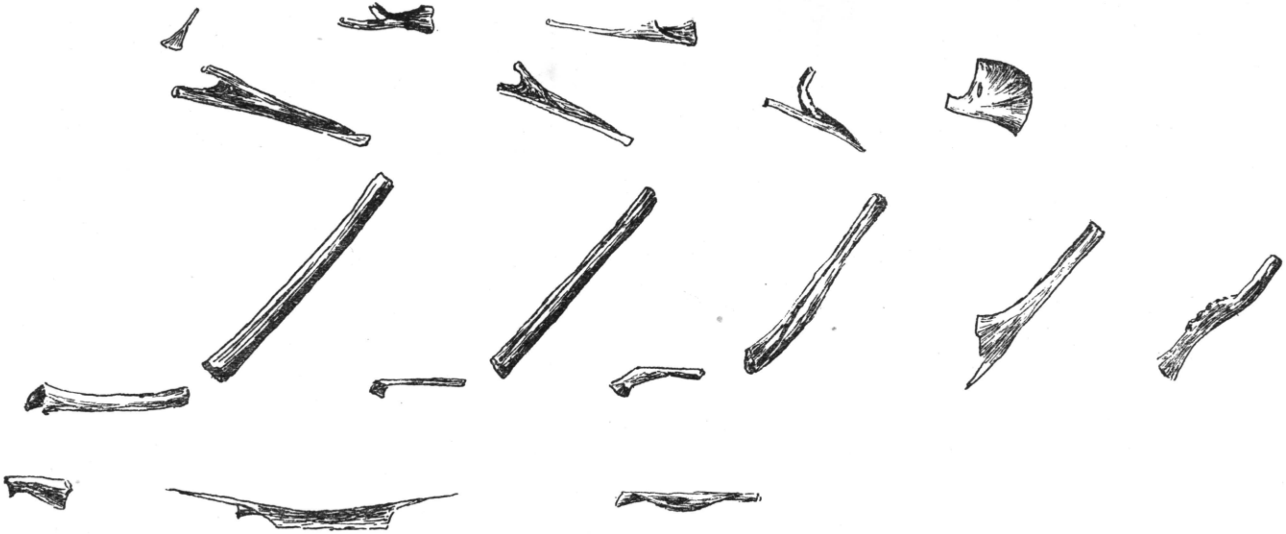


Fig. 72.—Bones of gills. The three bones in the lowest line are middle-line bones, basibranchials (3). The others are bones of the left side. The two rows next above the basibranchials are the hypohyals below (3) and the ceratohyals above (5). The two upper rows consist of the epibranchials (4) below, and the infrapharyngobranchials (3) above. The foremost infrapharyngobranchial is called the spicular bone. The hindmost epibranchial is called the epipharyngeal bone.

upper and lower bars of the gill-arches, and their sharp ends are practically in line with the teeth on the small plate of bone on the upper surface of the 'tongue'.

The roof of the mouth in front of the upper part of the gill-arches is formed by the stem of the parasphenoid bone with the entopterygoid bones on either side of it. The remains of muscles which ran to and from the hyomandibular bone obscure for the present the anterior extremities of the upper parts of the gill-arches.

By cutting through the muscles and rather feeble ligamentous bands which connect the gills with the skull, and then dividing the gullet and the vessels and muscles passing to the gills from behind and below—since these come from the region of the cleithrum—the gills can be turned forwards, and, with very little further dissection, removed *en bloc*. The heart and aortic arches are, of course, spoilt by this procedure. From below, the four laminæ of the gills on each side can be easily separated. If the gill-hinge be opened out by thrusting apart the upper and lower bones of the gill-arches, the palisade of gill-rakers can be well seen.

By removal of the gills we are left with only the skull, the fixed bones and the cartilage of the head, and the brain and organs of special sense.

The opening of the nostril, which is directly on the inner side of the lower end of the supra-orbital bone where the little adnasal bone below overlaps it, leads into a cavity in front of the eye, but not connected with any other space. Microscopical section of the lining of the inner wall of this cavity shows a small area where there are large deep folds, and these are clothed with the cells of the sense-organ regarded as olfactory.

The snout, which is all that region in front of the eyes, has a basis of hyaline cartilage. Running nearly the full length of the head, underneath, is the gracefully curved parasphenoid bone (*Fig.* 73). Its anterior end is flat, and is applied against the under aspect of the cartilage of the snout. Overlapping this end of the parasphenoid bone is the dagger-like vomer (*Fig.* 74). The thick anterior end of the vomer furnishes articular surfaces for the maxillæ. A short median ridge near this end projects downwards into the roof of the mouth, and carries teeth. The anterior end of each palatine bone forms a knob at the outer side of that of the vomer, and this knob on the palatine articulates with the mesethmoid bone (*Fig.* 75). The mesethmoid, being a middle line bone, has bilateral symmetry. It partly clothes the upper and outer part of the tip of the snout cartilage.

Fig. 73.—Parasphenoid.

Fig. 74.—Vomer.

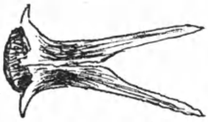


Fig. 75.—Mesethmoid.

Fig. 76.—Prefrontal, left.

Below and in front of the eye is a rounded prominence of gristle, part of the snout cartilage—and the root of this projection is partly enveloped by a very thin bone. This bone is the prefrontal (*Fig.* 76). It is of complex form, and one of its processes protects the eye from being injured by the upper edge of the lower jaw when the mouth closes.

Below the eyes, and on each side of the parasphenoid bone, is the long triangular entopterygoid bone, which is placed horizontally with its sharp end pointing forwards.

The lower part of the gristle of the snout (*Fig.* 77) forms a pointed process directed backwards in front of and below the eyes, close above the stem of the parasphenoid. A thin and narrow vertical septum of bone extends between the eyes from the trough-like portion of the presphenoid bone to the free margin of the middle of the front block of the snout-cartilage. It makes a partition between the oblique muscles of the right and left eye. These muscles take their origin from deep pits in the anterior block of the snout-cartilage. The upper surface of the snout-cartilage over the anterior block is narrow where the mesethmoid bone covers it, but a little farther back it broadens out and supports the frontal bones. Farther back still it forms an edging to the trough of the presphenoid bone, and thence extends as a Y-shaped bar to the anterior process of the supra-occipital bone. The two arms of the Y go to the edges of the trough, and in this way a somewhat quadrilateral space is completely encircled by the cartilage. The under aspect of the front block of the snout-cartilage presents four rounded eminences—two anterior ones, partly sheltered by the mesethmoid bone and articulating by a movable joint with the palatine bones, and two, more prominent ones, posteriorly, which articulate with another cartilaginous structure, viz., the gristle that lodges within the palatine bone and ectopterygoid.

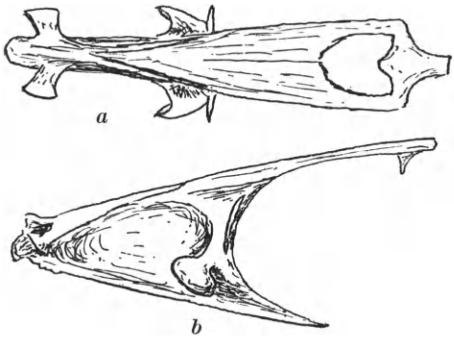


Fig. 77.—Cartilage of snout: *a*, From above; *b*. From left side. The mesethmoid, prefrontals, and vomer are still applied to it.

Behind the level of the eyes, the parasphenoid bone possesses a pair of wing-like processes which run back nearly parallel with one another. Their upper edges lie close against the proötics and basi-occipital, and help, with these, to form the walls of the eye-muscle canal. Immediately below their lower edges is the gullet, which is quite short. But farther back, across their tips, runs the arch of the gristly tube (*Fig.* 78) by means of which the cavity of the swim-bladder is put into communication with the small cone-shaped bulla in the exoccipital bones and through these with the bullæ in the proötic and squamosal bones. The straight legs of the arched tube of gristle run forwards and upwards to the skull in contact with the outer sides of the wing-like processes of the parasphenoid.

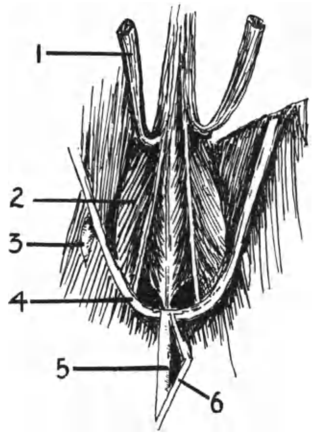


Fig. 78.—Cartilaginous U tube. The tube is actually about as thick as a stout bristle. 1, Muscle detached from ala of parasphenoid; 2, Ala of parasphenoid; 3, Transverse process of 1st vertebra, partly buried in muscle; 4, Cartilaginous tube; 5, Tip of swim-bladder; 6, Ventral ligamentous band pulled aside. The view is of a dissection with the fish placed belly upwards. The gills have been removed and the under aspect of the head exposed

If the remains of the muscles which connected the skull with the gills and hyomandibular bone be scraped away, the under aspect of the skull can be examined. In line with the eye, and close behind it, is seen the large grey bulla of the proötic bone (*Fig.* 79). The outer corner of this surface of the skull is formed by the sphenotic bone with its conspicuous white process pointing downwards. The sphenotic bone itself (*Fig.* 80) is of pyramidal shape, having three sides and a base, the base being chiefly articular for the proötic, squamosal (*Fig.* 81), and alisphenoid bones (*Fig.* 82). The hyomandibular nerve issues from the skull between the white process of the sphenotic and the bulla of the proötic.

Fig. 79.—Proötic, left.

Fig. 80.—Sphenotic, left.

Fig. 81.—Squamosal, left.

On the under surface of the sphenotic is the anterior end of the long articular groove for the hyomandibular bone; the rest of the groove is on the squamosal. The edge of the skull on the outer side of this groove is

Fig. 82.—Alisphenoid, left.

sharp and ends behind in a sharp spine which is imbedded in the strong muscular mass connecting the skull and the body in the roof of the gill-chamber.

Half-way between this sharp process and the parasphenoid bone, along the posterior edge of the under surface of the skull, is the small opisthotic bone (*Fig.* 83), which has a blunt process to which the stalk of the post-temporal bone is attached. Between this and the parasphenoid there is the small conical grey bulla of the exoccipital bone (*Fig.* 85) through which the tube of the arch of gristle enters the skull. Exactly in front of this is a squarish hole from which the vagus nerve emerges. At some distance from the outer side of this a small portion of the round bulla in the squamosal bone can be seen.

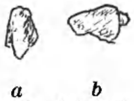


Fig. 83.—Opisthotic, left. *a*, From above; *b*, From below.

When the muscular tissue is removed from the back of the skull, the posterior semicircular canal can be seen arching outwards and backwards in the epiotic (*Fig.* 84) and exoccipital bones (*Fig.* 85). It is enclosed in a semicircular ridge which bounds a deep fossa on this aspect of the skull. A similar fossa is seen, partly bounded by the same ridge, on the outer surface of the skull, and at the lower part of this fossa another small portion of the bulla within the squamosal bone is seen. Projecting outwards, below this, is a shelf of bone perforated at its edge by canals connected with the channels of the neuromast or lateral line system. This shelf overhangs the articular surface for the hyomandibular bone.

Fig. 84.—Epiotic, left.

Fig. 85.—Exoccipital, left.

The study of the eye and of the muscles going to it involves the spoiling of other structures. To remove the eye, it is necessary to cut the thin membrane or conjunctiva which keeps it in place and to divide the muscles going to it, as well as the nerve. The parasphenoid bone is the chief bar to gaining a view of the eye-muscles, and it is firmly bound to the under surface of the head. The simplest way to remove this bone is to put the head of the fish into boiling water, after which it will be found easy to remove the bone. Along with it, the vomer is dislodged as it lies against the anterior end of the stem of the parasphenoid. Hidden till now by the stem of the parasphenoid was the tapering process of the snout-cartilage which runs backwards and fits like a wedge between the lower anterior quadrants of the eyes.

