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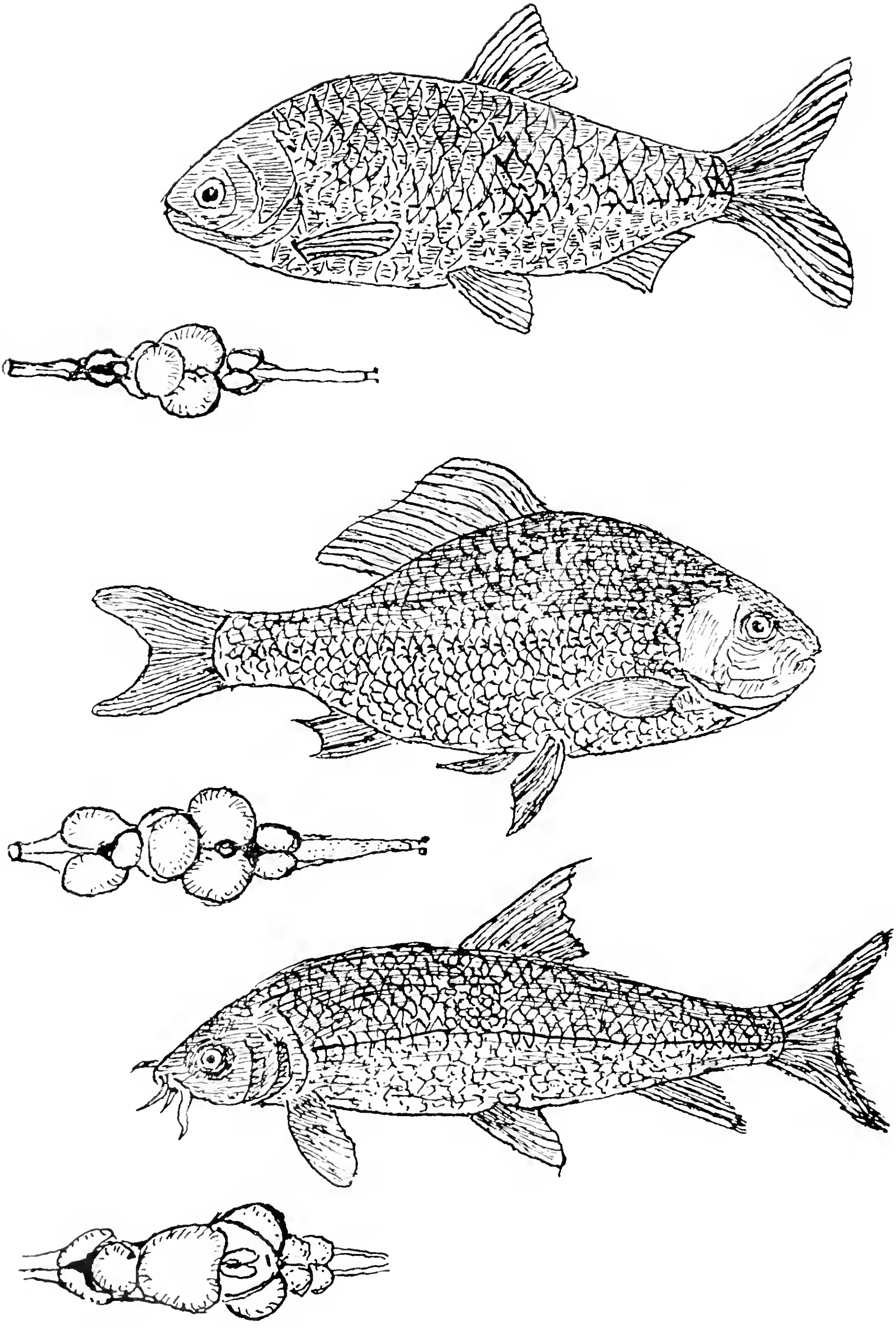
BRAIN AND BODY OF FISH



Brain and Body of Carps

ROACH

CARP

BARBEL

TASTE

HEARING

SIGHT

SMELL

BRAIN AND BODY OF FISH

A STUDY OF BRAIN PATTERN IN RELATION TO HUNTING AND FEEDING IN FISH

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FOREWORD

In this short introduction to the comparative study of the brain of fish we have confined our observations to bony fish. The reader will find no reference to the brain of the cartilaginous (elasmobranch) fish. Our old friend the dog-fish will not appear. This unpleasant animal may be the cause of the backward state of our interest in the neurology of fish. Fifty years ago Ray Lankester was making pioneer observations on the brain of the dog-fish, but there seem to have been few scientists who have followed his trail. It is probably true that if investigations had been made on the goldfish or the roach the interest in these attractive fish would have led to a wider knowledge of the brain structure of fish. This book is a study of the brain of our familiar fresh-water fish, and the common food fishes of the British Isles. Salmon and trout, having a publication of their own, do not appear. All the figures I reproduce are from my own specimens and drawings with the exception of two text-figures of the brains of the cod and mormyrus : for permission to redraw these I have to thank the Curator of the Royal College of Surgeons of England. In the discussion on the Silence of the Sea. I have referred to passages in Sir William Bragg's Lectures on "The World of Sound" and to Dr. Beatty's "Hearing in Man and Animals." I have also consulted Cunningham on this subject in the work "Reptiles, Amphibians and Fishes" edited by him. References to other authors are mentioned in the text. A large proportion of the observations described in this work have already appeared in the Proceedings of the Royal Society of London, but the text has been entirely re-written with a considerable amount of new material.

H. MUIR EVANS.

INTRODUCTION

In the course of a series of investigations into the physiology of the swim-bladder in the Carps or Cyprinoids, I was led to study afresh the functions of the Weberian ossicles, a series of small bones which connect the anterior sac of the swim-bladder in these fish with the internal ear. This latter study involved the dissection of the brain, and I thus became aware of the very diverse forms of the hind-brain in this family. In looking up the literature of the subject I came upon a reference to a paper by a Frenchman, P. Savouré, communicated to an obscure provincial society, the Bull. Soc. Sci. Ouest, Rennes, in 1912, which fortunately was in the library of the Royal Society of London. This paper described the brain of a number of members of the Carp family, and showed the diversity of form in the hind-brain, but the illustrations were on a small scale and semi-diagrammatic. On comparing these drawings with my own of similar species caught in English rivers, I found that my observations did not agree with those of the French observer in several instances, and further, that his descriptions were based entirely on superficial examinations and had not been supplemented by microscopic investigations of serial sections. This being the case it appeared to me that there was a fertile field for research into the neurology of the Cyprinoid brain, and for an attempt to associate the various forms or patterns of the brain with the habits and diet of fish, which presented so many opportunities for examination. I was thus led to undertake a series of neurological studies on fishes by means of comparative anatomy. This was the method employed by Sir Charles Bell, the first neurologist, as he has been called. When a child I was given by my mother " Bell on the Hand." When I became a medical student, Alexander Shaw, Bell's assistant and collaborator, gave me Bell's " Anatomy of Expression," with annotations in his own hand. Some years ago I purchased at the sale of Lord Lister's Library a copy of " Bell on the Nervous System," which had been presented to James Syme by the author, and bears his hand-writing : this I treasure, not only for its own sake, but for the triple association of three illustrious men. There are probably few medical students at the present day who realise that Bell's paralysis is named after the man who first described the true function of the facial nerve, and that the same man showed by dissection the nerves of muscle sense and described the fundamental difference between the anterior and posterior roots of the spinal nerves. Bell wished to be known to posterity as an anatomist, not as an experimentalist. "Anatomy is already looked upon with prejudice by the thoughtless and ignorant. Let not its professors unnecessarily incur the censures of the humane." "In a foreign review of my former papers the results have been considered as a further proof in favour of experiments. They, are on the contrary, deductions from anatomy; and I have had recourse to experiments, not to confirm my own opinions, but to impress them on others. It must be my apology that my utmost efforts of persuasion were lost, while I urged my statements on the ground of anatomy alone. I have made few experiments; they have been simple and easily performed, and I hope are decisive." In another place he says, in favour of anatomy, that "it is better adapted for discovery than experiment," and illustrates his contention by comparing astronomy and chemistry and considers that "anatomy is more allied to the former inasmuch as things are obvious."

Another paragraph extols the work of Monro and Hunter, and adds, "Let us continue to build on that structure which has been commenced by their labours, and which the undeserved popularity of the continental system has interrupted." "The whole history of medical literature proves that no solid or permanent advantage is to be gained either to medical or general science by physiological experiments unconnected with anatomy." We will quote another passage in full, "He who discovers a new nerve, or furnishes a more accurate description of the distribution of those already known, affords us information in those points which are most likely to lead to an accurate knowledge of the nervous system. For if we consider how various are the origins of the nerves, although all arising from the brain, and how different the circumstances attending them, we must suppose a variety of uses to arise out of this peculiar structure. In this manner is the nervous system to be studied. For there is an internal change in accordance with outward organisation, whilst the system or great plan does not alter. An animal, or class of animals, may have a particular organ developed, and with the external apparatus there is a corresponding or an adjusted condition of the appropriated nerve. Another class may be deficient in the external organisation, when we shall look in vain for the accompanying nerve; it is contracted or hardly visible; but with all this the system is unchanged." These profound truths were written over a hundred years ago. The experimental method is now predominant, and the morphologist is almost a museum specimen, yet there are still some minds who see in comparative anatomy a valuable aid in the investigation of function. The late Prof. J. H. Haldane said that comparative anatomy may be made as valuable as experimental physiology. "Future anatomy both normal and morbid will certainly set itself to investigate the physiological relationships which are inseparable from structural manifestations, and anatomy will then be as much an experimental science as is physiology." Experimental biology can only be pursued in a laboratory where the investigator can follow his pursuit within the law. But there is a vast field for a worker in comparative anatomy in its relationship to physiology and the investigation of function. My work embodies these suggestions, and has been carried out in the scant leisure allowed by a busy professional life. I have been encouraged by the interest and support of Sir Henry Dale, the late Prof. Boycott, Sir Leonard Hill and Dr. Tate Regan. I have also received much help from members of the Staff of the Ministry of Agriculture and Fisheries at Lowestoft, particularly I would mention Miss Thursby Pelham and Mr. Michael Graham, who kindly read the manuscript and made many valuable suggestions, and finally Mr. Clarke, the chief laboratory assistant, without whose technical assistance my work would not have been possible. My interest in the subject of hearing in fish dates from my young days when I studied Otology in Berlin, and worked on the literature of the cochlea at the British Museum, where I first became acquainted with the work of Bell on Hearing. It is often forgotten that the resonance theory of hearing first propounded by Cotugno, in 1761, was reaffirmed by Bell in 1826; but it was not until Helmoltz, in 1863, brought his physical insight to bear on these views that this theory was accepted, which has now become exclusively associated with his name.

CONTENTS

BRAIN AND BODY OF FISH

CHAPTER I

INTELLIGENCE AND BRAIN PATTERN OF BONY FISH

THE subject of behaviour in animals has in recent years attracted the attention of biologists in this country and also in America, and a large literature devoted to its discussion has arisen. Recent studies on fish have been made at the Marine Laboratory at Plymouth, in which experiments have been made to test the ability of fish to master the intricacies of a maze.

Another type of experiment has shown that if a predatory fish and its prey are put in the same tank, but separated from each other by a glass partition which prevents the hunter from reaching its would-be victim, after a short time the fish will keep to its own side of the partition, even after this obstacle has been removed. These observations seem to prove that a fish has a capacity to learn, to associate facts and direct its movements up to a certain point, according to experience. Nevertheless, one hears not infrequently the remark " I didn't know fishes had brains " ; and to illustrate the brainlessness of fish, or perhaps their want of feeling or perception of pain, the tale is told, how a fish hooked with a certain bait, may, when returned to the river, be caught again with the same bait after a short interval. This conclusion does not bear criticism, because when a fish is hungry or greedy, or, as a fisherman would say, is biting freely, there is no doubt it appears stupid, but that same fish when not hungry, will be most cautious in examining the bait and subject it to the closest scrutiny, so that the finest gut and cleanest bait are required to lure it to its capture. When hunger is in command, discretion is forgotten. As bearing on the intelligence of fish some remarkable studies have been recently made on the homing instinct of salmon. The most convincing experiments have been made on the chinook or king salmon in Canada, where in the Columbia River system we find the Lower Columbia River, ninety miles long, receiving the water of two systems. The salmon frequenting one system are "spring run," and those of the other are " autumn run " fish. If eggs were transplanted from one system and hatched in the other, the fish from the transplanted eggs, after their journey to the sea, returned to the river in which they were brought up and not to the river in which they were spawned. But they retained their hereditary habit of migrating in the spring instead of in the autumn as do the native fish (E. S. Russell).

Young salmon in fresh water get to know their home waters and recognise them on their return. They remember the way back to their home river after their extensive journeyings in the sea.

We see, therefore, that the behaviour of fish is not simply determined by seasons, currents, temperature, and their respiratory needs, as some biologists maintain. Their migrations are as difficult to explain as those of birds. Moreover, like birds, there are many fish which build most efficient nests. The sea stickleback not only builds a nest but binds it together with a thread spun from its own body. The male Lumpfish or Cockpaddle fans the eggs and drives away all intruders. In the Nile one of the Mormyridæ known as Gymnarchus, makes a floating nest of grasses, and the whole nest is somewhat like the ark of bulrushes which served as a cradle for the infant Moses (Cunningham).

So it appears that nest building, parental care, and the homing instinct are common to fish and birds. A further attribute common to both is song; it is true that our knowledge of sounds produced by fish is slight, but the hearing capacity of some fish has been studied by modern methods and reveals a remarkable range of hearing. The Squeatague produces a deep drumming sound, but only the male, so it is probably used in courting. The Maigre, a Mediterranean fish, is well known for its powers of "song," which it is believed to have given rise to the legend of the Sirens which beguiled Ulysses. Sounds are also produced by the Sea-robin Prionotus.

I have chosen the title of this book, "The Brain and Body of Fish," because this condenses in a phrase the remarkable fact that the external conformation of the brain of a bony fish indicates its habits and mode of feeding. In other words, the study of the external condition of the brain in bony fish is an index of the development of those organs belonging to the various sensory faculties. The life of a fish consists of two main activities which may be conveniently described under the headings feeding and breeding. The first is necessary for the life of the individual, and the second for the future of its race. In other words nutrition and reproduction make up the life history of a fish. We shall find that not only is hunting a highly specialised function in fish, but that the various methods of hunting are associated with a varying pattern of brain. For instance, if we come to study two familiar families of flat-fish, the sole and the plaice, it will be found that their hunting methods differ widely and that this difference is reflected in their brain structure. The sole is nocturnal in its habits, and it hunts by tapping the sand in its search for worms, just as the thrush does on the lawn in front of your window, and it has an acute sense of smell, which is evidenced by its elaborate nasal organ. Compared with the plaice its eyes are very small. The conclusion is reached, therefore, that the sole hunts by smell and touch.

This is not the whole story, but it is sufficient for our present purpose. The plaice on the other hand has large, prominent, and movable eyes, and, as we shall find later, a marked sense of taste, due to the presence of taste-buds, so we conclude that the plaice feeds by sight and taste. Corresponding to the increased importance of these different senses to these fish, the central areas in the brain connected with the sense organs are enlarged, and thus a definite type of brain pattern results. Other interesting correlations between feeding habits and form of brain are to be observed in the Cod family, in which there is a gradual change in the pattern of the brain as we pass from the shell-fish eating members, through the mixed feeders, to those purely predacious. The principle of the enlargement of special sense areas in the brain in accordance with an increase of function is also of service in elucidating problems like the question of hearing in fish. Certain fish have elaborate mechanisms which are supposed to be accessory to the organs of hearing; if it is found that in these fish there is a special area more developed than in fish devoid of these mechanisms, we may assume that this area has some acoustic significance. Examples of this condition are to be seen in the Carps and the Herring tribe among fishes of the British Isles and seas, and in the interesting family of fish known as the Mormyridæ of northern Africa. In fact, the comparative study of the brains of bony fishes is full of unexpected revelations. So much may be said as an introduction to the subject of brain form, in relation to hunting and feeding. Is there any area in the brain that can be identified as associated with the function of reproduction? Modern research into the function of the pituitary gland directs the attention to the condition of this gland in fish and evidence will be brought forward to show that this gland undergoes certain changes in those fish that are about to migrate for the purposes of reproduction.

The relation of form to function in determining the pattern of the brain of a fish will be described in the following pages. In order to help the reader to follow the argument it will be necessary to give an outline of the structure of the brain of a typical bony fish, and we shall endeavour to do this without introducing any but the most necessary technical terms.

The spinal cord of a fish may be likened to the long stem of a clay pipe, this, instead of being hard like baked clay, is of the consistence of a cream cheese and of the same colour. Instead of a bowl at the anterior end there are a series of thickenings of the walls, which for the most part appear on the upper or dorsal aspect. These swellings or lobes may be single, but more frequently there are two symmetrical protuberances facing each other, which is described as bi-lobed. These swellings are not necessarily associated with any increase in size of the central canal, although at two points of the brain, as the anterior part is called, the neural canal widens out into spaces called ventricles.

In the hinder part of the brain, which is known as the medulla oblongata, another condition is noticed. In the mid-line there is a longitudinal slit in the dorsal wall of the hinder ventricle, and the thickenings of the walls thus seem to take place in the free margin of the split tube; there is thus left an open space or hiatus, which, however, is covered in by a vascular membrane. This opening out of the fourth ventricle, as it is called. is known as the rhomboid fossa.

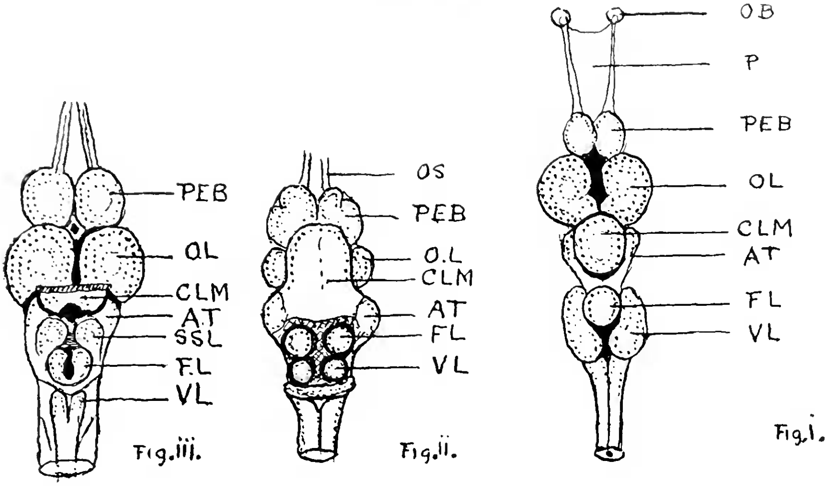
The various lobes will now be described, and starting from the simple spinal tube and passing forwards we first notice two lateral protuberances (Plate 1, Fig. i), the vagal lobes. This view is drawn from a specimen from which the roof of the bony cranium has been removed, and the brain is looked down upon from above. These lobes in the carp are pear-shaped in outline, and their anterior ends are seen to be separated by a central globular lobe known as the facial lobe. In the catfish (Plate 1. Fig. ii) the vagals are globular and there are two facial lobes lying in front of them. It is found that in certain of the carp family that the facial lobe has a partial median division, as in the gudgeon, so that the single median facial of the carp and most Cyprinoids is due to the fusion of two lateral segments. The condition in the cod (Plate 1, Fig. iii) is somewhat different, as the vagal lobes do not form so prominent a swelling dorsally, as we shall have occasion to note when the cod brain is discussed.

The vagal lobes receive nerves of sensation, afferent nerves and also efferent nerves which pass outwards and are nerves of motion; so that we say that the vagal lobes have both sensory and motor nerve roots.

The facial lobe in fish is peculiar in that it receives all the sensory fibres from certain peripheral sense organs known as taste-buds which are situated on the anterior part of the mouth, the lips, and barbels (when present) and even the skin. Its function is gustatory, i.e. the centre of taste perception, although the facial nerve still sends a few motor fibres to certain neck muscles.

This puzzles the human anatomist, who looks upon the facial nerve as predominantly the motor nerve of the face muscles; however, even in man the facial nerve still receives gustatory impulses from the anterior portion of the tongue by means of a recurrent branch, known as the chorda tympani.

PLATE I.



Cod. Catfish. Carp.

P.—Pallium. PEB.—Primitive end-brain. OL.—Optic lobe. C.—Cerebellum. AT.—Acoustic tubercle. S.S.L.—Somatic sensory. FL—Facial lobe. VL—Vagal lobe. OB—Olfactory bulb. CLM—Cerebellum (removed in Fig. iii, turned forwards in Fig. ii).

It is quite obvious how this apparent contradiction in function has arisen. In fish there are no facial muscles but an elaborate gustatory system, on account of the nature of the medium in which it lives; whereas in man the facial, which by Sir Charles Bell was called the respiratory nerve of the face, not only supplies the styloid and hyoid muscles of the neck, but also has taken on the supply of all the facial muscles as so fully described by Bell in his "Anatomy of Expression."

The course of the facial nerves within the brain of fish is so characteristic that they are a useful guide to the recognition of the facial lobe or lobes and their relation to other structures. In a position anterior to the facial lobes there is a bilateral area receiving sensory fibres from the skin, this can be seen in the drawing of the cod's brain, and it is known as the somatic-sensory or fifth lobe ; it is not apparent in the carp or catfish when seen from above, but it is clearly evident in sagittal sections.

The next prominent lobar swelling is a large central protuberance smaller in the carp than the catfish, and forming a tongue-like body overlapping the medulla oblongata in the cod ; this is known as the cerebellum.

From either side of the cerebellum leading to the sides of the somatic-sensory or fifth lobes are marked rounded prominences, varying much in size in different species, and known as the acoustic tubercles. Anterior to the cerebellum are two large globular swellings known as the optic lobes, which receive the large optic nerves on their ventral aspect, and at the anterior end of each optic lobe are smaller lobes which form the primitive end-brain into which enter the olfactory nerves, leading from the olfactory bulbs, or are in continuity with the olfactory lobes.

As this end-brain puzzles even a trained biologist, we will further explain that the end-brain in which the olfactory centres lie consists generally of two sections, the anterior being the olfactory bulbs which are the terminations of the olfactory nerves, and the posterior the larger, the primitive end-brain, in which the walls of the neural tube are thickened. The olfactory bulbs usually lie close to the end-brain as is seen in the drawing of the brain of a plaice, but in some bony fish the nasal sacs are far removed, as is seen in Plate 1, Fig. I, the drawing of the brain of a carp, where the bulbs appear separated by the pallium, and the olfactory stalks from the primitive end-brain.

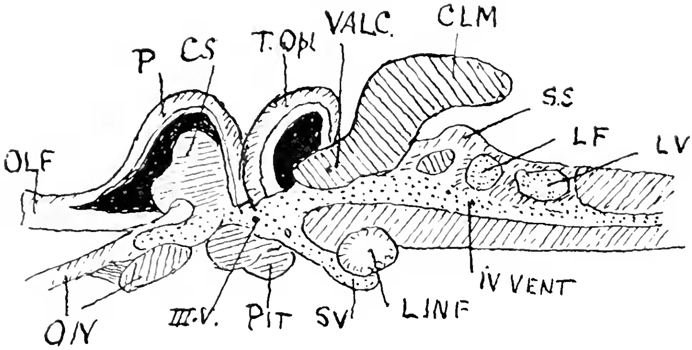
If we now look at Plate 2, which is a drawing of the brains of a carp and a cod viewed sideways when a sagittal section is made through one half of the brain we shall be able to visualise the above described organs in another dimension.

In man the sensory columns of the spinal cord lie posteriorly, but these columns become dorsal in fish and so we find the sensory centres of the brain appearing on the dorsal aspect in fish.

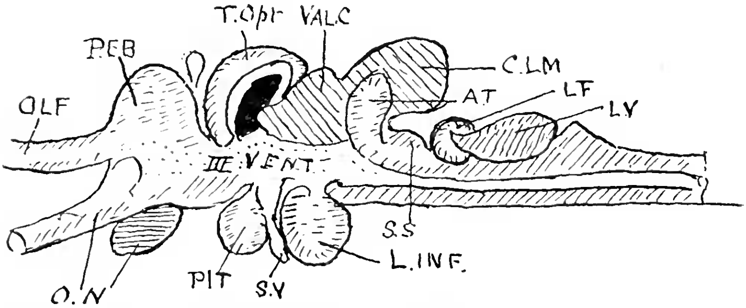
If we examine the diagrams of Plate 2 it will be seen that in both cod and carp the tecta optica which form the prominences of the optic lobes are similar, but the forward projection of the base of the cerebellum, known as the valvula cerebelli, is bigger in the carp than the cod and further in the carp tends to separate the tecta of either side.

When the medulla oblongata of the cod is examined, the skin area or somatic-sensory lobes are prominent, while the facial and vagal lobes make no prominent elevation: in the carp the skin area is small, but both the facial lobe and vagal lobes produce well-marked prominences. In the diagram it is clearly seen that all the sensory centres, namely the olfactory lobes, optic lobes, acoustic tubercles, the somatic-sensory lobes and the facial and vagal lobes are situated dorsally. Situated ventrally, are several important bodies: posteriorly the first enlargements are too well marked lobes, the lobi inferiores, in front of which lies the saccus vasculosus. Then comes the pituitary body or gland which in recent years has been recognised as an organ of great importance; immediately in front of this the optic nerves will be seen to decussate.

PLATE 2.



Brain of Cod in sagittal section.



Brain of Carp in sagittal section through the middle of a vagal lobe.

OLF—Olfactory tract. P—Pallium. CS.—Corpus striatum. T.Opt.—Tectum opticum. Val.C.—Valvula cerebelli. CLM—Cerebellum. SS—Somatic-sensory lobe. LF—Lobus facialis. LV—Lobus vagalis. ON—Optic nerve. PEB—Primitive end-brain. Pit.—Pituitary gland. SV—Saccus vasculosus. L.INF.—Lobus inferior. III.V.—Third ventricle. IV.Vent.—Fourth ventricle.

The functions and structure of these organs will form the material for a later chapter ; we have noticed that other authors dismiss the lobi inferiores with a few scanty remarks, but we hope to be able to point out the significance of this interesting but neglected structure.

CHAPTER II

BRAIN PATTERN—*Continued*

Having grasped a general idea of the layout of the brain, it is now necessary to consider its intimate structure, which is revealed by studying its tissue by microscopic methods. These methods are the same as those used in human anatomy, and involve an elaborate process which requires the use of a great variety of stains, which differentiate special cells and nerve fibres or neurons.

In this way certain cells can be distinguished, and we are entitled to assume that a motor nerve cell recognised as such in human histology, is a motor cell in a fish, and that a nerve cell of another definite type in man has the same function in fish. The lobes are thus found to consist of accumulations of nerve cells of different types, and these are so arranged that some receive impulses or messages from the sense organs of the body, both from the external parts and from the viscera or internal parts, while others send out impulses, which set the motor machinery in action. These messages are carried to and from the brain by the nerve roots and neurons as we have already mentioned. But, further, these groups of cells must of necessity have relations with the other groups, so that strands of nerve fibres, called tracts, carry messages from one centre to another; finally it is necessary that there should be a centre to correlate all these various messages, so that there are other tracts to carry messages to a higher centre which controls the whole nervous system. We have described the brain of fish as being an enlargement of a simple nervous tube which is known as the spinal cord; this also has tracts of fibres leading up to and from the brain. Around the central canal there is an accumulation of cells for the reception of sensory impulses and for the sending out of motor impulses. In all vertebrate animals the nerves given off from the spinal cord have two roots, and two columns of nerve fibres pass up the cord to the brain.

It was established by Bell just a hundred years ago that the anterior (in fish ventral or inferior) column of the spinal marrow and the anterior roots of the spinal nerves were for motion, and that the posterior (in fish dorsal) column and posterior roots were for sensation. There is a similar division, though more complex, in the brain, and so it is found that the lobes of sensation are found on the dorsal or posterior aspect. It will be understood that the term posterior in man becomes superior in fish owing to the upright posture of man, contrasted with the horizontal poise of fish.

The reader must forgive this rather elementary description, but it is necessary if he is to follow the more technical matter.

It may well be asked what means are to be adopted to understand the use or function of the lobes which have been enumerated? Are you justified in comparing the brain of a fish with what is known about the brain of man? As to the lobes which receive impressions from peripheral sense organs that have an exact counterpart in man there is no difficulty.

For example, the eye of a fish has much the same structure as in man, and is connected directly to the two optic lobes by large nerve trunks which cross each other as they enter the brain. There can be no doubt that this system is rightly assumed to be a visual apparatus. The truth of this assumption is further established, when the brains of two familiar flat-fish are compared. The plaice, which feeds by day and largely by sight, has very large optic lobes which tend to be convoluted, whereas the sole, which is nocturnal in its habits and feeds largely by smell and touch, has very small optic lobes.

It may be stated as a general rule that fish with nocturnal habits have small optic lobes; in the cod family this generalisation is well shown. The cod, whiting, and pollack have large optic lobes and are hunters by day; on the other hand the ling, burbot and rockling have small optic lobes.