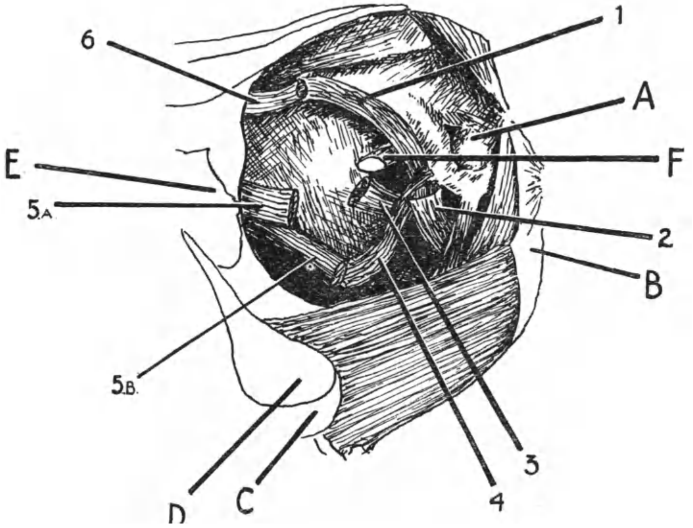


Fig. 86.—Muscles of eyeball, left: 1, Superior rectus; 2, Internal rectus; 3, External rectus; 4, Inferior rectus; 5A and B, Inferior oblique; 6, Superior oblique. A, Bulla of proötic; B Hyomandibular; C, Maxilla; D. Buccal; E. Nasal; F. Optic nerve. The eyeball itself has been taken away, leaving the cut ends of the muscles and nerve.

Two muscles arise within a pit in the cartilage of the snout, and run backwards, one to the upper and the other to the lower part of the sclerotic coat or hard outer shell of the eyeball (*Fig.* 86). A third muscle strand is also present, starting from the origin of the lower muscle and reinforcing the insertion of the upper one. The lower muscles of the right and left side are connected at their origin by a fibrous band. There is a small muscular band on the lower part of the eyeball, which looks like a detached portion of the lower muscle. The main upper and lower muscles are named, in accordance with mammalian anatomy, the superior and inferior oblique muscles. In the same way the muscles arising posteriorly to the eyes are classed as the rectus muscles. They are long bands. The external rectus and internal rectus arise from the second vertebra and even from the scale on the first rib close to its head. The inferior rectus arises from the transverse process of the third vertebra. These three pairs of muscles all lie in the myodome or eye-muscle canal. The superior rectus takes origin from the parasphenoid bone itself, near the anterior end of the canal.


Fig. 87.—Basisphenoid.

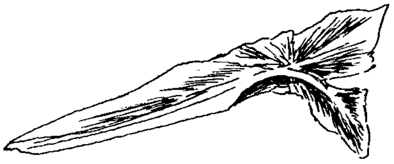


Fig. 88.—Frontal, left.

Between the two eyes is a thin septum. Its upper part is formed by the vertically set plate of bone which forms the front end of the presphenoid. It meets the cartilage of the snout and separates the right and left oblique muscles. The large opening in the skull from which the optic nerves emerge is between the alisphenoid bones above and the proötics below. The fine needle-like process of the basisphenoid bone (*Fig.* 87) separates the rectus muscles of the right and left sides at their exit from the eye-muscle canal.


Fig. 89.—Parietal, left.

By being gently worked up and down, the frontal (*Fig.* 88) and parietal bones (*Fig.* 89) can be loosened and lifted off. The mesethmoid, which covers the tip of the snout-cartilage, may also be removed in this way.


Fig. 90.—Supra-occipital.

Removal of the frontal and parietal bones opens up the cranium, the only remaining part of its roof being the scaly portions of the supra-occipital bone (*Fig.* 90) and the piece of cartilage which is in continuity with it and with the strips along the upper edges of the presphenoid bone.

The olfactory lobes of the brain occupy the trough of the presphenoid bone (*Fig.* 91). Their connection with the rest of the brain is easily broken. As seen from above, the brain lying in the main cavity of the cranium shows four large bulgings. No study of it will be made here. In the present state of the theory of dual constitution of animals, no use can be made of it.

When the brain is taken out of the way, there is to be seen at the back part of the cranial cavity, in the angle between the exoccipital and squamosal, a vertical stiff brown stem which at its upper end meets the upper ends of the posterior and anterior semicircular canals. These canals are easily seen, but the horizontal or external canal is less easy to come at. It runs in the substance of the squamosal bone, below and to the outer side of the bulla, where the shelf of bone which carries the articular surface for the hyomandibular joins the rest of the bone.


Fig. 91.—Presphenoid.

Below and behind the brain, a thin plate of bone helps to separate off a pair of fossæ from the rest of the cranial cavity.

These deep fossæ contain vascular tissue in which the large otolith (*Fig.* 92) is embedded, and a large bridge o similar vascular tissue connects the two masses in the fossæ across the basi-occipital bone underneath the brain.


Fig. 92.—Otolith. (× 6 diameters.)

The general impression that one gains as one looks at the skull after removal of its roof and its brain content, is that it is built up around the labyrinthine structures—utricle, saccule, and semicircular canals. Thus the supraoccipital bone, although it takes part in roofing over the cranium, yet is equally, if not more, concerned in ensheathing the posterior semicircular canal. The epiotic bones, which form the posterior corners of the upper surface of the head, on each side of the supra-occipital bone, wall in the same canals until they reach the exoccipital bones. The two exoccipitals together form an arch over the spinal cord, and they form the floor of the archway as well, for by their meeting they exclude, almost or entirely, the ridge on the dorsal surface of the basi-occipital bone (*Fig.* 93). The basi-occipital, being median in position, forms the inner wall of both the right and the left cavity wherein the large otoliths are lodged. The outer wall of these cavities of the saccule is formed chiefly by that part of the exoccipital lying to the inner side of the thick wall surrounding the posterior semicircular canal, but to a small extent the proötic helps to form part of this outer wall. The roof of the cavity of the saccule is made by a thin triangular shelf of bone belonging to the exoccipital. The upper fan-shaped portion of the exoccipital is the largest constituent of the back wall of the cranium. The outer wall of the cranium is formed by the squamosal, the front wall by the alisphenoid, which is a squarish plate standing edgewise on the proötic; its upper edge meets the sphenotic, but there is a gap between it and the squamosal which is filled up by a process of the frontal bone. The upper part of the middle region of the front wall of the skull is occupied by the presphenoid bone containing the fore-brain. Below this the large optic nerves emerge, separated from the eye-muscles by the basisphenoid bone—a bridge of bone with four articular processes spanning the interval between the alisphenoids and proötics.

Fig. 93.—Basi-occipital.

The floor of the brain-case is formed by the proötics, squamosals, and exoccipitals. The sphenotic bones, opisthotic bones, and the basi-occipital form part of the under surface of the skull, but they take no share in enclosing the brain.

When the opisthotic bone is dislodged, the position which was occupied by its anterior point is seen to have covered the meeting point of three bones. These are the proötic, the squamosal, and the exoccipital. They each possess one process of similar design in all three bones. This is a stout process semicircular in section. Its articular end shows two flat surfaces inclined to one another at an angle of 120 degrees; they meet along a vertical line which bisects the semicircular end of the process. Half-way down this line is the circular opening of a canal, which runs the length of the process and at its other end opens into the bulla which each of these bones possesses. Consequently, when these bones are in position in the skull they compose a star—a regularly triradiate suture alternating with a regularly triradiate canal—and the centre of this star is sheltered by the tip of the opisthotic bone.

It will be remembered that in the description of the stomach mention was made of the long tapering part, in line with the pharynx, which eventually becomes a fine tube turning sharply forwards to enter the swim-bladder. The tip of the swim-bladder as it lies immediately below the arch of gristle that embraces the wing processes of the parasphenoid bone communicates with the arch. The lumen of the swim-bladder opens into the tube of the arch (*Fig.* 94). In this way there is direct communication, through the mouth, pharynx, œsophagus, stomach, communicating tube, swim-bladder, and arch, with the cone-shaped bulla in the exoccipital bone. Now we see that this small bulla is directly connected with the bullæ in the squamosal and proötic bones. In these the remarkable passage comes to an end. The bulla in the squamosal has no other opening into or out of it. The bulla in the proötic has another opening into it, but a strong fibrous partition forms a bulkhead which completely closes off the part into which the passage from the swim-bladder opens. The part of the proötic bulla which does not communicate with the swim-bladder owing to the strong partition, has an opening which leads backwards into the cavity which lodges the labyrinth. Whether the utricle sends a prolongation through the opening into the bulla is uncertain.

It appears likely that the herring possesses the necessary apparatus for exactly adjusting its buoyancy in relation to the depth of water it may be in.

It has been shown,* both by experimental and histological means, that the carp (*Caprinus carpio*) can and does swallow air and pass it into the muscular portion of the swim-bladder through the pneumatic duct, the entrance of which into the swim-bladder is guarded by a sphincter muscle.

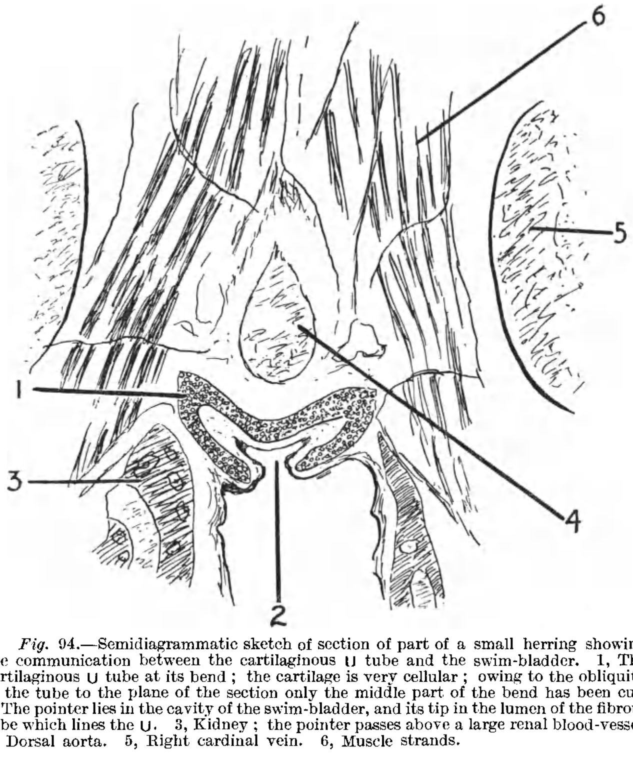


Fig. 94.—Semidiagrammatic sketch of section of part of a small herring showing the communication between the cartilaginous U tube and the swim-bladder. 1, The cartilaginous U tube at its bend ; the cartilage is very cellular ; owing to the obliquity of the tube to the plane of the section only the middle part of the bend has been cut. 2, The pointer lies in the cavity of the swim-bladder, and its tip in the lumen of the fibrous tube which lines the U. 3, Kidney ; the pointer passes above a large renal blood-vessel. 4, Dorsal aorta. 5, Right cardinal vein. 6, Muscle strands.

The herring differs from the carp and its relations by not having an arrangement of this sort. Its swim-bladder

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* Dr. Muir Evans, *Proc. Roy. Soc. Med.* (Otol. Sect.) 1930, xi, Sept., pp. 1549-1556.

is a simple long sac, opening posteriorly by a fine canal through a dense sphincter muscle, and anteriorly communicating through a cartilaginous arch with the interior of the labyrinth. The canal from the stomach enters the swim-bladder about its middle. It is curious to note that the communication from the stomach is actually in line with the pharynx, and that the passage to the labyrinth is through a tube of cartilage; for in this respect it impels us to remember the similar condition of things in mammals, with the Eustachian tubes running from the nasopharynx to the cavity of the middle-ear.

CHAPTER VI

THEORETICAL CONSIDERATION OF THE SKELETON

The reader who has followed the sketch of the main features of the anatomy of the Herring given in the preceding section should be in a position to recognize and locate the bones, which form nearly the whole subject matter of this chapter.

To regard the tail as a pair of fins may not be at all in line with present-day opinion. In this chapter, however, the tail is counted as a pair of fins (*Fig.* 95).