According to Cunningham the ling is somewhat nocturnal and the rockling entirely nocturnal in their habits, and according to Tate Regan the burbot goes in active pursuit of prey at night.

The above examples of the variations in the size of the lobes are simple and straightforward, and show well the relation of function to the central nervous system; they further establish a principle which enables us to unravel the more complex areas of the brain such as those concerned in the appreciation of taste which are known as the gustatory centres. These centres are very important in fish as the substances that give rise to the sensations of taste are always in solution. Therefore it is not surprising to find that fish, living entirely in a fluid medium, are furnished with an extensive gustatory system. Taste is a chemical sense, and the organs of taste enable the animal to recognise sweet, sour, salty and bitter substances.

By what means and by what structures is a fish enabled to make use of its surroundings, which must contain such a vast number of different sapid substances? The organs of taste in man are represented by certain patches or groups of peculiarly modified cells of the superficial layers of the skin, which are lodged in the thickness of the surface layers of the tongue. These groups of cells have a bud-like arrangement, and have therefore been termed taste-buds. Without going into details at the present stage, it may be stated that they are found on the tongue, the throat, and at the entrance to the windpipe. Leydig discovered in fishes flask-shaped organs, similar to taste-buds, in certain parts of the skin, and they also occur in the mucous membrane of the mouth and throat in those animals.

We shall describe later certain other sites in which they are found in fish.

Taste-buds have been compared in general form and appearance to the leaf-buds of a plant, but the arrangement of their cells may be also likened to the segments of an orange. They are flask-shaped bodies, the base of the flask lying in the depths of the skin or mucous membrane, and the neck projecting towards the free surface. The cells are enclosed in a sort of adventitious capsule, but the most superficial cells of this are perforated to allow of access of the apex of the taste-buds to the free surface: the cells that form the bud do not actually reach the surface, but from their apices arise fine hairlets which project into an opening called the gustatory pore. By this means the cells receive stimuli from the various substances in solution, and from these cells sensory impulses are carried to the centres in the brain.

The lobes that receive all these impulses are the vagal and facial lobes. The vagal lobes are both sensory and motor in function receiving sensory impulses from the gills and pharynx, and they have also a motor area known as the nucleus ambiguus from which efferent fibres pass by the vagal motor root: the facial lobes receive sensory fibres from the taste-buds situated on the skin, mouth, lips and barbels, but the facial nerve has also a small motor branch leading to the neck muscles.

A broad summary of the facts relating to these two lobes can be made in Herrick's words "the vagal lobe for mouth-tasting and the facial lobe for skin-tasting are local enlargements of the visceral sensory brain. All the taste-buds in the pharynx and back of the mouth are supplied by the vagal and glossopharyngeal nerves, those in front of the mouth the lips, the barbels, and outer skin from the root of the facial nerve."

It may well be asked what is this new nerve, the glossopharyngeal, which has not been mentioned hitherto. This nerve and the small lobe into which it runs, which may be regarded as a forward extension of the vagal lobe, supplies an anterior gill-arch so that for our present purpose it may be looked upon as functionally part of the vagal lobe, supplying a small anterior part of the gill-arches and neighbouring structures. But it is important to remember its existence, as in man as we shall mention later, it supplies a particular part of the pharynx and has a specialised function in the more complex structure of the higher vertebrates.

We are now in a position to apply the same process of reasoning to the vagal and facial lobes as was used in the interpretation of the function of the optic lobes. For this purpose the examples will be taken from three species of the large family of carps or Cyprinoids, of which there are many members in British freshwaters. Let us see what can be learnt from the comparison of the hind-brains of the bream, the roach and the gudgeon, to be more concise their facial and vagal lobes.

The habits of these fish are familiar to any coarse fisherman. The bream is found on the bottom in muddy waters, where reeds grow, and he sucks at the bait rather than bites, and lifting the bait up, tilts the float and drags it slowly along the surface before finally taking it into its mouth. It is able to extract food-stuffs from the mud. The roach is a more lively fish and often bites freely, but usually investigates the bait before actually closing its lips ; as a rule it feeds near the bottom, but it also takes a fly and feeds at times near the surface ; the gudgeon frequents gravelly bottoms and searches for its food among the stones with its sensitive barbels.

When the brains of these fish are examined the difference in size of their lobes is very evident. The bream has a very large vagal lobe, the roach a small one, and the gudgeon one of moderate size ; on the other hand the gudgeon has a very large facial lobe, the roach a very small one and the bream a small one. It has been observed that the vagal lobe is for mouth-tasting, so that the question arises what is the reason for this great enlargement of the vagal lobe in the bream, which is still more marked in the carp. The answer to this question is that these fish have a specialised organ on the palate, that consists of ridges lined with taste-buds which enables the animal to sift and sort, retain, or reject nutrient material from the mud and decaying vegetable matter, on which it feeds : this organ with its taste-buds is represented in the vagal lobe and is the cause of its great development. The size of the facial lobe in the gudgeon is still more easy to explain ; this fish has a pair of barbels richly furnished with taste-buds, with which it searches for shrimps, small molluscs, worms, and insect larvæ, in the sand and gravel. It has rather a curved snout and thick lips so that it is a typical "skin-taster," and therefore we find a very large facial lobe. But this is not the whole story of the facial nerve and lobe in the gudgeon. If the facial nerve is traced into the lobe it will be found to divide into two parts, an anterior bundle of fibres passes laterally into the front of the facial lobe, and a posterior bundle passes backwards into the hinder part of the lobe, thus dividing the lobe into two separate areas. There are other fish which have a similar division of the facial nerve within the brain; for example the barbel, which has two pairs of barbels; in this fish the bundles are of unequal size, the anterior is small, while the posterior is larger and enters a large division, forming the hinder part of the lobe.

The tench is also the possessor of a similar division of the facial nerve, but it has only a short barbel on either side of the mouth; associated with this small barbel we find that there is a large lateral bundle passing to the front of the facial lobe and a very small strand passing to the hinder portion. We see, therefore, that the size of the two parts of the lobe varies with the development of the barbels, in the barbel a large posterior portion with many barbels, and in the tench a small posterior portion with a single small barbel on either side. These conditions have also been found to occur in certain Cyprinoid fish of the Madras tanks as noted by Bhimachar, who describes a fish very like a tench with small barbels and a small division of the nerve passing posteriorly. The conclusion appears to be justified that fish with barbels have a division of the facial lobe, and that it is the posterior part of the lobe that receives the gustatory fibres arising from the taste-buds of the barbels, at any rate in the Cyprinoid family.

This observation concerning the differentiation of two bundles of the facial nerve reminds the writer of the remark of Sir Charles Bell, "he who discovers a new nerve or furnishes a more accurate description of the distribution of those already known, affords us information in those points that are more likely to lead to an accurate knowledge of the nervous system."

The brain of a roach is in sharp contrast with that of either bream or gudgeon. Both vagal and facial lobes are small, but to compensate the fish for this slight development of its gustatory centres, it has large optic lobes, and is very sharp-eyed, so that very fine gut must be used by the angler, if he wishes to be successful in his sport. But it must not be considered that the roach is lacking in the sense of taste, because every fisherman must have noticed how discriminating this fish is as regards baits. It seems, therefore, that the large size of the vagal in the bream is solely due to the large palatal organ and the large size of the facial lobe in the gudgeon is mostly due to the possession of a pair of barbels; and that the absence of these specialised structures in the roach is the cause of the smallness of both lobes.

In the spinal cord of man there are considerable enlargements in the cervical and lumbar regions and the mid-dorsal region is small in comparison. This is due to the large nerve trunks that go to the arms and legs respectively from these areas; but as a rule in fish the spinal cord is of uniform calibre throughout. But there is one family of fish, the gurnards, that gives us an example of a new function arising in a fin, associated with the formation of globular swellings of the cord. The gurnard appears to have adopted the method of protection employed by the crustaceans, and to have clothed its large head with a carapace like a lobster, and like a lobster has found it necessary to provide itself with feelers or antennæ; the three posterior rays of the pectoral fins have become separate and form three slender processes on either side, which possess extensive motion on a double row of joints, not connected with the fins. These processes or fingers are supplied with peculiar nerves, and are consequently in possession of special functions.

That they are organs of feeling cannot be doubted; but the fish has also been seen, according to Couch, " when resting on the ground, to close the pectoral fins and to creep by the help of these processes as if they were organs of motion that could be employed without exciting alarm to the prey which the motion of the fins might possibly do." What interests us particularly is the fact that the additional function which the anterior spinal nerves of the gurnard have to perform in supplying the sensitive pectoral appendages and their muscles has caused the development of a paired series of globular swellings of the corresponding portion of the spinal cord. On opening the spinal column it is easy to expose the cord, which is then seen to have six pearl-like swellings on either side immediately posterior to the medulla. The three posterior of these are the central connections of the nerves from the three sensory filaments, while the three anterior receive by a common trunk the nerves from the pectoral fin.

We see here in a simple way the principle, that is still further developed in the brain, namely an increase in the size of a nerve centre when it is called upon to deal with a new function. In the gurnard as soon as certain rays of the pectoral fin took on the new function of tactile organs there was developed a specialised areas in the spinal cord to receive the sensations of touch.

It must not be assumed that there is no tactile sensation in the pectoral fin, because the most posterior rays of the fin may be seen to approach in structure the sensory filaments. But the main function, propulsion, of the fin has been lost or altered by the development of the fingers, so that two functions can be distinguished, propulsion in the anterior portion and tactile sensations in the posterior, although according to Couch the fingers at times seem to act as organs of locomotion. Other examples of the change of functions in a fin will be described later, when it will be necessary to discuss the habits of the rocklings and their brain pattern.

CHAPTER III

THE CARPS

It is fortunate that the most suitable fish for the study of form and function, and the relation of bodily structure to brain pattern, are among the commonest fish in the rivers, lakes, and broads of our native land. We refer to the carps or Cyprinoids, and for our purpose we have examined the brains, both by the naked eye and by microscopical methods, of the following fishes, the carp, goldfish, bream, tench, roach, rudd, dace, minnow, chub, bleak, barbel, gudgeon, and the loach ; the last, though not strictly a Cyprinoid, is so nearly related, and so similar in many ways to the gudgeon, that it is included in the list. British Cyprinoids subsist on a mixed diet, some are almost entirely vegetarian, some feed on insects, shrimps, worms, flies, and larvæ and some on small shellfish. A few are at times predacious, as the chub, and others, found mostly in large lakes, are almost entirely surface feeders and might almost be called plankton-feeders.

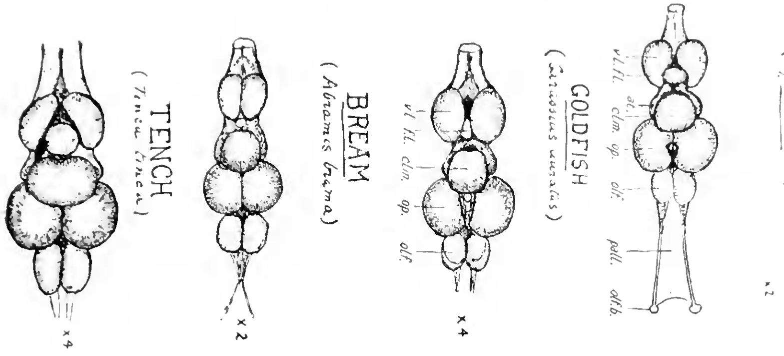
It will be found that these fish can be arranged into groups according to their diet and habits, and that each group has a characteristic brain-pattern ; and further it is found that these groups correspond to the groups given by Tate Regan in his synopsis, based on external characters only, of the British species of Cyprinoids. It is necessary to supplement the naked eye description of the brains of these fish by microscopic methods, but in the first place we will be content to describe the naked-eye appearances ; but it may now be mentioned that a lack of the study of serial sections has led to many erroneous statements in the past. A study of the Plate 3 will enable the reader to see at a glance the striking difference in the brain-pattern of the three groups ; but a short descriptive account will serve to emphasise the more important details.

Group I.—Carp, Goldfish, Bream, and Tench.

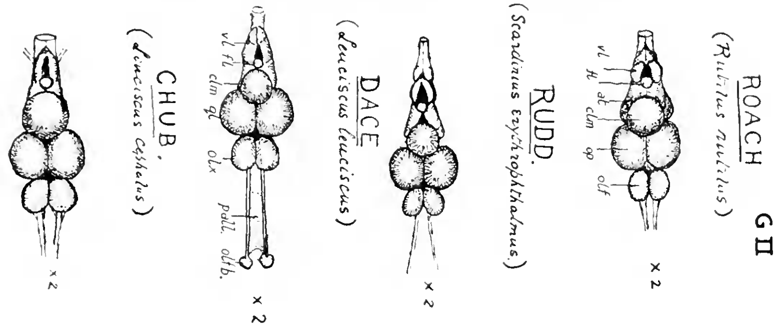
The vagal lobes are large and oval or crescentic in shape. In the carp the facial lobe is not overlapped by the vagal lobes, as it is in the goldfish. In the bream the facial lobe is small and lies further forward than in the other members of the group. In the tench

PLATE 3.

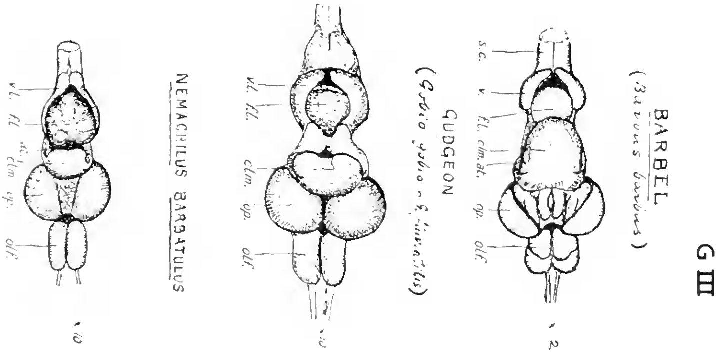
Group I.—Vagal Lobes, Large.



Group II.—Vagal and Facial Lobes, Small.



Group III.—Facial Lobes, Large.



V.L.—Vagal lobe. F.L.—Facial lobe. Clm.—Cerebellum. A.T.—Acoustic tubercles. OP.—Optic lobes. Olf.—Olfactory lobe. OLF.B.—Olfactory bulb. Pall. pallium.—The pallium is only shown in the Carp and Dace.

Note.—In the barbel, loach and goldfish the optic lobes appear large, as the tecta optica are separated by the valvula cerebelli. The olfactory lobes in the third group are large. The brain of the tench might almost be placed in Group III, as the facial lobe is large as well as the vagals.

the facial lobe is large and separates the anterior ends of the vagals. In fact the tench has some of the characteristics of Group III, as will be evident when we recall the facts given in the last chapter, when describing the division of the facial nerve.