The form of the tail is similar to the form of a pair of fins. The rays are not hinged each on to a separate somactid with erector and depressor muscles arising from it, as in the dorsal and anal fins, but they are connected with wedge-shaped bones of a different type.

The muscles which move the tail arise deeply in the body from the vertebral column and adjacent structures, which is much more in the style of the paired fins than in that of the unpaired fins.

The upper and lower sets of muscles each send tendons to both the lower and upper tail-fin rays. In other words, they have cross connections, which is a state of affairs that seems incomprehensible for an unpaired fin.

The strictly median position of the tail-fin is, surely, the result of physiological necessity rather than an index of kinship with the unpaired fins, and the presence of 'fulcra', for a similar reason, is an accompaniment of the median position.

If the tail be reckoned as a paired fin, then the Herring has three pairs of fins, and they cannot be thought of as corresponding to the limbs of four-footed animals.

From the point of view of use, the tail is much more like a paired fin. The bearing of these remarks will be seen presently.

During the process of acquiring familiarity with the shapes and features of the bones of the herring, a chance observation opened up a very interesting line of inquiry.

The cleithrum and the preopercular bone were found to show a curious similarity of feature. Both terminate at their upper end in a flattened spine formed by the continuation of their anterior margin. At the root of this spine, both bones show a more expanded plate projecting backwards and having a smooth curved edge, while the anterior border is formed by a turned-back lamina. This turned-over lamina ends below,

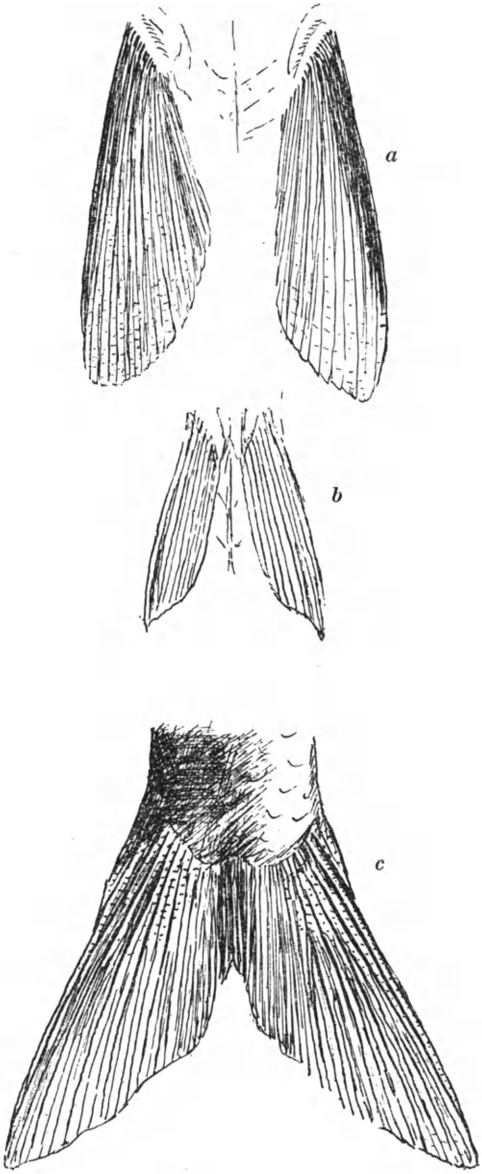


Fig. 95.—Paired fins : *a*, Anterior pair; *b*, Posterior pair ; *c*, Tail.

PLATE II

HERRING. BONES OF ANTERIOR PAIRED FIN, AND OF HEAD

Coracoid Cleithrum Mesocoracoid Scapula 1st Fin-ray

Admaxilla

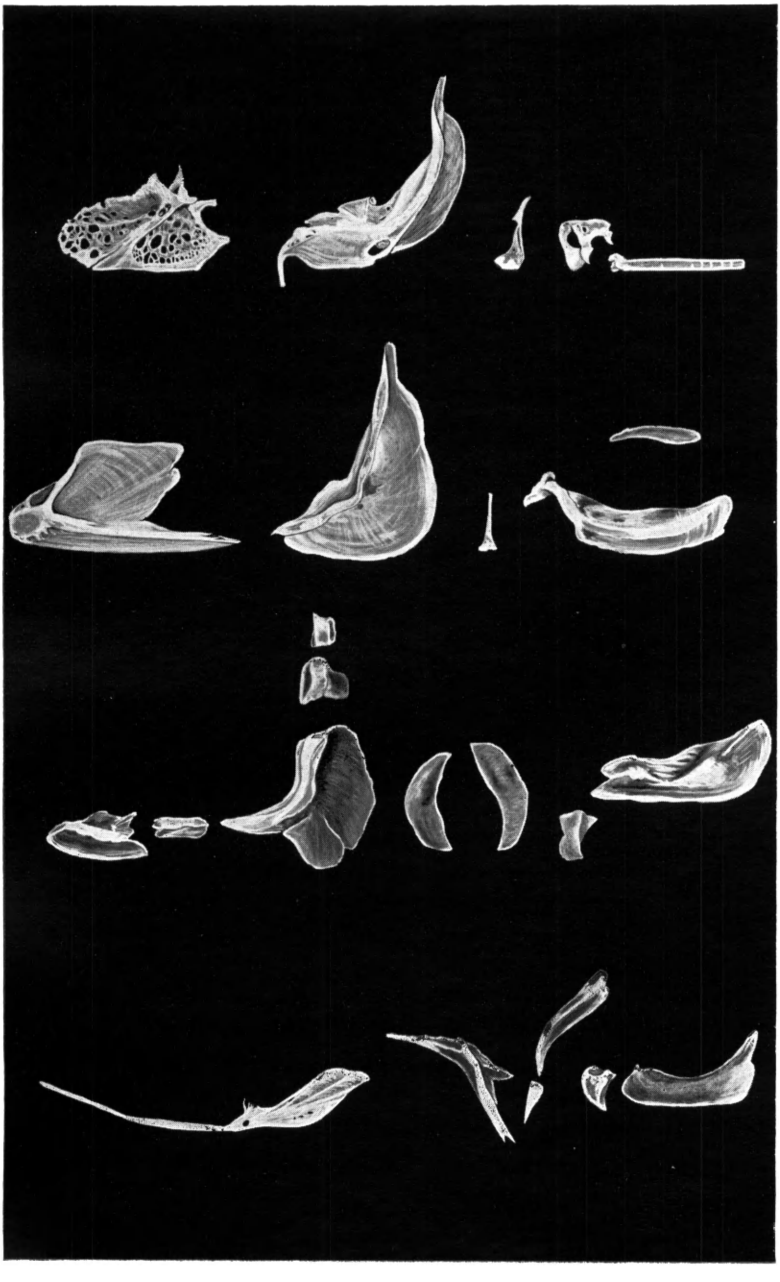
Dentary Preopercular Symplectic (upside down) Maxilla

Nasal Lachrymal 3 Suborbitals Sclerotic plates Lower hypohyal Interopercular

Supraorbital

Parasphenoid Ectopterygoid Adnasal Upper hypohyal Posterior gular

PLATE II



where it joins at a wide angle another turned-over lamina which forms a spine anteriorly. Opposite the point of junction of these two laminæ a triangular thin plate projects forwards and upwards. Thus we see that the main features of these two bones are similar in kind, though they are very different in degree.

Not long after this observation another similarity of this sort between two other bones was observed. Then a third one was recognized. After this the idea gained ground that there must be a large number of these resemblances between the bones, and they were deliberately sought out—and were found.

The next point was to determine whether there were groups of, say, seven or eight bones all pretty much alike, and others which could not be contrasted at all, or whether the bones could be all put into a few large similar groups. There certainly seemed to be more than just two such groups.

In view of the findings in the case of *Polygordius*, the possibility of there being four groups was favoured. In order to test this, it was necessary to take certain bones as the criterion by which to judge of the others. Here the only safe guide appeared to be similarity of function, and so the paired fins—including among them the tail—were taken.

The only possible way of finding likeness between many of the bones was by trial, i.e., direct comparison. Even then it required what might be termed a free translation of the observations to discern the likeness in some cases.

For instance, in the case of the cleithrum, the resemblance of the preopercular bone to it is easy to see (*Plate II*), but it only became evident later on, when other possibilities had been excluded, that a third member of the group was represented not by a single bone, but by the series of three or more thin flat bones which are called circumorbitals, and that the fourth member of the group was the diminutive ectopterygoid bone. The likeness of the ectopterygoid bone to the preopercular, or to the circumorbitals, is only recognizable when it and they are compared with the cleithrum.

The same kind of thing is seen in the case of the coracoid and its allies. The nasal bone is indeed a very good reproduction of the outline of the coracoid. But the likeness of the dentary is far less easily seen. Nevertheless the main features are the same, but in very different degrees of magnitude. The sharp spine in which the even lower border of the bone ends is huge in the dentary as compared with its size in the coracoid. The conspicuous ridge in the dentary running upwards and backwards from the anterior end of the lower border is copied in the coracoid by the oblique bar which runs from below and in front upwards and backwards to the articular part for the fin.

The parasphenoid bone has at first sight no resemblance to the coracoid, but through the medium of the dentary the affinity can be discerned. If the large spinous projection of the dentary were turned forwards, the shape of the bone would show distinct resemblance to that of the parasphenoid. The possibility of such an event being the case is greater than many people may be inclined to admit. In the animal a bone is not an inert mass of non-living material, but is just as much a living tissue as any other part. (See Chapter VII, p. 160.)

So far we have seen that the coracoid bone has the dentary, the nasal, and the parasphenoid bones resembling itself. And the cleithrum has for its allies the preopercular, the circumorbital bones, and the ectopterygoid bone.

Other bones which are found as components of the anterior paired fin and its root, are the mesocoracoid, the scapula, and the fin-rays.

The mesocoracoid bone is shaped something like the head of a spear with only one barb, which is at its upper end. The lower end of the bone broadens out and consists of two little wedges of yellow-coloured bone.

The symplectic bone, which is like a double-headed pin, resembles the mesocoracoid in its small size and in being composed of two tapering bars or wedges of yellow-coloured bone.

Less like it, the supra-orbital and adnasal bones come next. Their affinity to the mesocoracoid is shown in their close association with one another and their small size, and one might also perhaps include their outline.

By using the supra-orbital bones as intermediaries it is possible to accept the sclerotic plates as the fourth member of the mesocoracoid group. They consist of bone, are in close association, and are of unequal, but not of very unequal, size.

The next group is headed by the scapula as the type bone. The anterior end of the maxilla, which is composed of yellow bone, in contrast to the rest of the bone which is white or colourless, bears a striking resemblance in shape to the scapula. The other two members of the group are the two hypohyal bones. The upper one is like the scapula might be, if it were more folded up than we find it, and the lower hypohyal bone shows an even more extreme folding still.

The fin-rays, taken collectively, are the next things to be considered. Their counterparts are held to be the scaly portion of the maxilla, together with the narrow bony scale which lies along the upper edge of the maxilla, the large interopercular bone, and the largest gular bone. Seeing that only a small part of the fin-rays are bony, it is probable that not only the rays of the front paired fins, but those also of the hinder pair and of the tail ought to be comprised in this group. The sum total of all their bulk of bone would be more nearly the equivalent of the interopercular and the gular bones or of the maxillary counterpart.

Passing now to the hinder pair of fins (*Plate III*), there is only the one basal bone for consideration. It is triangular, with a straight wire-like edge forming a point at one end and at the other joining a mass of yellow bone.

The angular bone, which together with the dentary

PLATE III

HERRING. BONES OF POSTERIOR PAIRED FIN AND TAIL, AND OF HEAD

Bone of posterior paired fin (L.)

Hypurals (3)

Root-bones of middle tail-fin rays

Angular

Quadrate

Buccal

Entopterygoid

Metapterygoid

Premaxilla

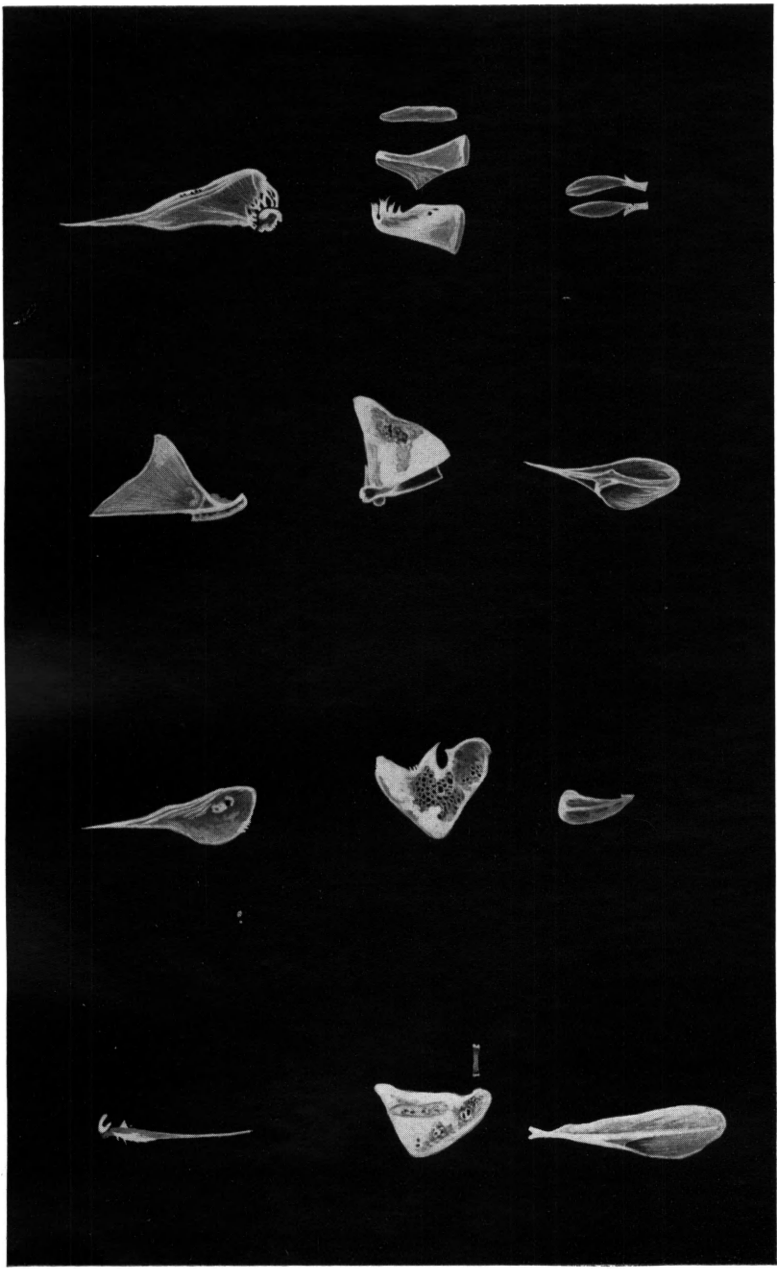
Interhyal

Vomer

Epihyal

Urohyal

PLATE III



makes up the lower jaw, presents a really remarkable parallel series of features.

The entopterygoid bone, which supports the eye—or seems to—is the next member of this group.

The fourth member is a middle-line bone, so that only one-half of it is to be considered. This bone is the vomer. It is much smaller than any of the other bones of the group. All these four bones are of narrow triangular form, and three of them have a mass of yellow bone at their broad end. The entopterygoid bone, which does not possess such a mass of yellow bone, is of nearly the same proportions as the basal bone of the hinder pair of fins.

In the tail there are the hypural bones which lie in the middle vertical plane between the upper and lower processes of the last vertebra or vertebræ, as the case may be. There are usually two large hypural bones, a third one considerably smaller, and sometimes one or more other very small ones. The two large ones lie opposite the end of the spinal column. They are of triangular shape and have a quill-like appearance, their posterior end being broad and square-cut. A thin scale runs along part of one edge near their anterior end. The smaller third bone is more rounded in section and has no thin scale.

The bones which are identified as corresponding to these hypurals are the quadrate, which looks as if it were made up of hypural bones placed edge to edge, the metapterygoid bone, and the epihyal bone, with which may probably be included the minute interhyal bone.

The epihyal, like the quadrate, looks like two hypurals joined edge to edge. But the resemblance of the metapterygoid to the hypurals is only seen on comparing it with the quadrate.

The only remaining bones of the fin series are the little blades of bone which form the proximal ends of the two middle fin-rays. Their counterparts are as follows. First, the thin bone which lies over the hinder end of the maxilla in the membrane which forms the outer wall of the mouth;

it may be called the buccal bone. Secondly the premaxilla, and thirdly the urohyal bone. The last is a middle-line bone, so that in its entirety it corresponds to all four of the little blade-bones of the tail-fin middle rays.

This completes the set of bones of the paired fins and their counterparts. It is convenient at this point to make some comments on these groups.

In the first place let us note that while the type series form one functionally entire group, the other three are not far behind in points of functional similarity.

Thus the second group consists of the dentary, preopercular, symplectic, maxilla and its attendant narrow scale, angular, quadrate, and buccal. These bones form the upper and lower jaws and their most immediate connections. They are strongly built bones, and except the quadrate and symplectic, which are under cover of the preopercular, they are under or in the skin.

The bones in the third group are, for the most part, thin and devoid of strengthening ridges. The nasal and circumorbital bones have a flat canal on them, but it is not very strong, and the rest of these bones is quite thin scale. The sclerotic plates, though apparently composed of yellow bone, are quite thin. The interopercular and entopterygoid bones are also notably thin. The lower hypohyal, the metapterygoid, and the premaxilla are all of more substantial build.

The classification which is given is a first attempt, made entirely upon the appearances of the bones of the Herring, without any control in the way of comparison with other fishes. It is therefore very probable that several bones have been wrongly placed. Perhaps, for instance, the buccal bone should be put in the third group and the premaxilla in the second, since the premaxilla is a more solidly built bone, and it is quite as closely associated with the jaws as is the buccal. The buccal bone, too, is thin and very superficial.

The bones of the fourth group, which are the parasphenoid, ectopterygoid, supra-orbitals, upper hypohyal, largest gular, vomer, epihyal and interhyal, and urohyal, are in general situated near or on the middle line. The parasphenoid, vomer, and urohyal are strictly median.

Apart, however, from the characters which have now been remarked upon, there is this interesting fact, that, with one or two possible exceptions, the bones in groups two, three, and four are all those constituents of the skeleton of the head which are capable of movement to a greater or less extent. They do not include any of the true bones of the gills or gill-cover, nor do they include any of the bones of the cranium. This remarkable uniformity in the position of these bones does much to justify the inclusion of the tail as one of the paired fins, although the reader will observe that the bones likened to the hypurals—namely, the quadrate, metapterygoid, and epihyal with the interhyal—are all of them a little irregular in respect of their groups. The quadrate is not a subcutaneous bone, the metapterygoid is not thin and scale-like, the epihyal and interhyal are not very nearly median in position.

If we take note of the orientation of the bones in the various groups, we find that the bones of the second group all agree with those of the first, with the exception of the symplectic and buccal. In the third group, the metapterygoid is the only one which undoubtedly differs in position from its type in the first group. The fourth group, however, shows marked difference. The vomer, epihyal, and urohyal, and half of the parasphenoid, are all reversed, and the ectopterygoid is turned through a quarter of a circle. The case of the vomer is particularly interesting, because it has obviously been carried round with the half of the parasphenoid when that was reversed, a thing which seems to indicate a close connection between these two bones. In the second group, the two bones corresponding to these—the dentary and the angular—make up the lower jaw, and Meckel's cartilage is found connecting them on their inner side, so here again the association is very close.

PLATE IV

HERRING. BONES OF HEAD (IMMOVABLE)

Parietal
Basi-occipital
Squamosal (pteroti̇c)

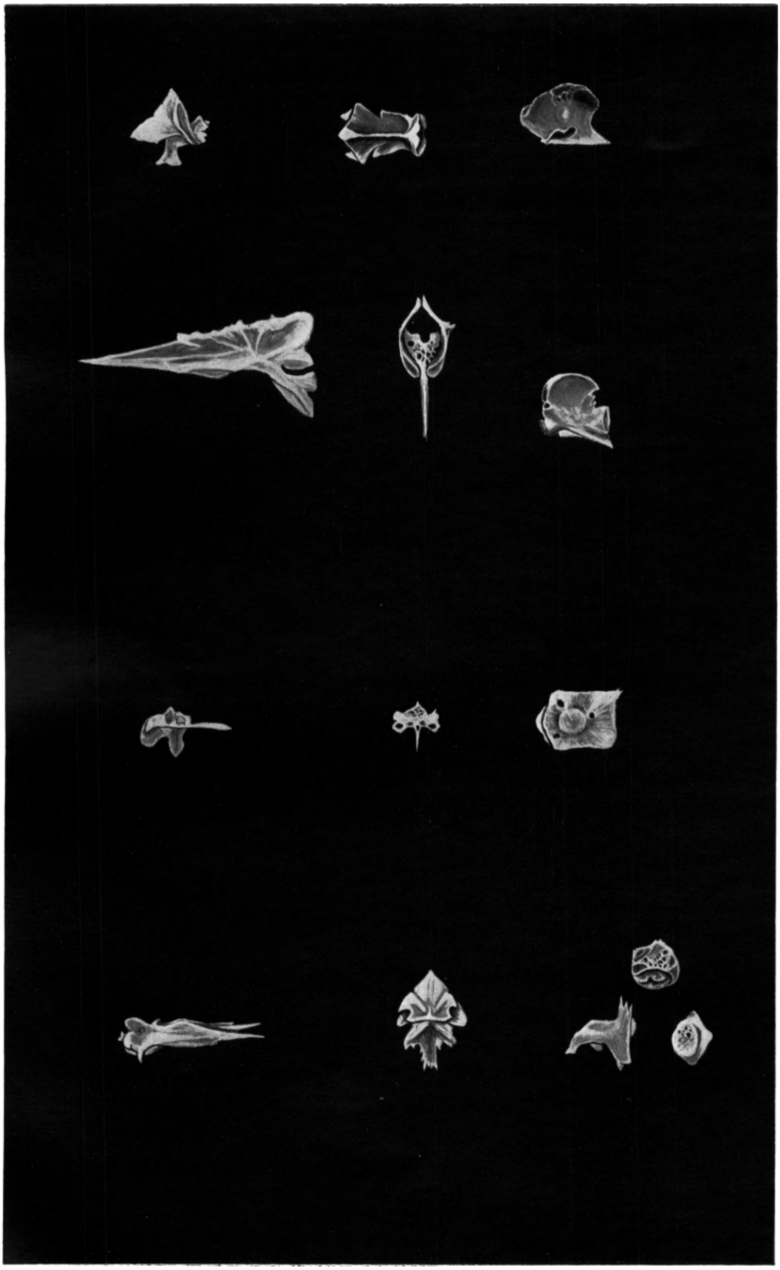
Frontal
Presphenoid
Exoccipital

Prefrontal
Basisphenoid
Proötic

Alisphenoid

Mesethmoid
Supra-occipital
Sphenotic
Epiotic

PLATE IV



An observation made by Ridewood concerning the jaws in another clupeoid fish, *Coilia nasus*, is illuminating. He says (*Proc. Zool. Soc.*, 1909, Part I, p. 480), "the mouth is so large that the ramus of the mandible is longer than the cranium. The dentary and articular components of the coronoid process are separated by a short interval. This separation, however, although striking, is evidently a feature of no great importance; it occurs in an exaggerated form in *Gonorhynchus*, it occurs in some percoid and berycoid fishes, and doubtless in many other groups."

The separation of the two bones noted by Ridewood shows that there is the possibility of such a thing, and greatly strengthens the case for regarding the bones of the anterior and posterior fin 'girdles' as representing in the first group the bones of the lower jaw in the second.

Without much effort it has been found possible to arrange all the bones of the skull into four groups also (*Plate IV*).

The parasphenoid bone, having been already allocated to the movable bone series, cannot be reckoned a second time. Another bone, too, the opisthotic, may or may not be rightly included among the skull bones. It is very small and does not help to cover in the brain; moreover, its connections seem rather to be with the gill-apparatus, and so it will be left out now.

There is no functional characteristic by which to determine which bones shall be taken as types, and there is not much indication as to which bones are in mutual association.