Group II.—Roach, Rudd, Dace, Chub.

The optic lobes are large when compared with the vagal and facial lobes. The vagal lobes are small, and the facial very small, but is really larger in depth than would appear from a superficial examination ; this is evident when serial sections are examined.

Group III.—The Barbel, Gudgeon and Loach.

In these three fish the vagal lobes are well-marked, but the facial lobe is very much enlarged, particularly so in the gudgeon and the loach ; but it will be found that the facial lobe of the barbel has a very considerable depth, and it widely separates the anterior ends of the vagals. In this group it will be noticed that the optic lobes are separated posteriorly, especially in the barbel. This is due to an extension of the cerebellum, inserting itself between the tecta optica, which form the roof of the optic lobes. This extension of the cerebellum is known as the " valvula cerebelli." As valvula has a very different application in human anatomy, its use here is unfortunate. The " valvula cerebelli " is peculiar to fish and its function is speculative. It is small in the cod, larger in the carp and still larger in Group III, reaching its maximum in the barbel among the Cyprinoids. It is of immense size in a family of African fishes, known as the Mormyridæ, which we shall have to describe in a later chapter, but we may note here the great development of the snout. The question of its significance may some day be solved by the study of its comparative anatomy ; for the present the only clue seems to be, that it is most developed in ground-feeding fish with a snout-like proboscis.

Mormyrus has a small mouth at the end of a more or less elongated snout, so that it is sometimes called the elephant fish. " The barbel has a rather long snout, with the upper profile decurved, and the gudgeon is rather similar to the barbel in general form as well as in the shape of the head " (Regan), and both grope and grub for their food.

Although the feeding habits of British Cyprinoids are similar, in that they subsist on a mixed diet, some are almost entirely vegetarian, while other are predacious. They can however be divided into three groups according to their diet.

Group I, which contains the same fish as appear in Group I of the table, is characterised by their habit of extracting nutrient material from mud. Yarrell gives as the food of the carp the larvæ of insects, worms, and the softer parts of aquatic plants. Shrimps are also eaten. Bream swim in shoals feeding on worms and other soft-bodied animals with some vegetable substances (Yarrell). Walton gives as baits for a bream " paste of brown bread and honey, gentles or the brood of wasps that be young." There is at the root of docks or flags or rushes in watery places " a worm like a maggot at which tench will bite freely." But for the carp or bream he recommends " as big a red worm as you can find without a knot " ; but this must be carefully cleaned with moss that must be changed fresh every three or four days. But the dominant characteristic of this group is the power of sifting mud and extracting nutriment from the organic matter it contains.

Group II.—This includes besides the fish, the brains of which are figured in Group II of the plate, the minnow. All will take a fly, and the rudd and the dace give good sport to the dry fly fisherman. The dace feeds on weeds, insects larvæ, and flies. The food of roach and rudd is very similar. But the chub is a predacious fish ; he leaps at flies or feeds at the bottom on weeds, shrimps, worms, or young frogs, and also preys on minnows and gudgeon.

According to Walton the chub will take a grasshopper. He recommends as baits, " a black with its belly slit to show its white or a piece of short cheese. Nay, sometimes a worm, or any kind of fly as the ant fly, the flesh fly, or wall fly, or the dor or beetle you may find under cow dung ; or a lob which you will find in the same place and in time will be a beetle ; it is a short white worm like to but bigger than a gentle."

Group III.—The feeding habits of the gudgeon and barbel are well described by Isaac Walton. The gudgeon frequents gravelly bottoms, " the Germans call him the groundling by reason of his feeding on the ground and on the gravel : and he there feasts himself in sharp streams. He and the barbel both feed so and do not leap for flies at any time as most fishes do. He is easily taken with a small red worm. The food of a barbel is partly of an animal and partly of a vegetable nature. He does not disdain any sort of vegetable matter, which he finds by rooting about on the bottom or banks with his snout often turning over stones and using the barbels as tasters in search of food." In general it may be said that their diet is one of shrimps, small mulluscs, insect larvæ, worms, and the eggs or fry of other fish.

A comparison of the groups described above and shown in the Plate with Tate Regan's Synopsis according to external characteristics only can now be made.

Group I.—Dorsal fin long, anal fin short. Last simple ray more or less spinous or serrated.

Carp with two barbels.

Crucian carp and *goldfish* with no barbels.

This corresponds with Group I according to brain pattern as above.

Group II.—Dorsal and anal fins short.

A.—Mouth with barbels.

Barbel, *gudgeon*, and *tench*.

This compares with Group III of brain pattern.

B.—Mouth with no barbels, scales small.

Roach, *rudd*, *chub*, *dace*, etc.

These correspond with Group II of brain pattern.

Group III.—Dorsal fin short, anal fin long Abdomen compressed and forms a sharp keel over which the scales do not pass.

Bream and *bleak*.

It is true that the bream has a brain of the carp type, but it is the only fish that does not fall into line.

This forms a fourth group from the point of view of brain pattern which will shortly be described. These relations of form to brain pattern are facts that are as interesting as they are remarkable. The apparent discrepancies are easily explained. As regards the tench we have already noticed that it has large vagal lobes, but also has a large facial lobe and that the facial nerve divides on entering the lobe ; my original view is, therefore, probably incorrect, and the tench should have been placed in Group III of brain pattern. The only fish that fails to fall in with my classification is the bream. Its relations to the bleak requires more research as the bleak and other fish with a keel have a very unique brain pattern and are, moreover, plankton-feeders.

An examination of the brain of a Cyprinoid inhabiting the large lakes of tropical Africa has furnished material which has enabled us to describe the fourth group of Cyprinoid brain, in which it will be found that the brain of the bleak can be included. In 1929, Mr. Michael Graham made a report on a "Fishing Survey of the Victoria Nyanza," and brought home a specimen of a Cyprinoid, Engraulicypris argenteus, which he kindly placed at my disposal for the purpose of an examination of its brain. An interesting fact noticed by Graham is that this fish has ceased to behave as a Cyprinoid, and has become entirely a plankton-feeder. Its name has an obvious reference to its habits and appearance, Engrauli- or anchovy, Cypris or carp, that is to say, an anchovy-carp, that recalls the habits of a Clupeoid fish, but is really one of the carp family. To quote the Report, "so far as the evidence goes this fish resembles the Clupeoid fishes in its pelagic or open water habitat, as well as in its structure. We frequently observed Engraulicypris apparently catching Copepods and other members of the plankton near the surface. Their stomachs contained Cladocera or Copepoda."

"This is an interesting example of fish belonging to a typically river family, the Cyprinoids, taking on a very different form, where the conditions resemble the sea, especially in the abundance and stability of a rich population of plankton, and adopting not only a pelagic existence but the shape and form of a pelagic family." The resemblance to marine fish does not end here ; "some floating segmenting eggs in the plankton, which evidence seemed to prove were those of Engraulicypris, were found," and this fact is commented on "as so far as I know this is the first record of a floating egg in a fresh-water fish."

On exposing the brain of this fish it was at once apparent that no facial lobe was to be seen in the usual position, not even a small one as is found in the roach group.

It was also found that the external appearance of the brain of a bleak was very similar to that of Engraulicypris, and we shall be able to show that these fishes have the same pattern of internal brain structure when they are examined by microscopical methods. My first observations on the bleak were made during a visit to the Lake Annecy. Both in this Lake and the Lake of Geneva the silvery scales were used for the manufacture of artificial pearls. This industry has almost died out as the Japanese culture of artificial pearls has driven it out of the market. I noticed a mass of bleak lying on a fishmonger's slab at Annecy, which was strikingly suggestive of a number of small herrings lying in a mess of blood-stained mucus with detached scales. In turning over the pages of the "Complete Angler," I was struck with the following passage, "The Bleak or freshwater Sprat, a fish that is ever in motion at the top of the water, ought to be much valued though we want Allomot-salt and the skill of the Italians to turn them into anchovies." Both the sprat and the anchovy belong to the herring family so that it was apparent to Isaac Walton that the bleak was similar in appearance to the plankton-feeding Clupeoids.

Now, after all these years, a study of the brain of this group of the carp family reveals that they have a brain pattern characteristic of plankton-feeding fish in addition to many similar external characters.

In the next chapter we propose to study the pattern of the brain of Engraulicypris and bleak by the method of serial microscopic sections, and we shall find the great importance of this method in unravelling the intricacies of the central connections of the organs of special sense and their relative size.

CHAPTER IV

THE CARPS—*Continued*

As sufficient information cannot be obtained of the various lobes of Engraulicypris by the naked eye, it becomes necessary to employ another method of observation; this is the method of examining the internal structure of an organ by cutting serial sections. To those who are unfamiliar with this method, the following sketch of the process may be useful. The tissue to be examined is first "fixed," that is to say, put in a solution, which prevents distortion or destruction of the cellular elements, which might occur in the later stages of the process. After being fixed, the tissue is "hardened" by various reagents; in the case of brain tissue, the cheesy consistence is changed to that of soft leather. The specimen is now embedded in paraffin of low melting point and allowed to stand in an incubator until the paraffin has thoroughly permeated the tissue. It is then taken out and allowed to cool. The solid paraffin block is then put in a proper position on a microtome and very thin slices are cut in series, which come away from the microtome in ribbons, lengths of which are placed on slides, and numbered. The paraffin is then dissolved out, and the sections stained in the appropriate manner to show up details. These are examined seriatim and successive drawings made under the microscope.

Suppose the first drawing was made of a transverse section of the hinder end of the medulla, each section, as you pass forwards, is studied and, when a modification of the picture occurs, a fresh drawing is made and so on, until you have examined and made pictorial notes of the whole of the medulla. In this way it is possible to make a mental picture and build up the structure of the various lobes and plot them out. Also the intimate details of the tissue are made clear, and the different types of cells recognised, and the course of the connecting strands of nerve fibres followed. The latter often form definite tracts to which terms are applied, signifying their supposed functional significance.

To help the reader to follow the interpretation of the series of transverse sections of the medulla oblongata and cerebellum of the roach, we give a half-a-dozen diagrammatic drawings of this area of the brain. The series begins at the bottom of the Plate 4, and Fig. i is a section of the hinder end of the medulla across the vagal lobes, where they are most prominent. These are separated by a deep cleft, the rhomboid fossa, which is the opening out of the fourth ventricle. At the base of the fossa on either side there is a group of large motor cells, known as the nucleus ambiguus from which pass the efferent fibres of the motor root of the Xth or vagal nerve. External to this motor nucleus on either side is a large bundle of longitudinal fibres cut transversely, which are a prominent feature of the medulla and can be traced in four of the sections of the plate. This bundle is known as the great longitudinal secondary gustatory tract, and in it can be distinguished three divisions, an upper (that is most dorsal), known as the spinal root of the fifth nerve, a middle known as the descending gustatory tract which receives fibres from the facial lobe, and the lower the ascending secondary gustatory tract. In the middle line just below the rhomboid fossa are a number of bundles of nerve fibres known as the longitudinal median bundles (or the fasciculus medialis).

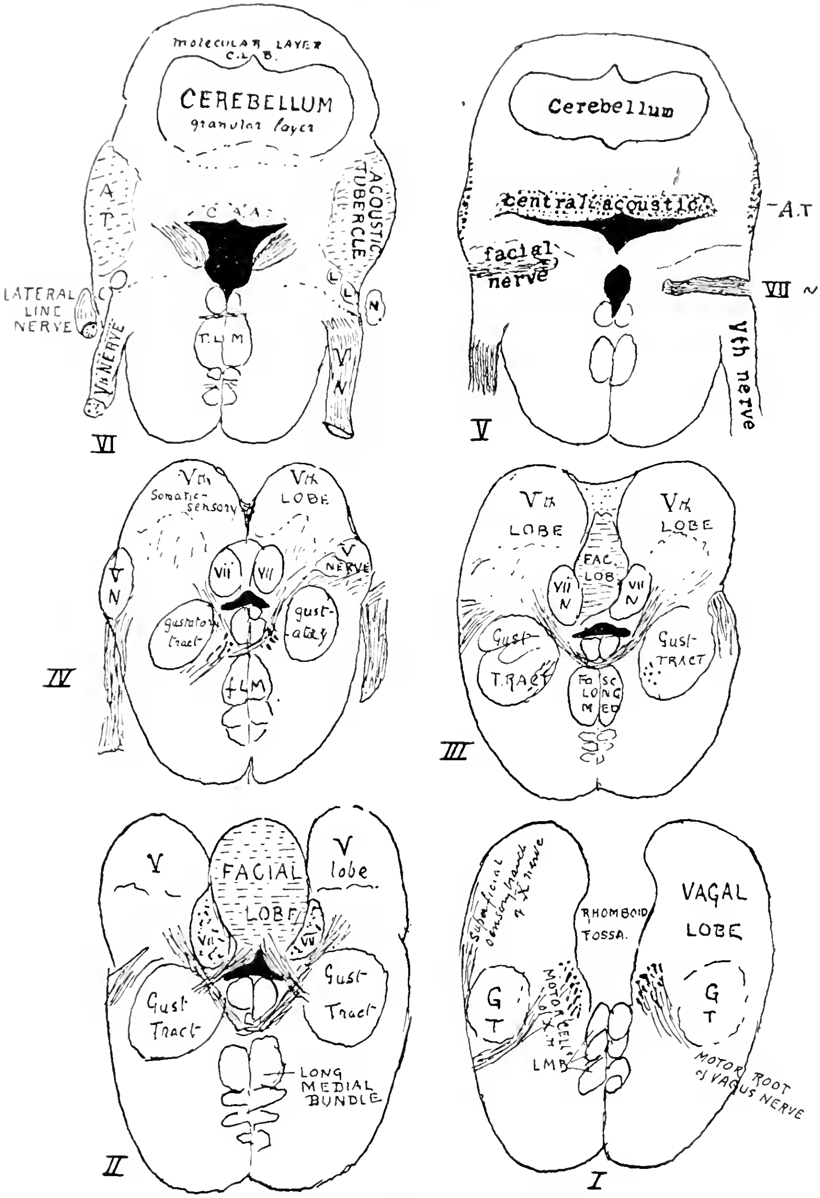
Fig. ii is a section somewhat anterior to the preceding and the vagal lobes no longer appear. In the site of the rhomboid fossa is now seen the facial lobe, and below it is the central canal or ventricle. On either side of the central lobe we see the commencement of the fifth lobes. These represent the skin areas, so are usually called the somatic-sensory lobes. Descending fibres pass on either side into the gustatory tract from the facial lobe, and crossing these descending fibres pass from the fifth lobes to cross each other through the median longitudinal bundle. The facial nerves are also to be seen at the base of the facial lobe into which their fibres gradually pass.