In the bones shown in *Plate IV* the arrangement is as follows :—

Parietal
Frontal
Prefrontal
Mesethmoid

Basi-occipital
Presphenoid
Basisphenoid
Supra-occipital

Squamosal
Exoccipital
Proötic
Alisphenoid, Sphenotic, Epiotic

A better arrangement as regards the position of the bones in the skull would be :—

Parietal	Supra-occipital	Squamosal
Frontal	Presphenoid	Proötic
Prefrontal	Basisphenoid	Alisphenoid, Sphenotic, Epiotic
Mesethmoid	Basi-occipital	Exoccipital

In the first column all the bones are thin and scaly. Examination of the bones will show that the frontal and the parietal bones point in the opposite direction, so that the two notches between the downward pointing process and the rest of the mass of the two bones come together and form a window.

The folding of the prefrontal bone is so complex that it is difficult to be sure of its true orientation. The mesethmoid, however, or rather one-half of it, points in the opposite direction to the frontal.

The bones in the second column are all middle-line bones, and it is a curious thing that they are none of them in contact with each other. They are all composed chiefly of yellow bone and have a scaly portion in front, except in the case of the basi-occipital, in which bone the scaly part is represented by an articular piece of white bone at its posterior end. The likeness of the basisphenoid to the back portion of the supra-occipital is quite remarkable. The cancellous structure of the presphenoid renders its points of resemblance to the other bones in this column obscure. It is a curious thing that the presphenoid bone and the coracoid are the only bones which show a generally cancellated structure. In spite of its very much perforated condition it is possible to recognize that the presphenoid is built up of parts similar to those of the other bones in this column.

In the third column are the three bones which possess an auditory bulla. The bullæ in the squamosal and proötic are globular, that in the exoccipital is a small narrow cone and may be almost non-existent sometimes. But all three bones have other features in common.

There are fan-shaped slabs of yellow bone, and each bone also has a spine-like process of white scaly bone. In addition, the three bones articulate with one another by means of a stout process, semicircular in section, perforated lengthwise by a canal leading to or from the bulla. There can be no doubt of the resemblance of these three bones.

In place of a fourth bone of similar type, we have to be content with three lesser bones which perhaps are equivalent to such a fourth bone but have become separated and dispersed. The epiotic consists of a somewhat fan-shaped slab, which encloses part of the posterior semicircular canal. The sphenotic has a spine-like process of white scaly bone, and the alisphenoid appears in nature and quantity to make up the residue of detail and volume that is necessary.

Although the bones of the skull are in this way seen to be capable of arrangement into four similar groups, there is little or nothing to show whether any one of these groups is particularly associated with any one group among the movable bones.

In passing to consider the bones of the gills and gill-cover (*Plate V*), we leave the quadruple arrangement, and find instead that there are two sets of two groups each. This finding, then, rather confirms the idea of the dual structure of all metazoan animals; whereas, had all the bones been capable of being put into four similar groups without exception, the case for the dual origin would not have been so strong.

Along with the bones of the gill-cover is reckoned the hyomandibular to which the operculum is articulated by a movable joint. The only bone at all comparable in number of parts to the hyomandibular is the large ceratohyal bone.

Associated with the hyomandibular in its group are the opercular bone, which articulates with the hyomandibular by a movable joint, the subopercular bone, which fits on to the lower edge of the large opercular and completes the free edge of the gill-cover, and the gular bones, except

PLATE V

HERRING. BONES OF GILLS AND GILL-COVER

Hyomandibular Opercular Subopercular Branchiostegals (5) Gulars (2)
(The two anterior
gular bones)

Spicular Infrapharyngobranchials (2) Epipharyngeal

Epibranchials (3)

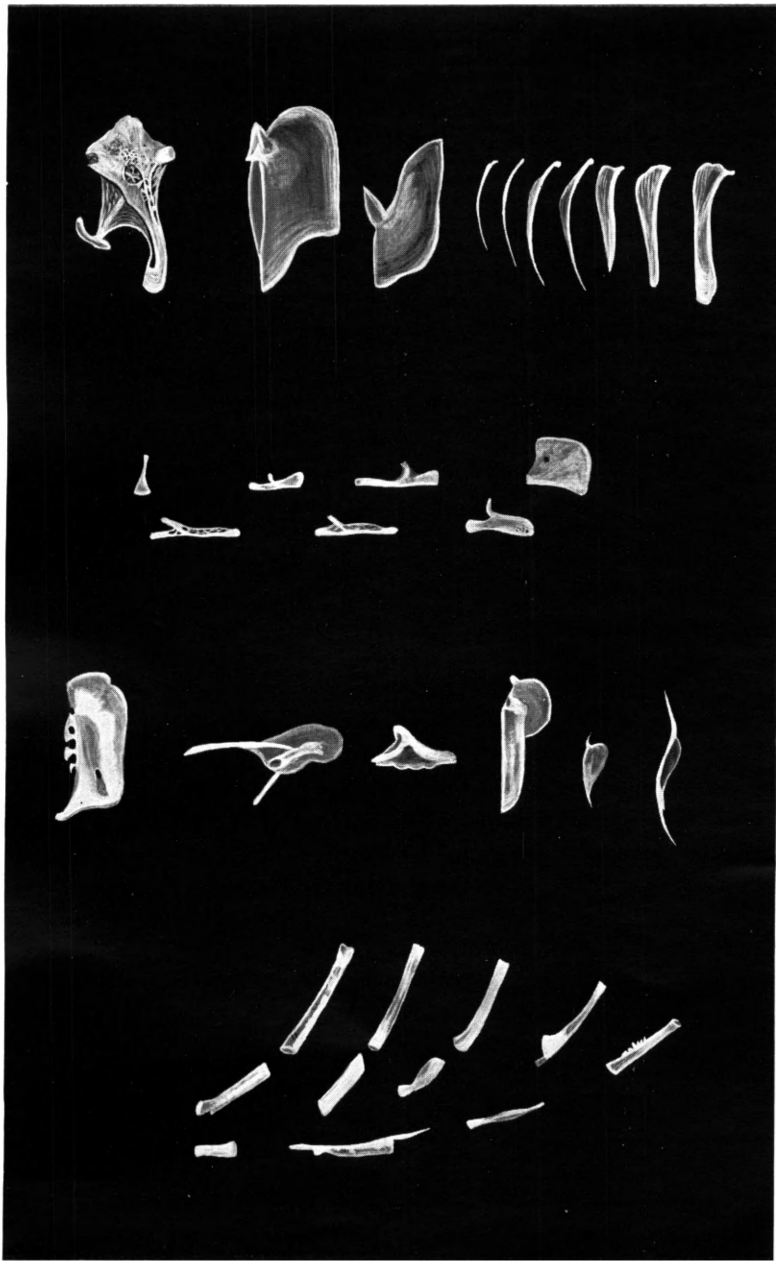
Ceratohyal Post-temporal Supratemporal Epicleithrals (3)

Ceratohyals (5)

Hypohyals (3)

Basibranchials (3)

PLATE V



the largest of the three, which has already been included among the other movable bones.

In *Plate V* the branchiostegal rays are shown in this group along with the gular bones, but in view of their peculiarly intimate association with the ceratohyal it is more likely that they belong to its group.

The bone in the ceratohyal's group which resembles the opercular is the post-temporal. The long sharp spine on this bone is comparable to a much elongated postero-inferior angle of the opercular, and instead of a sessile cup as possessed by the opercular, the post-temporal has its long stalk by which it is articulated to the odontoid process of the opisthotic bone. It is quite probable that the opisthotic bone should have been included with the ceratohyal as equivalent to the hyomandibular. The triangular supratemporal bone corresponds to the sub-opercular in the hyomandibular group. Then to correspond to the gular bones of the hyomandibular group are the supracleithral bones—three or four in number—and finally the five curved bones known as the branchiostegal rays.

The only remaining bones in the head now are the bones of the gills. The sword-shaped gill-rakers are actually bones, but they can be stripped off with the membranous ribbon which runs along the gill-arches and so are not considered to be really part of the bony framework of the animal. A superficial examination of the gills shows that they are divided by the hinge of the arches into an upper and a lower set.

The bones of the gills below the hinge are more or less straight simple bars running downwards and inwards towards the middle line, where they meet a chain of three bones and two rods of gristle. This chain of structures forms the middle of the floor of the pharynx. There are five gill-arches, of which the anterior three are composed of two bones and the posterior two of only one bone each, below the hinge.

The last arch has no bone above the level of the hinge ;

in fact, it has not got a hinge, but the opening of which it forms the posterior boundary is of crescentic shape. In the fourth arch a nodule of gristle occupying the recess in the lower end of the bony bar represents, or seems to, the lower bone that is seen in the arches in front.

The bones of the middle line of the floor of the pharynx are so perfectly adapted to fit in with the scheme of the gill-bars that there can be little doubt but that they and the bones below the level of the hinge, at any rate, have acquired their shapes as the result of use, quite as much as from the result of inherited features.

There are seven bones of the gills above the level of the hinge. The foremost of these bones is the minute os spiculare which sits upon a block of gristle in front of the upper bone of the first arch. The spicular bone points upwards and lies almost over the foramen in the root of the wing process of the parasphenoid bone.

The most posterior of the bones above the hinge of the gills is the epipharyngeal bone—a thin plate of yellow bone of approximately quadrilateral outline.

All the other bones, five in number, are branched, and the two arms formed by the branching in every case point forwards. Minute bars or nodules of gristle help to complete the formation of the arcades of this part of the gills, and a cartilaginous edging to the epipharyngeal bone completes the upper part of the fifth arch.

The branching of the bones situated above the hinge of the gills is taken to mean that these bones are compound in nature, and it does not appear too improbable that they may represent the closed-up arches of a former set of gills. So that, although now they are only the upper elements of the gill-arches, in some ancestor, or perhaps one should say predecessor, of the type 'Herring', they were the bones of the whole arches. It is even possible that the two smaller bones with the very small side branch —the infrapharyngobranchial bones—are relics of a still earlier set of gill-arches. If this were the case, then there would be evidence of at least two perfected types of vertebrate animal in the formation of the type which we now know as the Herring.

The statement made above with reference to the epibranchial bones, that their arms in every case point forwards, is hardly exact. It would be better to say that the angle between the arms looks forwards and upwards, or inwards, but does not face backwards.

Every one of the bones of the head, of the gills, and of the paired fins, has now been dealt with. The evidence which they afford for the support of the theory of the dual constitution of animals appears to me to be strong. The similarities between the bones which have been described are too numerous and too well marked to be accidental. The reader will remember that exact resemblance is almost as much denied by the theory as close resemblance is postulated.

One finding to which this review of the bones has led is that the terms 'pectoral fin girdle' and 'pelvic fin girdle' seem to be complete misnomers. Like the names of many of the bones in the fish, they have been applied from mammalian anatomy, a proceeding which is about as rational as trying to apply the terms used for the parts of a motor car to the parts of a chariot and horse of Roman times.

The large remainder of the bones of the Herring consists of the vertebræ and their processes, the ribs, the root-bones and rays of the unpaired fins, and the bones embedded in the muscles of the body.

The study of these last-named bones I have not undertaken. The task of determining their number, form, and exact locality would require an enormous amount of time, and probably trouble too.

But something has been done with the other bones of the body (*Plate VI*).

The number of vertebræ which the Herring possesses is differently stated by different authorities. As in all animals the actual number does vary, although the great majority of any one race will have the same number.

PLATE VI

HERRING. BONES OF BODY REGION

‘False’ ribs (2)

Branched ‘tendon-bones’ from muscles of body (2)

‘Tendon-bone’ from occipital region

Basi-occipital (viewed from above)

Basi-occipital (end view)

1st vertebra

Dorsal and dorsilateral spines (R. and L.)

Vertebræ of approximately the following sites, Nos. 6, 27, 30, 36, 43

One of the anterior vertebral bodies

3rd rib

1st rib

Anterior root-bone of dorsal fin (side view)

Gill-raker

Supporting bone of gill fringe

Root-bone from dorsal fin (front view)

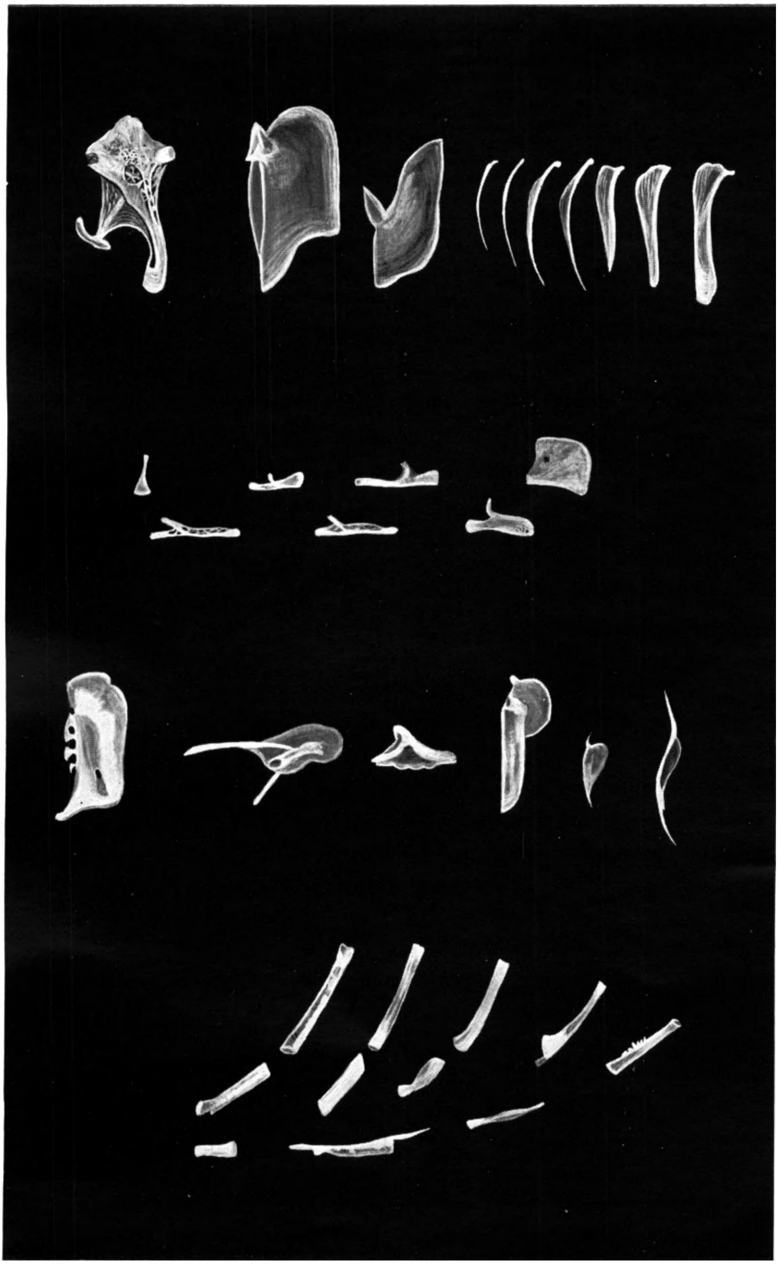
Two fin-rays from anterior paired fin

Root-bone of dorsal fin (side view)

Two vertebræ, about Nos. 31 and 32 (side view)

Vertebræ of tail region and hypural bones

PLATE VI



But another source of difference in the statements is due to difference in the reckoning of what shall, and what shall not, be called a vertebra.

Counting as a vertebra the terminal little vertebral element which some people call the urostyle, the Herring has usually fifty-eight vertebræ.

The first two vertebræ do not carry ribs.

The next twenty-two vertebræ have ribs articulated to them, and the last two of these vertebræ (sometimes more, sometimes less) have ventral processes.

Behind the rib-bearing vertebræ are sixteen or seventeen which possess delicate side processes. The first fourteen of these vertebræ are connected with the 'false' ribs, and vertebra No. 26 usually has an arch of bone, as do all the vertebræ behind it. In front of it, however, are three or four vertebræ which have ventrally directed points of bone, which correspond to the pillars of the arches not as yet connected together. By the time the tenth bony arch is reached the two pillars have met to form a single ventral spine, and this ventral arch, if it were separate from the body of the vertebra, would be a chevron bone.

The remaining seventeen vertebræ do not have any side processes, nor do they have any ribs connected with them. It therefore seems highly probable that the side processes of the sixteen vertebræ or so are really homologous with the side processes of the true ribs, but that when the 'false' ribs failed to connect up with the vertebræ the lateral processes corresponding to them dispensed with their rib partners and attached themselves to the vertebræ.

Of the last seventeen vertebræ the last two or three show a peculiar quill-like thickening of the tip of their ventral process. The next two or three vertebræ in front of these, though having sharp-pointed ventral processes, are like the terminal vertebræ in having their dorsal and ventral processes nearly straight, and in front of these again the next few vertebræ show a very gentle curving of their processes. At about the eighth or ninth vertebra from the last, the dorsal processes begin to exhibit a distinct sudden change in thickness and an angular bend at about half their length, and it may be noted that the side branch of the intermuscular bone is connected by ligament to the dorsal spine at this point.

From this description of the backbone of the Herring it is evident that it is divisible into definite regions, and to recognize only two groups of vertebræ—those of the body, and those of the tail—is to understate the case.

It is not possible to give anything like a complete or satisfactory account of the bones of the body of the Herring, but some attempt may be made to show that there is reason to believe that these bones of the body will ultimately prove to be susceptible of a similar type of grouping to that of the bones of the head and paired fins.

By way of introduction it will be convenient here to give a table of certain details of seventeen herrings which are all random samples.

Sex	Submerged Fin	Dorsal Fin	Tail Fin		Anal Fin	Keeled Scales	Posterior Pair of Fins	
			Upper	Lower				
♂	17	18	9	9	18	14	9	9
,,	17	18	9	9	18	15	9	9
,,	17	17	8	9	17	14	9	9
,,	17	17	9	9	17–18	14	9	9
,,	17	18	9	8	18	15	9	9
,,	17	18	9	8	16–17	14	9	9
,,	19	17	8–9	8–9	18–19	14	9	9
,,	16	18	9	9	18	14	9	9
,,	17	19	8	8	17	14	9	9
,,	11	16	7	8	16	15	9	9
♀	18	16	9	9	16	14	8	8
,,	17	19	9	9	18	14	9	9
,,	17	18	9	8	18	14	9	9
,,	17	18–19	8	9	17–18	14	9	9
,,	17	19	8	8	18	14	9	9
,,	17	19	8	7	18	14	9	9
,,	16	18	9	8	18	13	9	9

The table shows that the number of rays and of ray-bones is far from constant, but that the variations are not great as a rule. The herring which showed only eleven bones for the submerged fin was probably less abnormal than it seems from the figure given, because the posterior six or seven bones were absent ; the bones which were present were in their usual place, and there was no attempt to make eleven bones spread out to occupy the space normally taken up by seventeen bones.

The table shows that there is about the same amount of variation in the two sexes.

A few other details besides those that are shown were ascertained in some cases. In two the rays of the anterior pair of fins were counted : they were eighteen and eighteen in one case, and seventeen right, sixteen left in the other. The U-shaped scales in the first case were nineteen, and in the second eighteen.

Even allowing for the personal element in making counts of these rays and scales, there can be no doubt that no one particular number is constant. That is the verdict of the letter of the law. But is it the spirit ? Surely the reality of the phenomenon is that there is an attempt on the part of the tissues concerned to repeat these structures nine, or some multiple of nine, times.

For the anterior paired fins there are eighteen rays each, for the posterior pair nine rays each, for the tail fin nine rays in the upper and nine in the lower part ; dorsal fin eighteen rays, anal fin eighteen rays, U-shaped scales eighteen.

If there is anything in this principle, it should also be applicable to the spine and ribs. There are fifty-eight vertebræ, twenty-two true ribs, fourteen 'false' ribs : none of these numbers seem capable of conforming to the rule.

As regards the vertebral column, there is good reason to think that the number of the bodies of the vertebræ depends more upon physical conditions of environment than upon the inborn tendencies of the tissues. The number of vertebræ is known to be greater for fish in one habitat than it is for the same kind of fish in another. (B. Storrow, Review of Three Books, *Nature*, 1925, May 16, p. 756.) But apart from this, there are further reasons, to be dealt with in another chapter.

The work of H. Gadow and E. C. Abbott (" Evolution of the Vertebral Column of Fishes ", *Phil. Trans.*, 1896) shows, in teleosts at least, the dominating importance of the processes of the vertebræ in the matter of ossification. It is then to the processes rather than to the bodies of the vertebræ that attention should be paid.

The number of bones of what is here termed the submerged fin is usually seventeen, and an X-ray photograph of a herring shows that each of these little rods corresponds in position to the tip of the dorsal spine of a vertebra. This is rather a curious thing when it is observed that the space occupied by the length of the bodies of the eighteen vertebræ is shorter than the length of the space occupied by the submerged fin.

The dorsal fin appears to be definitely connected with the submerged fin ; the median keel on the foremost of its root-bones is almost in contact with the last bone of the submerged fin.

In spite of this the dorsal fin shows no such relationship to the spines of the vertebræ as the submerged fin does. Some of the spines of the vertebræ are a little bent down under the dorsal fin as if it had intruded itself on their domain. This is all the more interesting because at the back of the dorsal fin is a small muscle with several long tendons. It is an obvious thing known to every dissector that a tendon is a physiologically active, inextensible connection between a muscle and its site of insertion or origin, so that there shall not be an excessive amount of contractile tissue, while at the same time all the energy of the muscular contraction shall be employed exactly where it is required. The presence of the long tendons of the muscle behind the dorsal fin, therefore, betokens that the little muscle has changed its position relatively to its points of insertion, and instead of being close to them it has moved forwards away from them, having been transported by the bone from which it arises—the last bone of the dorsal fin root.

The first two vertebræ do not carry ribs ; they are short from front to back and broader than the other vertebræ by a slight amount, but apart from these characters they have nothing about them like the atlas and axis of quadrupeds. Yet their existence seems to call for some explanation, and the fact that the submerged fin is closely related to their dorsal processes and to the processes of the vertebræ which follow them may be the governing reason for their persistence, since the submerged fin, though no longer functioning, has controlled the position of the dorsal fin, as shown above.

The complete system of the submerged fin and dorsal fin together consists of about thirty-six bones arranged in series.

There are twenty-two ribs which are attached to the spinal column. The lower extremities of these ribs, except the first one and last two or three, are attached to the U-shaped scales along the ventral border of the fish. There is thus an intimate association of the ribs with a series of epithelial structures, eighteen in number.

Behind the true ribs is another set of bones of similar nature called here the 'false' ribs, and they with the true ribs complete the protection of the viscera in the cœlom.

There are fourteen false ribs, so that the total number of ribs on each side of the body is thirty-six.

When in the course of dissection the region of the terminal part of the cœlom is reached, then it is found that there are three rods of bone lying parallel with the false ribs near the lower end of the last one, and these three bones form a gradation between the false ribs and the root-bones of the anal fin.

The actual number of the false ribs and of these intermediate bones may vary considerably, but there can be little doubt but that here again the total number is seventeen or eighteen, and since there are eighteen root-bones to the anal fin, we again get a series of thirty-six bones.

The last three vertebræ present a quill-like modification of the tip of their ventral spine; otherwise all the posterior vertebræ possess a ventral arch which terminates in a sharp spine. Farther forwards this arch has two points and the arch itself broadens out, and still nearer to the head the vertebræ show only two little sharp points directed downwards. The sum total of all these vertebræ is thirty-six. The two or three front ones of this series correspond to the last vertebræ which carry true ribs.

But if we take into consideration the last vertebræ of all, which are those showing the peculiar modification of their ventral spines and the adjoining vertebræ, we may note that their dorsal and their ventral spines are nearly straight, and that the anterior ones are of evenly diminishing thickness. There can be said to be nine vertebræ of this type in all. The next nine vertebræ in front of these have their dorsal and ventral spines of nearly equal size, and they show a marked unevenness in the thickness of these processes, and a distinct angle where the sudden change of thickness occurs. In front of this second lot of nine vertebræ there are a set of eighteen which have a small lateral spine attached to their bodies; the attachment, however, is not a bony one, so that the presence of these little bones is only seen on dissection. Once more, then, we see that there is a set of thirty-six bones forming a continuous group.