Fig. iii is very similar to the section which has been just described, but the fifth lobes are much more prominent and almost entirely embrace the facial lobe, which is much diminished in size.

Fig. iv.—The facial lobes are replaced by the two trunks of the facial nerves which are passing backwards to enter the lobe as was seen in Fig. iii.

Fig. v.—Here the cerebellum first appears and is joined to the medulla laterally by the acoustic tubercles. The facial nerves are now cut longitudinally and appear to pass transversely towards the ventricle ; the fifth also are seen on either side.

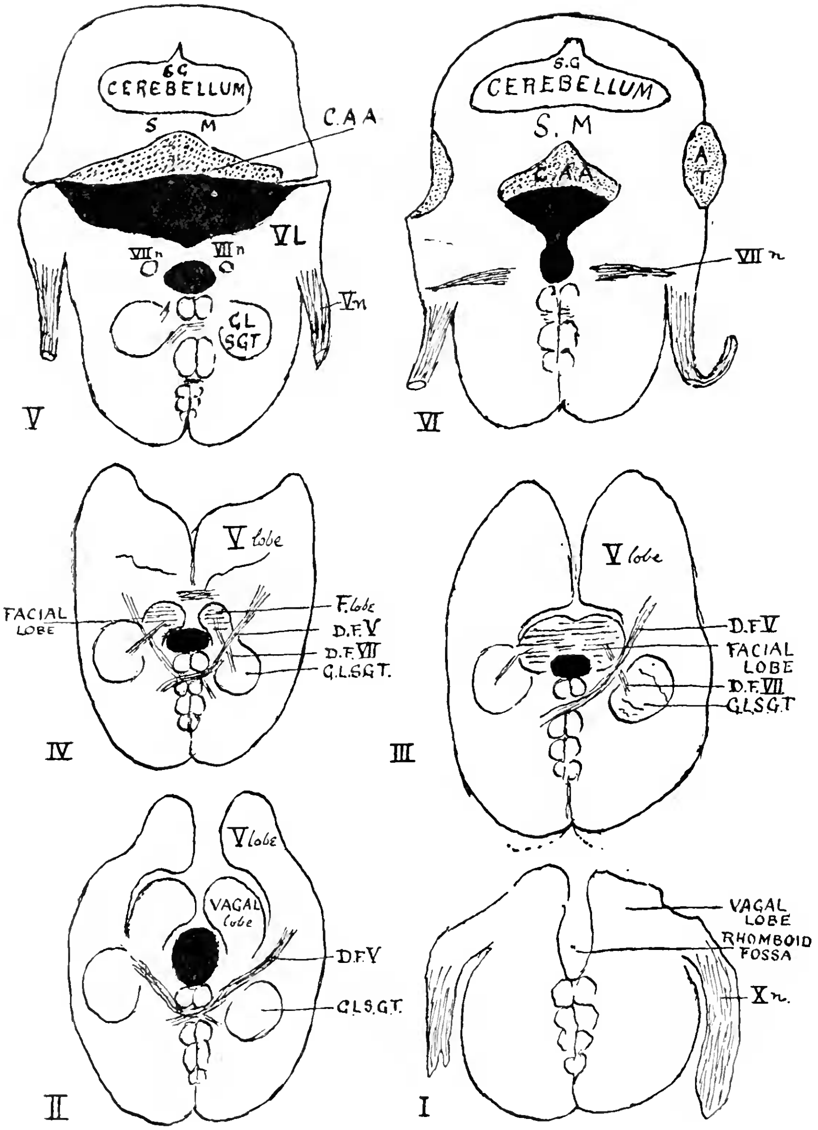
If we study a similar series of sections of the madulla oblongata of Engraulcypris, a very different picture will be observed. We have seen that the naked eye appearance of the medulla shows the absense of a facial lobe as seen in the roach, and the vagal lobes are not easily identified.



Sections of medulla of Roach.

S.G.—Stratum granulare. S.M.—Stratum moleculare. C.A.A.—Central acoustic area. A.T.—Acoustic tubercle. L.L.N.—Lateral line nerve. VII.—Seventh or facial nerve. Vth.—Fifth or somatic-sensory lobe or nerve. G.T. and G.L.S.G.T.—Great lateral secondary gustatory tract. Xn.—Tenth or vagal nerve. D.F.V.—Descending fibres of fifth lobe. D.F.VII.—Descending fibres of facial lobe.

PLATE 5.



Sections of medulla of Bleak.

S.G.—Stratum granulare. S.M.—Stratum moleculare. C.A.A.—Central acoustic area. A.T.—Acoustic tubercle. L.L.N.—Lateral line nerve. VII.—Seventh or facial nerve. Vth.—Fifth or somatic-sensory lobe or nerve. G.T. and G.L.S.G.T.—Great lateral secondary gustatory tract. Xn.—Tenth or vagal nerve. D.F.V.—Descending fibres of fifth lobe. D.F.VII.—Descending fibres of facial lobe.

The serial section Plate 5, Fig. i, shows the vagal lobes, which are very small compared with the vagals of the roach, as figured in Plate 4, Fig. i. The first lobe to produce a definite prominence dorsally in Engraulcypris is the Vth or somatic-sensory lobe, and on either side this lobe hides the vagal as seen in Plate 5, Fig. ii. The vagals are here club-shaped in section, with the rounded dorsal portions tending to meet in the middle line. In Plate 5, Fig. iii, the junction is complete, and the fifth lobe have also approached the middle line. The presence of a small facial lobe is now recognised by descending fibres passing from the central lobe, formed posteriorly by the united vagals, but now formed by the medium fusion of two very small facial lobes. Descending fibres passing laterally downwards and outwards into the great longitudinal secondary gustatory tracts, an important bundle very obvious in the cyprinoid medulla.

This identification of the facial lobes is confirmed if the section shown in Plate 5, Figs. v and vi are examined. In Fig. v, the VIIth or facial nerve is seen cut in section, and in Fig. vi the same nerve is seen cut horizontally as it passes in its usual course from the periphery to the margin of the ventricle. To enable the reader to follow the differences in the medullæ of the roach and the plankton-feeding type as illustrated by Engraulicypris we will summarise the matter.

In the roach the naked eye examination shows two lateral prominences posteriorly the vagal lobes, and these embrace anteriorly a small facial lobe. The sections confirm this picture ; in Engraulicypris neither vagal nor facial lobes are seen superficially and can only be recognised microscopically.

We now come to that part of the brain which lies between the medulla and the optic lobes and consists of the cerebellum and its lateral supports connecting it with the medulla, which give rise to the prominences known as the acoustic tubercles or the acousticolateralis areas. These can be seen on either side of the base of the cerebellum in Plates 4 and 5, Fig. vi. The acoustic tubercles receive afferent fibres from the eighth nerve or auditory and from the lateralis nerve which is the nerve of the organs of the lateral line of which we shall speak later. The function of the cerebellum and acoustic tubercles has been the subject of a great deal of theoretical speculation, but the former is usually held to be associated with the perception of position in space, as recorded by the semicircular canals of the internal ear. The cerebellum may be simply a globular protuberance or may be tongue-shaped, but it always has a characteristic internal structure ; it has a core which consists of darkly staining cells, called the stratum granulosum, which is surrounded by a marginal layer of peculiar cells, which lie in an outer layer varying very much in thickness, which has a uniform consistence, and stains with difficulty, called the stratum moleculare (*see* Plates 4 and 5, Figs. v and vi). In Fig. v the cerebellum is separated from medulla, but in the last section, Fig. vi, the cerebellum is no longer separated from the medulla and the tissue that unites it has two large lateral prominences, the acoustic tubercles, which have a granular structure rather finer than the granular layer of the cerebellum, but also staining deeply. Below on either side Plate 4, Fig. vi, are seen the lateral line nerves entering these lobes.

We have deferred from speaking of the lateral line system till now as it is a controversial subject. There is present in fishes a system of small sensory canals widely distributed under the skin. These contain sensory organs somewhat similar to those of the semicircular canals of the internal ear and their functions are probably intermediate between those of the organs of touch in the skin and those of the internal ear, responding to water vibrations of low frequency, and probably in the orientation of the body in space. These are the lateral line canals and we are all familiar with the lateral line in fish, which is so clearly seen running along the side of fish nearly midway between the dorsal and ventral margins and often made more obvious by being pigmented. Similar canals are also found on the head. These canals are supplied by special roots of the following cranial nerves which all finally enter the acoustic tubercle or acoustico-lateralis lobe ; these are the seventh or facial nerve, the ninth or glossopharyngeal nerve, and the tenth or vagal nerve. These, together with the eighth or acoustic nerve, are associated with the reception of vibatory sensations of a greater range from those of hearing proper to slow vibrations such as are felt by the skin of man and also by what is known as bone conduction.

It will be our aim to see whether the methods of comparative anatomy may not help to unravel the central areas which must presumably be associated with these various functions, and with this object in view we must draw the attention of the reader to an area of small cells interpersed with transverse nerve fibres which appears at the base of the cerebellum just before its free portion joins laterally with the medulla. This area is known as the central acoustic area and at times forms a definite lobe. It is well shown in Plates 4 and 5, Fig. v, and it will be observed that it is more prominent in Engraulicypris than in the roach. In the bleak it is still more prominent. Fibres pass to this area from the eighth nerve, and there are also fibres passing from it to the acoustico-lateralis area.

Besides the lateral line organs there are diffusely scattered sense organs in the skin also innervated by the lateralis system and both arise from a " common rudiment in the epidermis of the embryo in the position of the future auditory organ. This rudiment grows backwards along the side of the body and also forwards." (*Camb. Nat. Hist.*). This seems to be an important fact in the discussion of the acoustic tubercles. There is very little known about the acoustico-lateral area of fishes, except the fact that it receives all the nerve fibres from the internal ear and from the several kinds of lateral line organs. Herrick states " that the central terminations of these different kinds of fibres are so intertwined within this area, that it has not been possible hitherto to separate completely the reflex centres of the many diverse functions, represented in this complex system of peripheral sense organs. There is, however, an incomplete separate localization within this area of several specific functions, but the reflexes, served by all of the organs of the acoustico-lateral complex, are evidently in very close physiological association. These reflexes fall into three groups : I.—Postural and equilibrial, served chiefly by the semicircular canals of the ear ; II.—Auditory, served by the end-organs of the saccule ; III.—Reactions following excitations of the lateral line organs by slow water vibrations and by other agents as yet imperfectly known."

But before we enter on further discussion of the function of the acoustic tubercles it will be necessary to give a short description of the organ of hearing in fish, and also mention the various accessory organs of hearing which are found in certain families. This subject deserves a special chapter, as it is rather a long story, and it treats of many facts which have only been firmly established by recent research.

CHAPTER V

HEARING IN FISH

Hitherto, very little has been said about hearing in fish, and the function of the eighth or auditory nerve ; most people will not be surprised by these omissions, and the more knowledgeable among them would say, fishes cannot hear they only perceive vibrations ; this, however, is not correct, as accurate anatomical investigations supported by the most convincing physiological experiments have proved that many fish have a wide range of hearing and that the minnow can recognise notes of as wide a range as can the human ear. The ear of a fish can be best understood by a reference to the two diagrams which compare the general structure of the internal ear of a typical fish with the human ear.

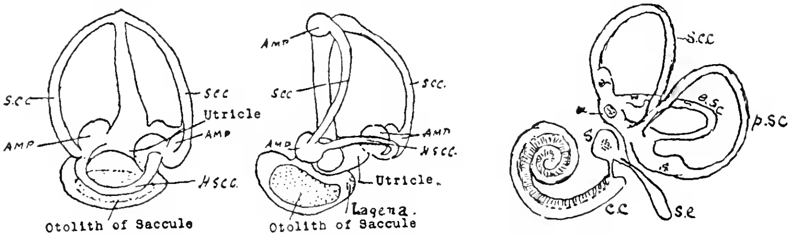


Fig. i.—Two drawings of the ear of Herring from specimens prepared by the author, and internal ear of man after Schäfer.

S.C.C.—Semi-circular canals. H.S.C.C.—Horizontal semi-circular canal. AMP.—Ampullæ. c.c.—Canal of cochlea. e.s.c.—External Canal. s.e.—Saccus endolymphaticus.

The lettering which accompanies these diagrams will be sufficient to make clear all that is essential for the reader to understand for our present purpose. But there are many fish that have an accessory organ, in addition to those parts of the organ of hearing, known as the saccule and utricle with its three semicircular canals. We should expect that these fishes would be provided with a more specialised centre in the brain, and, therefore, before studying the central connections of the auditory nerve, it would be wise to consider the nature of these accessory organs. In pursuit of this idea we are led to the study of the air-sacs or swim-bladder of fish, and it is found that this organ is capable of presenting a great variety of methods of increasing the auditory function in different families of fish.

PLATE 6.

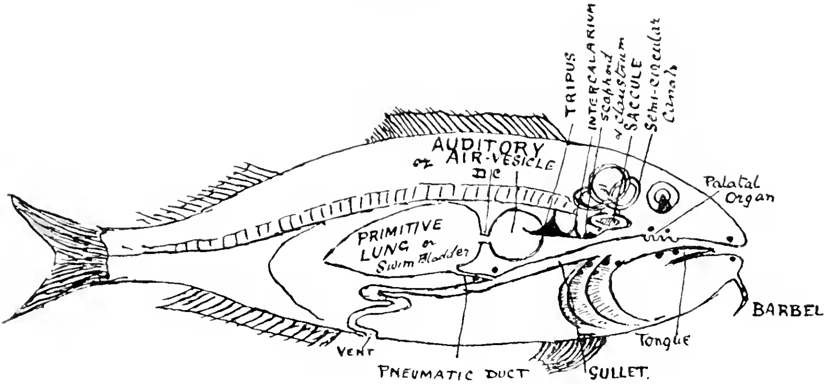
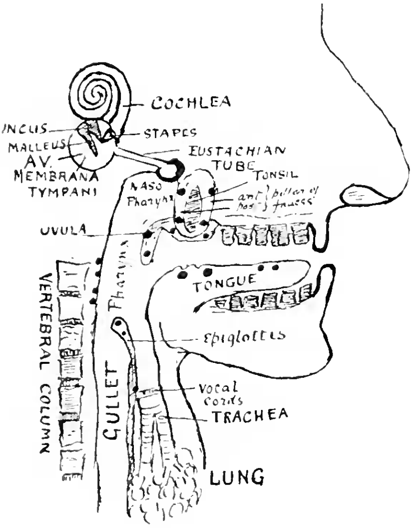


Diagram of Fish to show relations of swim-bladder and auditory vesicle to internal ear and distribution of the taste-buds.