It is very likely that a study of the slender bones of the musculature would provide other instances of a similar kind, and it certainly seems legitimate to reckon the paired fins in this way, viz., eighteen rays in the anterior, nine in the posterior, and nine in the tail, since the bones of the roots of these fins have been found to correspond to the dentary, angular, and quadrate, which are all continuous as far as they can be.

A feature of all these groups of thirty-six is that they all contain one set of eighteen similar structures, while the other eighteen are generally split up into two groups of nine each. The number nine seems to be the basic feature, and the reason for there being a basic number does not appear to be difficult to understand. The nine structures are in every case a series of similar bones differing but little from one another.

From the study of *Polygordius* the conclusion was reached that serial repetition without the appearance of new structures is characteristic of an asexual phase of growth. So that the recurrence of the number nine merely indicates that the proximal ancestors of the type *Clupea* all possessed the same power of production in their asexual phase, just in the same way as the proximal ancestors of the type *Polygordius* were each able to give rise to five sets of micromeres.

An interesting thing about the Herring is the overlapping that occurs. The fitting is not exact. The bones of the submerged fin seem to have necessitated the lengthening of the vertebral column to at least two more vertebræ beyond those required for the ribs. The crowding out of three bones of the false rib series between the anal fin and the cœlom has apparently been the reason for the occurrence of twenty-two true ribs instead of only eighteen. The hæmal arches along the ventral aspect of the vertebral column trespass upon the region of the true ribs.

These seeming inequalities are probably of great use in giving strength to the whole; they are like lapped joints in structures built of metal. The two penultimate vertebræ show a peculiar quill-like formation of their ventral spines which is comparable to the quill-like structure of the hypural bones in their immediate vicinity. It is an interesting phenomenon that this quill-like appearance, which the microscope shows to be due to ossification around cellular cartilage, should have been actually located in the place of the hæmal spines. It points to there being much more than a casual relationship such as might have been assumed to be the case if the hypurals alone were the only bones of this sort in the root of the tail. Furthermore, the only other place where this type of structure is clearly seen is in the region of the gills and the hyomandibular bone. This state of affairs seems to me to show that the same thing has happened in the herring as happened in *Polygordius*. The serially repeated structures have not been permitted to extend back indefinitely, but have been limited in their backward extension by being produced in between parts of the previously existing animals. In *Polygordius* the long body of the worm is produced between the upper and the lower parts of the trochophore; in the Herring the body is enclosed between parts of the gill system. Incidentally it may be remarked that the gills are themselves serially arranged structures, and therefore probably represent asexually repeated structures of some earlier ancestor.

There are, I doubt not, many other things that might have been said, and many other details of structure which could have been made use of, but I have given to the reader practically all the points which seem to be sufficiently well supported to be of value as evidence in favour of the theory of the dual constitution of animals.

NOTE.—The figures of the *bones* in the text of chapters V and VI show them magnified 2 diameters.

CHAPTER VII

THE BEGINNING OF BONES

IN the silt and drift along the banks of the Oswego River which flows into Lake Ontario there may sometimes be found white rods of gristly material, about 2½ in. long. These rods, which are about $\frac{1}{20}$ in. thick, are none other than the notochords of defunct lampreys.* The lamprey is hardly to be reckoned as a fish, although it has an eel-like form and possesses gills. The notochord, which corresponds to the backbone of higher animals, is one continuous rod, and bends readily according to the needs of the animal; it is not divided up into segments as it is in sharks and rays and all the higher animals.

The doctrine has been attributed to Gegenbaur that all cartilage originates from without (Dr. Gadow, " Discussion on ' The Origin of Vertebrates ' ", *Trans. Linn. Soc.* 1910 : " Aller Knorpel kommt ursprünglich von Aussen "), and this implies that the cartilage of the notochord must, in some period in the ancestry of the lamprey, have had a representation on the surface.

The lamprey has an elaborate gill-skeleton of cartilage, and since the gills of necessity are surface organs, in the sense that they must come into direct contact with the water in which the animal lives, it may well be the case that here is the site of formation of the first skeletal cartilage. This view has been put forward by Ayers.

The physical properties of cartilage, its strength, flexibility, resilience, and solidity, are characters which fit it for its use as a frame and support to other softer structures.

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* Prof. S. H. Gage, *A Biological Survey of the Oswego River System*, State of New York Conservation Department, 1928, p. 171.

But it is neither a uniform substance—there being several kinds of cartilage: hyaline cartilage, fibro-cartilage, elastic cartilage, cellular cartilage—nor is cartilage very definitely demarcated from mucus and its related substances. There is every gradation to be found among these from the liquidity of white of egg to the brittleness of glue.

The mucoproteins, which are the nitrogen-containing bodies characteristic of these substances, are combinations of a protein with a carbohydrate group which is conjugated with sulphuric acid.

To give some idea of the study which chemists have made of these substances the following quotations from the work of Dr. P. A. Levene on hexosamines and mucoproteins (*Monographs on Biochemistry*, 1925) may be given.

Page 82: "DISTRIBUTION OF CHONDROITIN SULPHURIC ACID AMONG TISSUES OF THE ANIMAL ORGANISM.—Correctly stated, mucoproteins of this type (chondroproteins) occur in the connective tissue of various organs, though it would be misleading to say that mucoproteins of all connective tissue belong to the same type. Up-to-date mucoproteins of this type were found in:—

1. Cartilage.
2. Tendons.
3. Aorta.
4. Sclera.

"Although no effort has as yet been made to analyse osseomucoid in this respect, it is, however, quite likely that it belongs to the same group."

Again on page 84: "TYPES OF MUCOITIN SULPHURIC ACIDS. At present mucoitin sulphuric acid has been isolated from the mucoproteins of the following tissues:—

A. 1. From Mucin of gastric mucosa.
    2. From Serum mucoid.
    3. From Ovomucoid.
B. 1. From Funis mucin.
    2. From Humor vitreous.
    3. From Cornea."

These two quotations merely show the wide range of connective tissues which have been studied, but they give no idea of the careful chemical work that has been done, nor of its difficulties, nor of its achievements. Nor is there any mention of the rôle of hexoses and phosphoric acid which are also dealt with.

In elasmobranch fishes the cartilaginous vertebral column is partially calcified, and Ridewood showed that the calcification takes place in that part of the sheath of the notochord which is formed by the cells which have invaded the sheath from without. The innermost zone of this sheath cartilage is hyaline, and if it calcifies it does so in an irregular manner. The middle zone is very cellular ; it calcifies evenly and forms the double cone of the biconcave vertebra. Its cells are fusiform and their long axes are circumferentially disposed. The outer zone, likewise, shows circumferential calcification.

In the case of the notochord, Sedgwick (*Textbook of Zoology*, 1898, Vol. I) points out that the cells are vacuolated and develop cuticular structures, so that they have much the appearance of plant parenchyma, and moreover partake of its nature in so far that they are able to act as a supporting structure. In the embryo the notochord is budded off from the mid-dorsal line of the endoderm, and in some animals a hypochord or secondary structure of similar nature occurs—an echo of the true notochord, so to say.

The main function of the notochord is as a support. It reaches a relatively extreme degree of presence in Amphioxus, in which animal it is coterminous with the body. Perhaps this is an accidental occurrence due to the means taken by the cells to acquire their power of giving support—that is to say, due to their vacuolation, which by enlarging all their dimensions may have increased the total length of the notochord beyond the real needs of the animal.

Vacuolation itself seems to be due to a dehydration of the protoplasm leading to a more resistant material—the protoplasm becomes harder through being dried.

If the white albumen of a hard-boiled egg be cut into small cubes, and these are put into a solution of pepsin in 2 per cent hydrochloric acid, the cubes are easily digested in a few hours at the temperature of the body, 37.5°C. But if the cubes are allowed to dry in air so that the edges harden, they can be kept for days in the acid pepsin solution and remain unchanged. This seems to lend colour to the view that the vacuolation of the notochordal cells may be caused through some process of dehydration conferring powers of resistance to change and at the same time hardening the original matter.

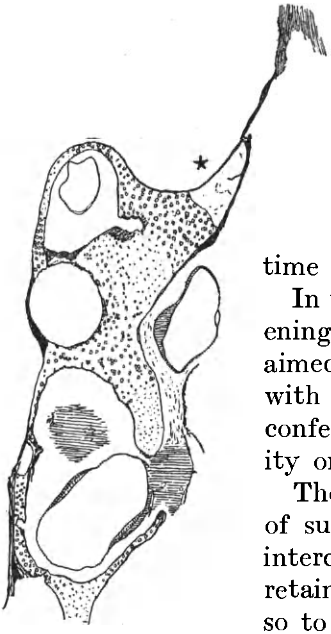

Fig. 96.—Ossifying skull of young herring in section. At the upper end adjacent to the asterisk the cartilage has been replaced by bone.

In the elasmobranch fishes a hardening of the cartilage is evidently aimed at by means of impregnation with lime salts, the mineral matter conferring a certain amount of rigidity on its own account.

The rôle of cartilage as a means of support seems to be due to the intercellular substance being able to retain a large amount of water and so to obtain rigidity from its incompressibility. Sections of the ossifying portion of the skull of a young herring (*Fig.* 96) show that the form, which has been fully filled out by cartilage, is now maintained by a thin but dense shell of bone, the interior of this bone containing scarcely any tissue. Again, then, the strength of the tissue—in this case bone—is obtained, in part at least, through a process of dehydration.

About one-third of the substance of bone is albuminoid or protein-like material known as ossein, or, under another name, as collagen. Collagen, when boiled in water, produces gelatin. Chondrin, the substance obtained from hyaline cartilage, is a mixture of gelatin and mucinoid substances. The cartilage which forms much of the skull of the young herring is hyaline cartilage, although it contains a large number of cells. It gives rise to the substance which has often been referred to in this book as yellow bone.

Gelatin, then, or a near relative of it, is an important constituent of the skeleton, and it is interesting to recall the well-known effects of slow drying on the configuration of regular-shaped masses of gelatin.

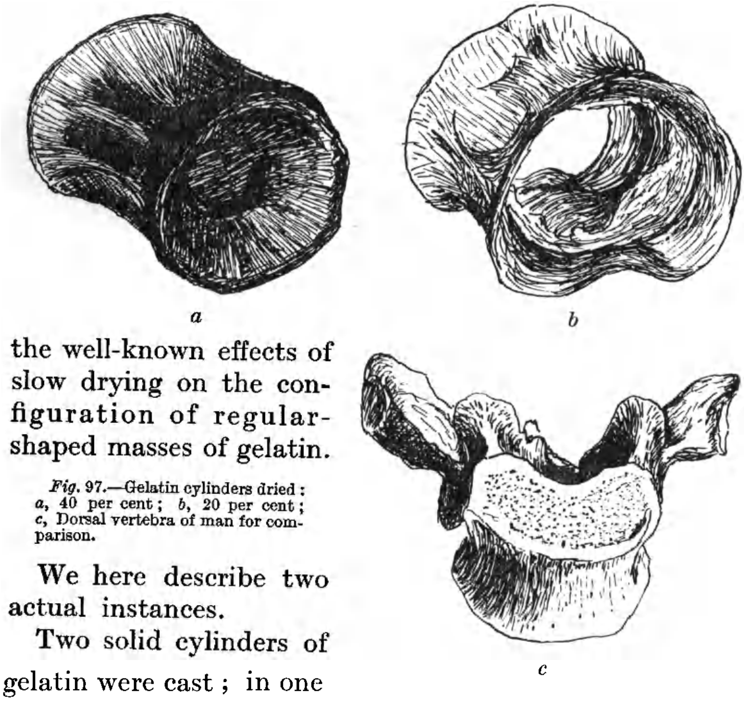

Fig. 97.—Gelatin cylinders dried: *a*, 40 per cent; *b*, 20 per cent; *c*, Dorsal vertebra of man for comparison.

We here describe two actual instances.