Distribution of taste-buds in Man and relation of air-passages to the middle-ear.

Black dots signify site of taste-buds.

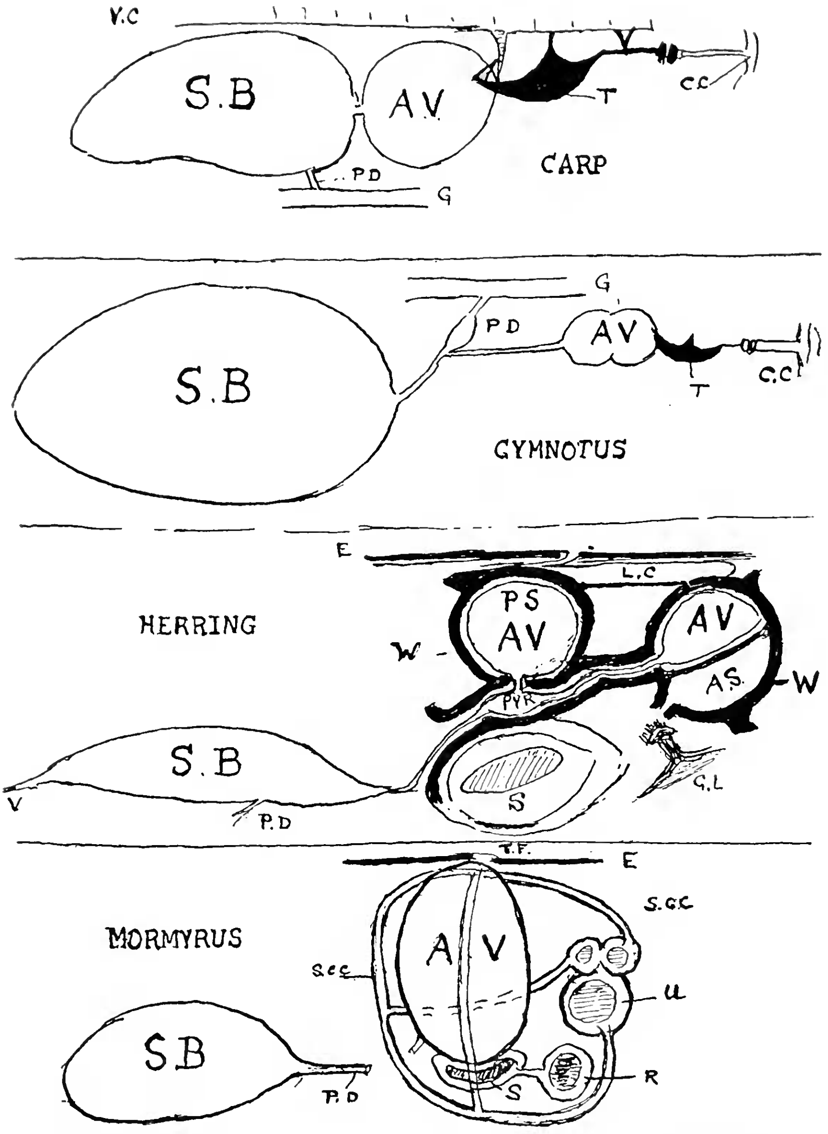
The history of the swim-bladder is one of the most remarkable tales in the development of present day fishes. Although the swim-bladder was originally a lung, it is now largely used as a hydrostatic organ or buoyancy tank ; nevertheless, there is often a vesicle or secondary air-bag given off from its anterior end, which is connected by various means with the internal ear. The very large family known as the carps or Cyprinoids have a swim-bladder lying free in the upper part of the abdominal cavity only attached to a small plate of bone projecting downwards from the vertebral column to which the anterior sac or air vesicle is not only attached by its outer wall, but also by a very important muscle rising from an ossicle, the first of the chain of small bones leading from the anterior sac to the internal ear. These are known as the Weberian ossicles. (Plate 7.)

In the carps the posterior air-sac, which acts as a buoyancy tank, has a tube connecting it with the gullet, and this duct, known as the pneumatic, allows swallowed air to be not only introduced into the bladder by means of the pneumatic bulb or pump, but also to be discharged when necessary in accord with the hydrostatic requirements. Between the two sacs there is a communicating duct which is kept closed by a sphincter muscle, controlled by a nervous ganglion ; this enables the gaseous pressure in the anterior vesicle to be kept at a level most suitable for the reception of vibrations ; the function of the anterior sac is that of a drum, which acts as a hydrophone. It may be said that this drum combines the functions of a vibrating membrane and that of a middle ear, while the " ductus communicans " has the same physiological use as the Eustachian tube in the human ear. Vibrations received by the body wall of the fish are communicated to the anterior sac directly and not by any external ear, which does not exist in fish. There is another important fact to be noted, namely, that the orifice of the pneumatic duct as it enters the gullet is surrounded by a ring of taste-buds, which act as sentinels protecting the orifice, and only allow bubbles of swallowed air to pass into the posterior sac.

If the two diagrams (Plate 6 and 7) of the connections of the lung in man, and the swim-bladder in fish, with the auditory organ are studied, a remarkable similarity in general arrangement can be traced. In the human ear there is an external ear which leads to a drum which forms an outer wall to the middle ear. To this drum is attached a chain of ossicles or small bones which transmit vibrations to the internal ear, and the gaseous pressure in the middle ear is controlled by means of a tube, the Eustachian tube, that leads into the upper part of the pharynx which may be looked upon as an extension of the air-passages upwards.

In the carp, an external ear being non-existent, the anterior sac or air-vesicle receives the sound vibrations directly through the body walls and from its anterior end there arises a chain of ossicles that transmit these vibrations to the internal ear. Weber, who first described these ossicles, named them after the small bones of the human ear, malleus, stapes and incus ; but those comparative anatomists, who followed him, did not consider that these bones

PLATE 7.

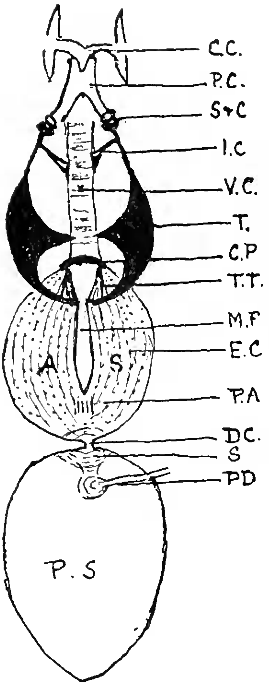


Accessory auditory organs of Carp, Gymnotus, Herring and Mormyrus.

W.—Wall of auditory vesicle. S.B.—Swim-bladder or buoyancy tank. A.V.—Auditory vesicle. T.—Tripus. P.S.A.V.—Posterior spherical air vesicle. A.S.—Anterior spherical with transverse membrane. PYR.—Pear-shaped air vesicle. P.D.—Pneumatic duct. C.C.—Cross canal. G.—Gullet. S.—Saccule. R.—Round vesicle. U.—Utricle and ampullæ. S.C.C.—Semi-circular canals. E.—Epidermis. T.F.—Tympanic fenestra. G.L.—Ganglion with papilla. V.—Vent.

had any auditory function so that a new terminology was given to them, the tripus, scaphoid, and claustrum. But we have now returned to Weber and it has been proved that his views are correct.

At the hinder end of the anterior vesicle we have noted the ductus communicans and here we have the representative of the Eustachian tube as it controls the gaseous pressure in the middle ear. The posterior sac as we have already stated was primitively a lung and this is connected with the gullet by the pneumatic duct, which corresponds to the larynx and, just as the larynx is guarded by the epiglottis with its taste-buds, so the pneumatic duct is guarded by its ring of sentinel buds.



—Canalis communicans.
—Posterior cavity.
—Scaphoid and Claustrum.
—Intercalarium.
—Vertebral column.
—Tripus.
—Central plate.
—Tensor tripodis.
—Membrana flaccida.
—External coat of A.S.
—Anterior sac.
—Posterior attachment of A.S.
—Ductus communicans.
—Sphincter.
—Pneumatic duct.
—Posterior sac.

Fig. ii.
Dorsal view of swim-bladder and Weberian Ossicles of Carp.

There are many other interesting details which make this comparison of the organs of hearing in man and fish very striking. We may mention two : The tripus or malleus of a fish is kept tense by a small muscle, by which it is attached to the central plate, and in the human ear there is a small muscle that controls the malleus, the tensor tympani. The outer wall of the anterior vesicle in fish consists of a very friable membrane composed of fibres running in a criss-cross fashion, while the inner wall, which is only loosely adherent to the outer wall, can be removed with its contained gases without interfering with the attachments of the ossicles. The membrana tympani of man has a very similar fibrous structure to that of the external coat. Other minute details might be described, and these can be studied in the more technical papers that have appeared in the Proceedings of the Royal Society and the Transactions of the Royal Society of Medicine (Evans).

Before we leave the subject of the accessory organ of hearing in carps, it will be of great interest to study the modifications of the swim-bladder and Weberian ossicles in a tropical air-breathing fish. We were very fortunate to be given by Mr. Burne, the physiological curator of the Royal College of Surgeons, a specimen of the electric eel, which belongs to a family closely related to the carps. The diagram (Plate 9) of its swim-bladder and the auditory connections will enable the reader to follow these modifications, and to compare them with the corresponding organs in a carp. The most striking fact is the very large size of the posterior sac, or buoyancy tank, which has a volume ten times larger than an average sized carp. If the pneumatic duct is traced back to the gullet it will be found to enter an ovoid chamber before it actually enters the oesophagus. This chamber is the air-pump, which pumps the swallowed air into the sac. From this chamber there also passes a fine duct that runs forwards and enters a small air-vesicle which lies in the anterior part of the abdomen. From the front of the air-vesicle the small bones, or Weberian ossicles, pass forwards to end in the duct that communicates with the internal ear or saccule.

The most striking point in this arrangement is the complete separation of the hydrostatic sac from the auditory vesicle which makes the similarity of the duct leading to the air vesicle, to the Eustachian tube of man, very convincing.

In the course of our dissection of this fish other points were observed of interest which hitherto had not been completely investigated. The famous surgeon and scientist, John Hunter, noticed and described a number of foliate projections in the floor and roof of the mouth ; he did not, however, recognise the function of these outgrowths. When these foliate papillæ were examined microscopically, it was found that they had a superficial layer of air spaces like the alveoli of a lung, and there can be no doubt that, when the mud flats are parched by the sun, the electric eel is able to obtain air by this accessory mouth-breathing organ.

It is not necessary to go into the details of the connections of the Weberian ossicles with the saccule by means of certain ducts which lead to a space called the "atrium sinus imparis." But it will be interesting to quote some conclusions arrived at by Sörensen :

"I.—The wall of the air-bladder is capable of vibrating synchronously with rapidly recurring sound waves.

"II.—The tripus is thrown into vibrations when the wall of the bladder is vibrating.

"III.—All movements, also, vibrations of the tripus are transmitted, by means of the tight inter-ossicular ligament, to the rest of the Weberian ossicles and in this way to the atriun sinus imparis.

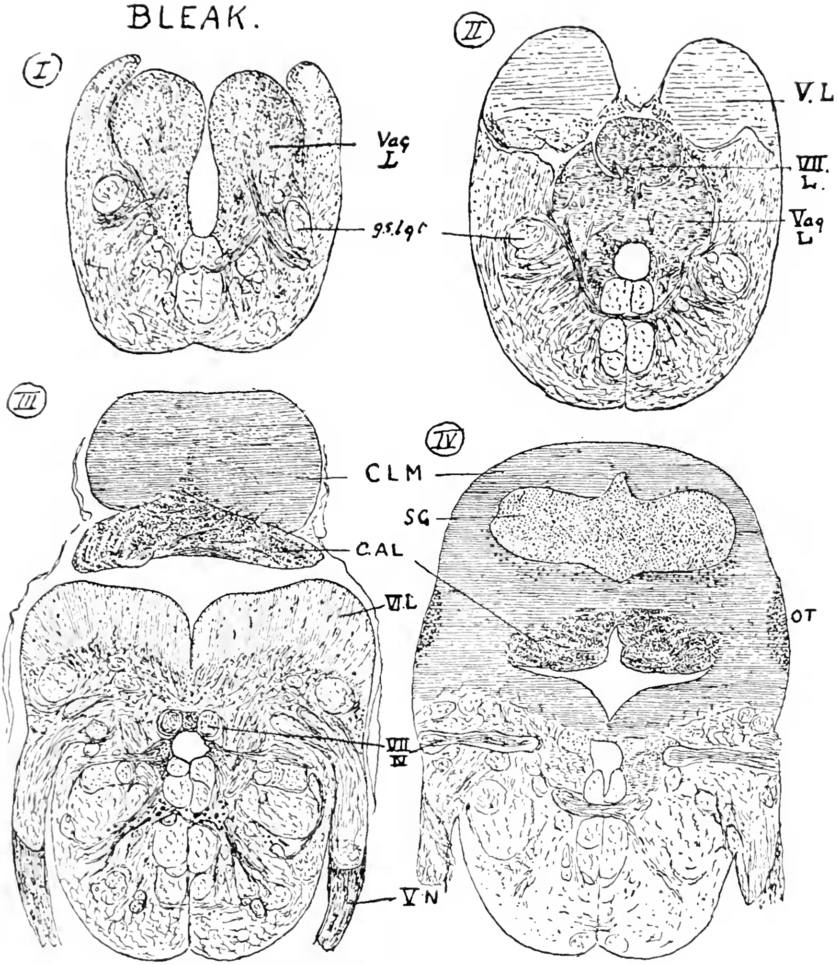
"IV.—The tones of the air-bladder can be transmitted to the water without losing much in strength, and if so, vice versa, sound waves can be transmitted from without to the air-bladder."

Recently, Prof. K. von Frisch has shown by experiments that have been conducted on the principle of Pavlov's conditioned reflexes that the minnow has a range of hearing as wide as has the human ear. But we are the more indebted to him for putting on an experimental basis, the fact that the swim-bladder has an important share in the hearing of those fish with a Weberian apparatus. He tested the range of hearing in minnows both before and after removing the swim-bladder and found that hearing remained in those fish which had had the swim-bladder removed, *but that it was weakened.* "We see, therefore, that those fish in which the swim-bladder is connected with the labyrinth by Weberian ossicles, have an apparatus through which the acuteness of hearing is increased."

We are now able to turn to the discussion of the methods of feeding of the fourth group of Cyprinoids as typified by the African fish Engraulicypris and the bleak, which, as far as we were able to judge, were mostly dependent on sight in the search for food. When the serial sections of the roach and Engraulicypris were described in a previous chapter there was noted a central area of round cells with interlacing transverse fibres at the base of the cerebellum connected laterally with the acoustic tubercles ; this we termed the central acoustic area. When we come to discuss the auditory organ of the herring and its central representation in the brain it will be possible to give more fully the arguments in favour of adopting this term and of associating this with audition.

It has already been pointed out that Engraulicypris has a rudimentary facial lobe, and that the gustatory function must be small ; that it has large optic lobes and that it has a surface habitat and is a plankton feeder. The study of its central acoustic area, however, seems to indicate that hearing may be of importance in regard to its

PLATE 8.



Four transverse sections of the medulla oblongata of the Bleak.

I.—Posterior across the vagal lobes. II.—More anterior across the small facial or VIIth lobe. III.—Across the central acoustic lobe. IV.—Most anterior across the cerebellum, acoustic, tubercles and central acoustic area. Vag.L.—Vagal lobe. V.L.—Fifth or somatic-sensory lobe. VII.L.—Facial or seventh lobe. C.L.M.—Cerebellum. S.G.—Stratum granulosum. A.T.—Acoustic tubercle. VII.N.—Facial nerve. V.N.—Fifth nerve. C.A.L.—Central acoustic lobe.

surface feeding habits, as this area is very highly developed ; this is also the case in the bleak, which has a similar habitat and method of feeding. In fact, in the bleak figure, the central acoustic area becomes a definite lobe which projects backwards from the base of the cerebellum. The central acoustic area is also seen in the roach, but is less marked ; but in the bottom-feeding Cyprinoids it is only feebly represented. These facts suggest that surface feeding fish find it advantageous to have an increased power of hearing. It is of great interest to find that these considerations receive strong support from observations made by Bhimachar on the Cyprinoids of the Madras tanks.

In a paper which was published in the Proceedings of the Royal Society, he states, " The acoustic area or lobe is the terminal centre in the brain of the auditory function. This area is very prominently developed in all the sight feeders, and fairly well developed in the ground feeding fish which come to the surface to take in air. But in the purely ground feeding fish as Nemachilus, which is not exposed to the influence of external sound waves this area is almost completely absent. Compared with the central acoustic area of the British plankton feeding fishes, such as the bleak, the Indian forms like rasbora, nauria, etc., have not only a larger central acoustic area but also an extension of this area behind the cerebellum in the form of a distinct central acoustic lobe. This is evidently due to a more perfect sight-feeding habit of the tropical fishes and their consequent exposure to the effects of external sounds. In the accessory air-breathing Cyprinoids and Siluroids the extent to which the central acoustic area or lobe is developed gives a strong indication of the air-breathing habit."

This confirmation of the observation of a British observer by an independent Indian naturalist makes the conclusion, that the auditory function of the central acoustic area or lobe in surface feeding Cyprinoids is justified, will be supported by further observations on several other families of fish as we shall have occasion to describe in the following chapter.

We have now reviewed the relations of all the special senses to the various lobes of the carp family and we arrive at a certain conclusion which may be expressed as a law, "The pattern of the brain of a bony fish is determined by the proportional representation of the special senses in its feeding or hunting equipment."

CHAPTER VI

ACCESSORY ORGANS OF HEARING

We have seen in the carps that from the anterior end of the primitive lung, represented by the posterior sac, there grows a vesicle which lies in the abdominal cavity. In two important families of present day fishes, namely, the herring family or Clupeidæ, and an African family the Mormyridæ, we find a duct given off from the swim-bladder anteriorly, which divides into two finer ducts, and these end in a vesicle or vesicles connected with the internal ear. The connection of the vesicle with the bladder is not permanent in the Mormyridæ, but its rudiment remains; whereas in the herring it persists in the adult. In these families the connection with the auditory organ is within the cranial cavity, so that there is no need for a series of ossicles, as is present in the carps. We propose firstly to describe the more simple and less controversial of these two accessory organs of hearing.

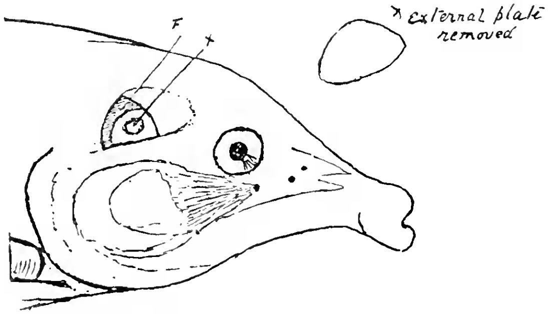


Fig. iii.—Head of Mormyrus Kannume (Worthington) to show position of external auditory orifice.

Diameter of eye ·9 cm. Distance eye to ant. foramen 1·5 cm. *X* Exposed portion of sac ·5 cm. *F* Vertical diam. foramen ·7 cm.

The African elephant fish or Mormyrus (Fig. iii) has a small fenestra in the lateral wall of the skull which is closed by a very thin osseous membrane loosely attached to the margin of the window, except at one point. Immediately beneath this lies an ovoid vesicle (Fig. iv), about the size of a small pea in its longest diameter, which lies in a vertical plane; this contains gas; attached to its base is an almond-shaped sac, containing an otolith; leading from this and connected to it by a short duct, is a round sac the diameter of which is less than the long diameter of the other sac; this also contains an otolith. In the floor of the cranial cavity anterior to the air-vesicle are three impressions which lodge the utricle and two ampullæ, the spherical terminations of the semicircular canals; and posterior to the vesicle is another impression for the ampulla of the horizontal semicircular canal. These canals embrace the vesicle, but do not communicate with it.

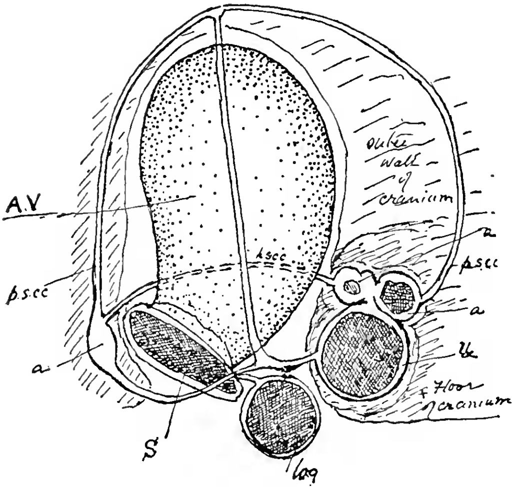


Fig. iv.—Air vesicle, ampullæ and canals of Mormyrus—enlarged.

A.V.—Auditory vesicle. p.s.c.c., h.s.c.c. and a.s.c.c.—Poserior, horizontal and anterior semi-circular canals. S.—Saccule. lag.—Round sac with otoliths. U.—Utride. a.—Ampullæ.

The almond-shaped sac must be regarded as the saccule, and the round sac presumably represents the lagena, which is the term applied to a specialised portion of the saccule, which is supposed to represent the cochlea of higher vertebrates. This is the nearest approach to the ear of an air-breathing vertebrate that is known in fish. It is true there is no external ear, but there is a tympanic membrane communicating directly with a middle ear represented by the air-vesicle, and this is in direct contact with the internal ear, represented by the saccule and lagena and their otoliths. There is another interesting fact that must be noted; projecting from the base of the vesicle is a small blind rudimentary duct ; this has been shown by a study of the development of Gymnarchus, one of the Mormyridæ, to be the vestigial remains of the original swim-bladder connection.

We shall find when we describe the spherical air vesicles of the herring that the posterior vesicle is surrounded by the semicircular canals, just as we have described in Mormyrus ; this seems to point to the probability that the posterior vesicle is functionally similar to the air-vesicle of the latter fish. It may be asked why has the swim-bladder connection been lost in Gymnarchus but remains in the herring ; the explanation is that the herring has a wide range of movement, at times swimming rapidly from the depths to the surface ; if there was no connection, the gas in the vesicles would expand to such an extent as to put the mechanism out of gear when the fish comes to the surface ; moreover, there is a special orifice in the swim bladder of the herring which allows of a free discharge of gas, directly near the vent. We know little of the habits of the Mormyridæ, except that they are bottom-feeding fish, and keep approximately at the same depth, so that there is no necessity for any contrivance to release the pressure in the air-vesicle.

The accessory organ of hearing in the herring, which we shall now attempt to describe, has never been quite satisfactorily investigated. In an endeavour to throw more light on this very complicated mechanism, we have dissected a very large number of fresh specimens and have been struck by the number of details that can be made by simple anatomical methods. But the most important contribution to the interpretation of its structure has been made by the study of a series of horizontal sections which were given us by Dr. Hillier, who has made a detailed study of the bones of the cranium of this fish. These sections are very beautiful and seem to solve many of the difficulties that have arisen in the correct understanding of the function of this organ.

In order to simplify our description, it is proposed to describe this complex mechanism under three headings, the ear proper, the swim-bladder, and the accessory air-vesicles by which the first two organs are connected. The two drawings of the ear proper (Fig. i) are made from the dissections of a fresh specimen, and show the usual type of internal ear that is found in fish, namely, the utricle with its three semicircular canals, and the saccule with its otolith. There are two other facts or relations that do not appear in the drawings : the bony cavity of the saccule has a specially modified external wall which is known as the auditory fenestra ; this is closed by a membrane which has the characteristics of a tympanic membrane, as found in the higher vertebrates; this allows the incompressible fluid in the cavity to vibrate. It must be understood that the membranous wall of the saccule lies in the central cavity of the bony labyrinth of the ear, known as the vestibule; in the herring an appendix of the vestibule meets the anterior spherical air vesicle, which we shall shortly describe, and comes in close contact with it. The long silvery looking tube that we see in the upper part of the abdomen of a fresh herring is the swim-bladder. Hillier gives a very concise description of this organ as follows:

"It is a simple long sac, opening posteriorly by a fine canal through a dense sphincter muscle, and anteriorly opening through a cartilaginous arch, into the fine duct that leads into the interior of the labyrinth. A canal from the stomach, the pneumatic duct, enters the swim-bladder about its middle. So that the swim-bladder is unique among fishes in having three openings into its cavity. 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 ring of cartilage; for in this respect it suggests the similar condition of things in mammals, with the Eustachian tube running from the naso-pharynx to the cavity of the middle ear."

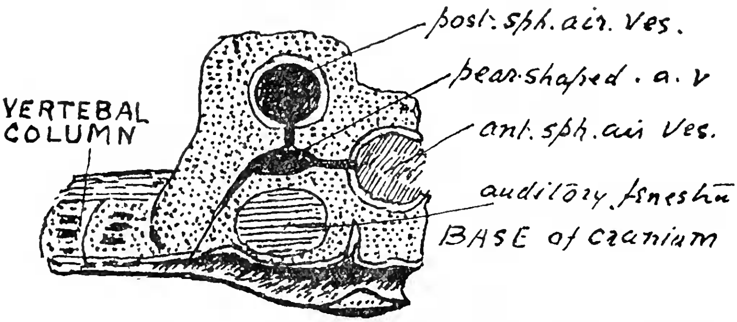
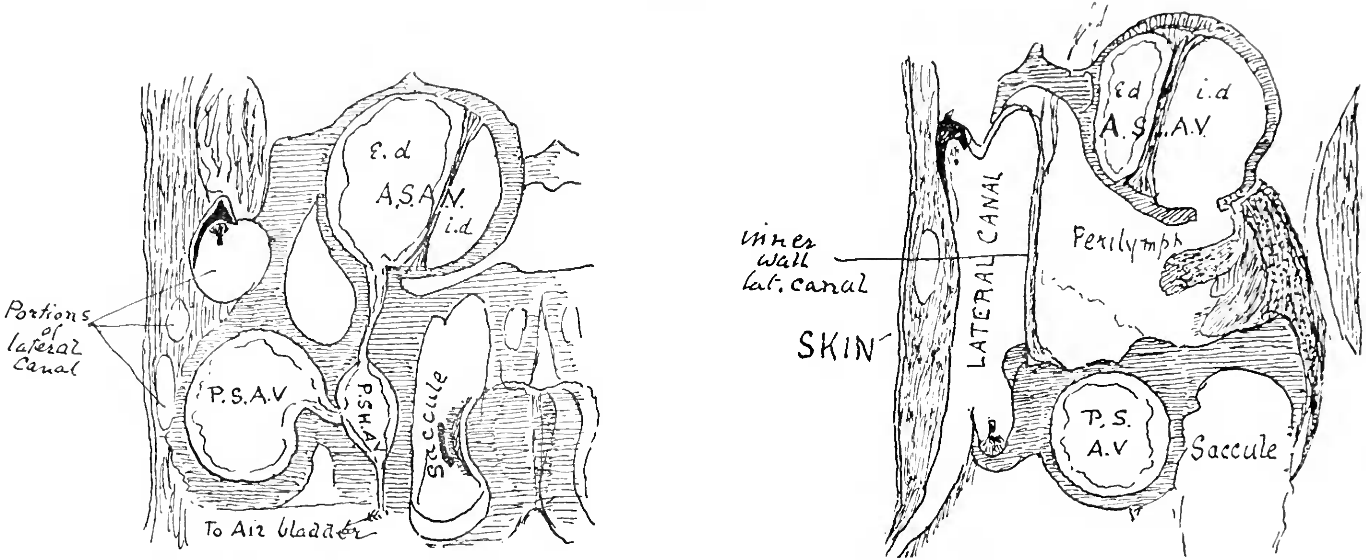


FIG. v.—A dissection of the lateral wall of the Herring (enlarged) from within to show the accessory auditory apparatus.

The front wall of the anterior spherical air-vesicle has been chipped away so that india-ink could be injected into the posterior air-vesicle through the canal leading into the pear-shaped vesicle. The ink has also passed into the canal leading into the swim-bladder. Below the pear-shaped vesicle is the outer wall of the saccule closed by the auditory fenestra.

The accessory portion of the auditory organ commences by the fine duct given off from the anterior end of the swim-bladder; this almost at once divides into two finer ducts, which pass forwards

PLATE 9.



Two drawings of sections in a horizontal plane of the accessory auditory organ of the Herring.

To the left is a section made ventrally through the saccule and the three air-vesicles showing the extension of the inner lining of the swim-bladder into their vacuities. The anterior spherical air-vesicle is divided by a transverse membrane and the lining only occupies the external segment. The saccule is also shown with its auditory papilla and otolith.