Two solid cylinders of gelatin were cast; in one case the gelatin was strong, e.g., about 40 per cent; in the other it was weaker, about 20 per cent. The initial size of the cylinders when cast was something like three inches high and two inches in diameter. They were allowed to dry slowly, and their ultimate form is depicted in *Fig.* 97.

The first effect of the gradual drying was a hardening of the sharp edges top and bottom, since these were the parts which exposed the greatest amount of surface to the air. They therefore shrank a little, and their hardening shaded off rapidly into the more uniform, but less well marked, hardening of the entire surface which took place during the first few days. The drying was done at room temperature in an ordinary cupboard. As the result of the shrinking at their circular edges each of the cylinders became to a slight degree globose, the one of 40 per cent gelatin to a less extent than the one of 20 per cent gelatin.

In the case of the 40 per cent gelatin the drying, having hardened the edges, made them more resistent than the rest of the mass to change of shape, and so henceforward they shrank very little, but the wall and ends of the mass went on shrinking continuously, and since the parts near the edges, being more exposed, dried and hardened first, the middle parts steadily sank inwards until finally the original cylinder had acquired the biconcave form of a fish's vertebra.

The fate of the 20 per cent cylinder was quite as instructive. This mass had not the same tensile strength as the other, and the rapid shrinking of the edges in the first day or two diminished the total volume and so increased the pressure inside more than the strength of the material could withstand. It therefore gave way at one end and some of the more liquid central portion escaped. Thereafter, drying went on not only from the outer surface, but also from within, and one part of the wall being a little feebler than the rest, caved in slightly, and since it was thinner, dried and hardened more quickly. The final result of the drying was that the original cylinder finished up with a shape almost exactly that of the centrum of a dorsal vertebra of man.

The lesson to be learnt from these two cases is a simple one, surely. The forms of the vertebral bodies may be purely the result of some dehydrating agency, or rather agencies, acting upon cartilage.

The uniform rods of notochordal cartilage acquire their strength by drying and vacuolation ; but in higher animals, where hyaline cartilage forms the basis of the vertebral column, it first of all maintains its strength by virtue of the incompressibility of its water content, but later on it is dehydrated by the action of serially arranged dehydrating agencies, and the resulting shrinkages give rise to the double-cone segments, while at the same time additional rigidity is conferred upon each block by the deposition of lime salts.

The agents which cause the dehydration can hardly be other than channels through which liquid can flow, and one is naturally inclined to think that these must be the blood-vessels. But there is some evidence that these are not the immediate path by which dehydration is effected. In sections of a young herring in which the cartilage is being replaced by bone, I have never been able to satisfy myself that there is even a capillary blood-vessel in the immediate vicinity of the part where the cartilage is disappearing, though there is the appearance as of a fine channel of some sort.

The usual description of the structure of bone to be found in text-books on histology is that of bone as it is found in mammals. This bone exhibits what are known as Haversian systems (named after Clopton Havers, who first accurately described them). If the bone of the shaft of the femur is ground down to a thin ‘section’ and examined microscopically, there can be seen in a transverse section a number of nearly circular holes surrounded by several concentric belts of lacunæ. These lacunæ are narrow oat-shaped spaces of minute size from which fine tubules run out, for the most part at right angles to their long axis. These lacunæ are occupied by ‘bone-cells,’ and it is said that the fine channels communicate and so form a continuously porous structure, with the fine channels next the central space communicating with channels therein. In longitudinal section the blood channels are seen as short lengths of nearly straight tubes arranged parallel with the long axis of the bone except where the channels bend round to communicate with one another. The layers of lacunæ form sheaths parallel with the blood-vessels.

I have never discovered any Haversian systems in the Herring, but in those bones which are transparent the bone-cells or their lacunæ are readily seen. Very careful examination with an oil immersion lens shows that the fine branches of the bone-cells always avoid meeting. In other words, there is no general permeation by fine tubes as ascribed to mammalian bone. The preparations of mammalian bone from which the classical descriptions have usually been taken have probably all been made by grinding down opaque bone until it is thin enough to be transparent, and it is easy to understand that such treatment would often cause breakage of the very minute thickness of material which intervenes between the fine branches of adjacent bone-cells.

There is, therefore, reason to doubt the existence of a continuous system of channels throughout bone in direct communication with the lumen of the blood-vessels. Such being the case, it may be that the Haversian system has a different signification.

May it not represent an organic calcification of the outer coats of fine blood-vessels ? The regular arrangement of the lamellæ and spacing of the cells would then depend upon a nicely adjusted balance between the tissue involved and its affinity for lime salts. If this be so, then it would seem that the one and only part of the system not liable to calcification is the endothelial wall of the blood-vessel itself.

On the strength of these observations there seems to be the possibility of the existence of a series of channels or spaces apart from the blood-vessels, specially concerned with abstracting water from certain tissues.

The lens of the herring's eye, when boiled in water, goes opaque white like hard-boiled white of egg. When this softer opaque matter is scraped away, the inner layers which are revealed are found to be more transparent, until the most central part of the lens is found to have a consistency and transparency almost of a bead of glass.

The lens of the human eye is firm, elastic, and clear as water. On drying it becomes yellowish.

If the white of a hard-boiled egg be suffered to dry slowly, in the same way as were the cylinders of gelatin, it becomes hard, pale straw-yellow in colour, and translucent if not even transparent, but it is full of minute cracks.

There is on the whole, however, a good degree of resemblance in physical qualities between the dessicated albumen coagulated by heat and the lens of the human eye. The lens of man is devoid of blood-vessels, but apart from this there is the physiological fact that its moisture must be regulated by some means, and that part of the system at least is represented by the canal of Schlemm and the spaces of Fontana which contain aqueous humour.

The central clear part of the lens of the Herring seems as if it could only have attained its hardness by a process of dessication, but how far the mechanism is like that of the human eye I do not know.

These things strengthen one's belief in the existence of a set of channels whose main function is that of maintaining a proper degree of dehydration of certain tissues.

It is quite likely that such a system is of epiblastic origin and is concerned in the production of the dense scaly bone which forms the facial armour of the Herring, and possibly it may also operate in the formation of the scales which cover the body.

In view of these various findings, the reader will not be surprised to see the opinion put forward that the shapes of bones in the Herring depend upon the distribution of certain channels, and that these channels are not the blood-vessels, though they may usually accompany them. Nor can they be connected with the lymphatics, since these are in communication with the blood-system on the one hand and the serous cavities on the other, with neither of which do these supposed channels directly communicate.

Since blood-vessels undergo changes in position—appear, disappear, fuse, break up, and so on, in the course of development of the body, so too may these channels be supposed to do. Hence there is no extravagance in imagining the stem of the parasphenoid bone of the herring to be homologous with the long spine of the dentary, nor in imagining the fusion of two elements into one bone in the formation of the upper gill-bones.

Marrow, epiphyses, and Haversian systems are characters of bones of animals higher in the scale of life than the fishes. Evidently, then, bone is a tissue of manifold structure, and progresses from a simple to a very complex arrangement. As far as this book goes, its story can only be partly told. Most of this has already been done in the present chapter, albeit more by argument than from the solid foundation of well-ascertained fact. But a few things concerning the skeleton remain yet to be said.

In the Herring the hinge of the gills is entirely a cartilaginous structure. It is found on section that the flexibility required is obtained by an absence of cells and a partial liquefaction of the cartilage in the central part, so that these characters seem to be purely physical effects induced in hyaline cartilage by usage. There does not appear to be any particular histological structure involved in producing the condition of flexibility which is required.

To persons who are familiar with the Haversian systems of mammalian bone, the question will arise as to how blood-vessels came to invade bone and form so intimate a part of it, seeing that it is possible to have bones without any blood-vessels at all in them.

Of course it might be argued that one reason for the presence of blood-vessels is to enable the bones to grow to a much larger size. The total mass of the largest bone of the Herring is scarcely equal to that of the smallest bone in the human skeleton with the exception of the auditory ossicles, so there is good reason for the need of blood-vessels. But to say that this is the cause of their entry into bone is, surely, to put the cart before the horse. The question therefore remains, How did they gain admission ?

The question would not have been raised here were it not for the fact that the histology of the Herring seems to be able to give an answer to it.


Fig. 98.—Supporting rod of gill-membrane. (× 8.)

The gill-fringes consist of a series of closely-set, very thin membranes permeated by capillary blood-vessels. The thickness of the membrane which separates the blood from the water outside, even when magnified four hundred times, looks to be no more than that of tissue paper. Such delicate tissue would be quite unable to stand of itself, and so it is fixed to a little rod of bone which stands out at right angles to the bone of the gill-arch and supports the membrane as a staff supports a flag.

There are a great number of these little bones, and they vary to some extent in size, but an average-sized one is about a third of an inch long. The length is about twelve times the thickness, and the end of the bone by which it is attached to the gill-arch is bent round like the lower end of a hockey stick. On the outer side of the bend, when the bone is in the body, there is the large blood-vessel which runs along the gill-arch. The lower part of the stem of the little rod near its bend shows a number of deep grooves in its edge, which thereby becomes divided up into a number of 'teeth' like the cogs on a wheel (*Fig.* 98, *and see Plate VI*). In a dried bone they are very conspicuous, and some of the grooves may even be converted into holes by a bar of bone on the far side.

Sections of the gill-tissue with the bone in position provide an explanation of why this curious formation occurs, for it is then seen that these grooves form part of the wall of the capillary blood-vessels of the gill-membranes, and that they come off from the large vessel running the length of the little supporting bone and itself a branch of the main vessel which runs along the arch (*Plate VII*). Probably the minute vessels which groove the edge of the supporting bones have a complete wall of flat endothelial cells, but next to that comes the bone directly without any intermediate tissue, so that it seems as if we actually witness here the beginning of the invasion of bone by capillary blood-vessels, which in higher animals form the perfect Haversian system.

It is interesting to reflect that, just as the skeleton may have had its beginning in the gill-arches, so the advance in bone formation which permitted bones to attain a great size may also have originated at this site.

The Herring has about 600 bones apart from those of the gill-rakers and supporting rods; probably the sum total would be about 800. But the bones, though so numerous, are of very small size, and so do not form a very great proportion of the animal's bulk. The reader, however, will have perceived that it is neither their number nor their bulk which makes them so important from a theoretical point of view, but it is their form and their arrangement.

It is frequently stated that the scales are in reality bone. I know of no evidence in the Herring to show that this is the case, except in the little keeled scales which occur between the hinder pair of fins and the anus; the ridges on these show the structure of bone.

The sources from which the bones of the head and paired fins of the Herring are derived have not been determined. Since there are four groups of them, they cannot have originated in the proximal ancestors of this type, nor is it likely that they first took form in the phylogenetic ancestors which proceeded the proximal ones. But more than this cannot be said at present. It is a matter for future study. The mere presence of bone

PLATE VII

HERRING. TRANSVERSE SECTION OF PART OF GILL.

Drawing of section of part of the gill of an adult herring showing the relation of the supporting bone of the gill-membrane to the blood-vessels. *a*, Parts of gill-membrane; *b*, Bone supporting gill-membrane; *c*, Bone of gill-arch; *d*, Large blood-vessel of gill-arch; *e*, Branch to gill-membrane of blood-vessel of gill-arch; *f*, Bone supporting gill-membrane (pointer crosses blood-vessel in groove). (×20.)

in practically every part of the Herring points to its physiological importance.

In higher animals bone becomes still more important by virtue of additional circumstances both intrinsic and extrinsic. The fact that the skeleton is all that is found of many extinct animals confers great interest upon bone from a biological point of view.

The higher vertebrates are of such vast importance to human life that their study in relation to the theory of dual constitution would require a volume to itself.

TERMINAL NOTE

The theory of the dual constitution of all metazoan animals offers a ready explanation of the method of production of generic, and perhaps even of greater, differences between animal forms.

It is adequate to explain the appearance and disappearance of organs during ontogeny provided certain assumptions are allowed. One of these is the postulate that the blastula represents the primitive form of all metazoan animals. Another is that the alternation of generations persists throughout the ancestry of animals. The third assumption is that the design as made by the 'active meridian' is the ruling power in the construction of organs. This assumption is the only means by which interpretation of the facts is found possible.

INDEX