To the right is a section cut more dorsally. A large lateral canal leads from an aperture inwards and is bounded internally by a tense band, passing from the wall of the posterior air-vesicle anteriorly to an extension of the external margin of the anterior spherical air-vesicle. An aperture leads from the inner division of the anterior vesicle into the perilymth cavity, and abuts on an auditory papilla which lies on a ganglion close to the medulla.

e.d. and i.d. A.S.A.V.—Internal and external divisions of the anterior spherical air-vesicle. P.S.A.V.—Posterior air-vesicle.
P.S.H.A.V.—Pear-shaped air-vesicle.

in the bone just above the auditory fenestra of the saccule and enter on either side a small pear-shaped cavity ; from this again a small duct passes upwards and outwards into the posterior spherical air-vesicle, while from its anterior end another duct leads forward into the anterior spherical air-vesicle. Both of these membranous extensions of the swim-bladder are enclosed in bony capsules ; in the bony capsule of the posterior vesicle are embedded the semicircular canals which thus surround this vesicle just as we have seen the semicircular canals of Mormyrus surround its air-vesicle. If the anterior wall of the anterior air-vesicle is carefully chipped away, the shiny coat of the anterior extension of the swim-bladder will be seen to occupy the outer half of the bony capsule, which is divided by a transverse membrane ; the inner half of the bony capsule communicates by a slit-like opening with the perilymphatic space and near the medial margin of the orifice there lies an end-organ with a layer of hair-cells surmounted by an otolith ; from the base of this organ nerve fibres pass into a ganglion connected with the auditory nerve.

If we consider the position of the posterior air-vesicle and its connections with the exterior it will be noted that it lies in the pterotic bone near the surface of the cranium and that immediately in front there is a temporal foramen occupied by a bay-like expansion of a lateral-line canal, and that the inner wall of the lateral-line canal belonging to the lateral wing of the frontal bone is absent. The place of this wall is taken by a tense membrane, which is attached posteriorly to the front of the bony capsule of the posterior air-vesicle, and anteriorly to the bone which connects the anterior capsule to the outer wall of the cranium. How are we to construct a reasonable theory as to the physiological use of this complicated mechanism. Looking at the position of the posterior air-vesicle, its site in the temporal region, and its proximity to the external surface, suggest the theory that its function is to receive vibrations from the surrounding water, which may also be received through vibrations received from the tense membrane which forms the inner wall of the adjacent lateral-line sinus, as this membrane is attached to its capsule. The analogy of its envelopment by the semicircular canals, as is seen in the air-vesicle of Mormyrus, also supports this view.

Vibrations received by the air in the posterior vesicle would, according to this suggestion, be carried to the air in the outer segment of the anterior spherical air-vesicle, and so to the transverse membrane which divides the bony capsule ; this membrane would convey the vibrations to the perilymph in the inner division, and would pass out through the slit-like aperture and be received by the otolith lying on the hair-cells close to this orifice and so to the auditory ganglion. The membrane tends to take a somewhat spiral course in the anterior capsule, so that the relative size of the two compartments vary ; the inner division being large at the base and the outer division being large at the apex. If this view be correct the anterior vesicle would appear to be constructed somewhat on the plan of a rudimentary cochlea.

We regard the connection with the swim-bladder as simply a means of regulating the pressure of gases in the system of air-vesicles. The theory of an auditory function attributed to this mechanism is nothing new. This was the view expressed by most of the older writers. Weber considered that the septum in the anterior osseous capsule functioned as a tympanic membrane. Another theory held that the mechanism is part of a reflex system which through efferent visceral nerves transmits impulses to the swim-bladder, in order to adjust it to changes in hydrostatic pressure. Another modern and very careful anatomist does not consider the posterior air vesicle of any importance ; he dismisses it with the statement, " Since the posterior vesicle has no apparent relation to the labyrinth or other structure outside the bony capsule it will not be discussed further in this paper."

Other objections have been raised to the theory which has been expounded above, namely, the slight variations in the posterior vesicle found in the pilchard and sprat. But we consider these variations do not invalidate our view and hold that the herring presents the most perfect adaptation of the accessory auditory system to the function of hearing to be found in the family of Clupeoids.

CHAPTER VII

THE CENTRAL ACOUSTIC LOBE

Having described the accessory organ of the herring we can now turn to the consideration of the brain pattern of this fish, a typical plankton feeder, and see whether it throws any light on the central acoustic area we have described in the surface-feeding carps. The medulla of a herring is much concentrated and has a well-marked median lobe, projecting from the back of the cerebellum. This lies in the position of the facial lobe of a carp, but microscopical examination shows that it is connected with the acoustic tubercles and has no anatomical relation with the facial nerve. When serial sections are traced beginning at the hinder margin of this lobe, we find that, resting on the fifth lobe, are two wings of tissue that meet dorsally. These consist of groups of round cells between which nerve fibres run, to meet at the apex, while an interrupted layer of round cells forms a cortex. As the sections are followed forwards these wings become thicker and finally have the shape of a pear in section, surrounded by a dorsal extension of the basal tissue, from which it springs.

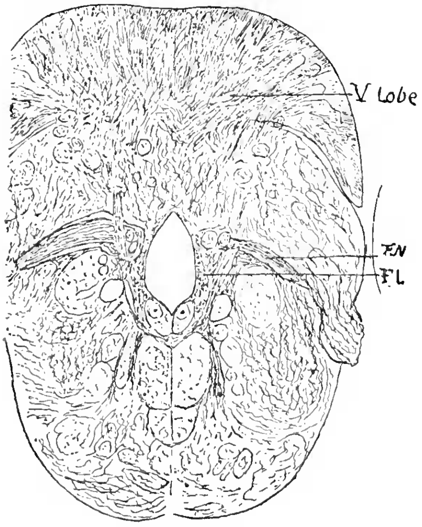
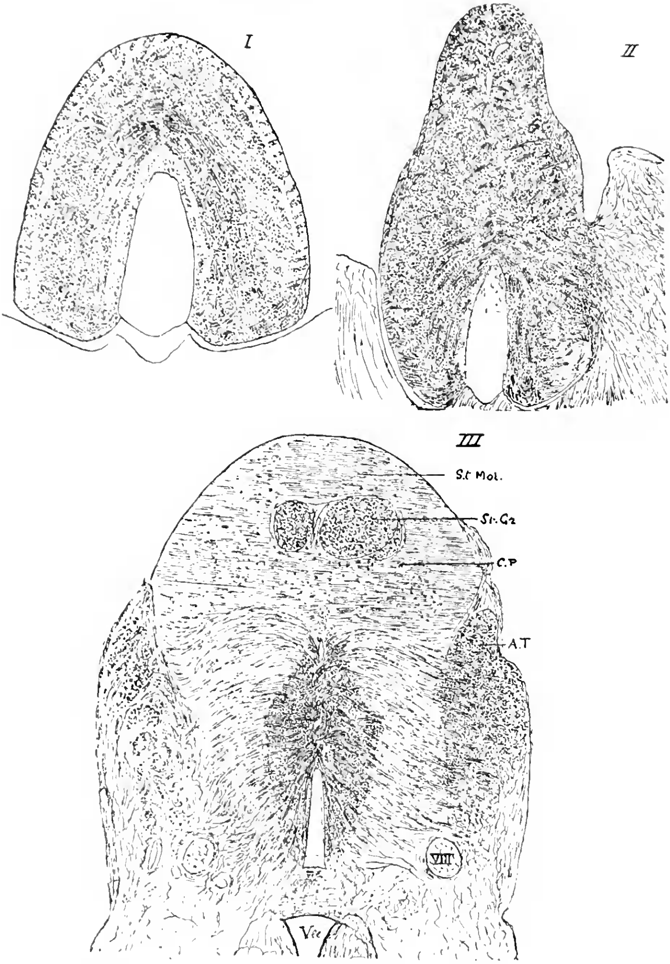


Fig. vi.
Section of Brain of Herring.
V.—Lobe (somatic-sensory lobe). F.N.—Facial nerve. F.L.—Facial lobe.

Further forward the commencement of the cerebellum is seen lying dorsal to this central lobe, and at the lateral margins the acoustic tubercles commence to make their appearance; nerve fibres are seen passing from these transversely towards the central lobe. The eighth or auditory nerve is seen entering laterally and forming a distinct bundle of fibres which approaches the central

PLATE 10.—Herring.



Three drawings of the acoustic lobe of Herring. Fig. I.—Commencement of lobe resting on the anterior end of somatic-sensory lobe. Fig. II.—A little anterior to Fig. I, the lobe is now partly surrounded by the crura cerebelli. Fig. III.—Shows the commencement of the cerebellum with the stratum granulosum surrounded by cells of Purkinje lying in the middle of st. moleculare. The acoustic tubercles are prominent and fibres pass inwards to the central acoustic lobe. The eighth nerves are also seen.

St. Mol.—Stratum Moleculare. St. Gr.—Stratum granulosum. C. P.—Cells of Purkinje. A. T.—Acoustic Tubercle.

lobe while rather more anteriorly the large lateral-line nerve enters the acoustic tubercle. It is thus apparent that this lobe is part of the acoustico-lateralis system. The small facial lobes (Fig. 17) can be recognised by tracing the facial nerves which pass on either side into a small area, triangular in section, which abuts the ventricle. From these areas descending fibres pass outwards into the great longitudinal gustatory tracts ; the course of these fibres and that of the facial nerves prove that these triangular areas are the facial lobes ; these lobes do not appear on the surface. This detailed description is given, as the central lobe has been mistaken for a facial lobe.

Certain interesting facts concerning the lateral-line organs must now be mentioned. The herring has no lateral-line. There are lateral-line organs on the head, and, as we have seen, one of these makes a deep bay in the temporal region and appears to form an accessory part of the auditory organ. This being the case it is clear that the large central lobe cannot be explained by an increased functional importance of the lateral-line system. But as the herring is a surface feeding animal and has an elaborate auditory mechanism the most reasonable conclusion to be drawn is that this central lobe has an acoustic function and should be termed the central acoustic lobe.

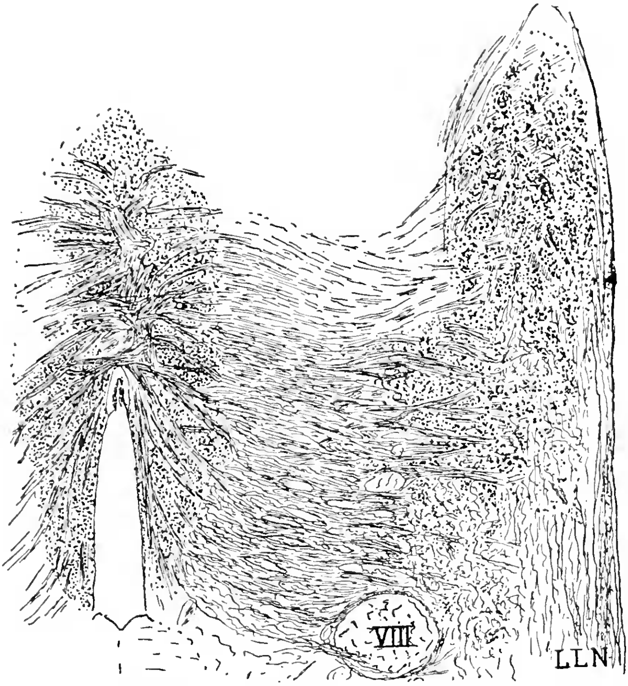
The conclusion to be drawn from the above facts is that the brain of the herring is characterised by large optic lobes, a large central acoustic lobe, and a small facial lobe, not apparent by naked eye observation. This type is also found with slight modifications in the sprat and pilchard and as the latter has a central acoustic lobe very similar to that of the bleak it may be assumed that it is characteristic of plankton feeders, as far as our present knowledge allows this generalisation.

If this pattern is compared with a typical ground feeder, such as the loach, a near relative to the Cyprinoids, it will be at once evident how marked is the difference. The facial lobe is very large, with a lobulated surface, and overlaps the vagal lobes. The facial nerves, also very large, divide at the inferior surface of the lobe into an anterior branch which splits into two bundles, one passing centrally and the other laterally to the dorsal area of the lobe. The posterior branch on either side passes backwards close to the ventricle and enters a large posterior lobe. Large descending fibres from the lobe pass into the middle division of the great longitudinal secondary gustatory tracts. The central group of cells described in the bleak and herring at the base of the cerebellum does not appear, but a few cells forming a narrow band across from one side to the other and become slightly more prominent at the outer margin.

The acoustic tubercles are well developed. The optic lobes are apparently large, but this is due to the tecta optica being widely separated by a large valvula, just as in the barbel. In this fish the pursuit of food is obviously mostly by taste, touch, and smell.

What conclusions can be drawn from the study of the herring's brain of the functions of the central acoustic lobe? This problem can be attacked by the method of elimination. The positive facts point to the conclusion that sight is an important fact, as witness the large optic lobes, and that taste and the gustatory organs can take but little part, as shown by the insignificance of the facial lobe.

PLATE 11.—Herring.



Base of cerebellum (high power) showing desussating fibres and round-celled tissue of central acoustic lobe. One acoustic tubercle with lateral line nerve and fibres connecting the lateral and central lobes. The eighth nerve is seen and fibres to it from the central acoustic lobe.

It would be contrary to the general rule that appears in our study of the carp family, if there was not some functional significance in the presence of the large central lobe we have described. The herring, in the first place, possesses a very elaborate organ of hearing which communicates with the swim-bladder. It has an anterior and posterior spherical vesicle, and we have shown that the posterior vesicle has certain anatomical connections with a large lateral line organ near the pterotic bone, which enables vibrations to be received by the air in this vesicle, and these are conducted to the air in the anterior vesicle. This vesicle is divided into two sections by a transverse membrane which receives the vibrations and communicates them to the perilymph occupying the other section, from whence they pass by a foramen into a space connected with the saccule, and pass over a special endorgan which has a direct connection with the medulla by a nerve ganglion. It seems probable that this elaborate organ must have a special representation in the medulla. It is highly improbable that the central lobe can be due to any increased functional activity of the lateral line system, because the herring is peculiar in that it possesses no lateral line. A possible explanation of the large central area might be that it is for the control of the swim-bladder, but this view is shown to be untenable when we examine the functions of this organ in other families as will be described later. The evidence so far seems conclusive that the central area has an auditory function, and we propose to call it the central acoustic lobe or area according to the extent of development into a definite lobe or not.

The hind-brain of a sprat has a similar pattern to that of the herring. The central acoustic lobe appears as a large area, pear-shaped in section, and fibres pass outwards to the acoustic tubercles and also a definite strand of fibres leads to the lobe as described in the herring.

The examination of the hind brain of the pilchard provides a sort of connecting link which binds the central acoustic lobe of a Cyprinoid with the Clupeoid. It is hardly to be distinguished as regards this lobe from the bleak, but the relative size is larger ; a further point is the large size of the acoustic tubercles which coalesce very early after their appearance with the lateral margins of the granular area of the cerebellum. The special tract noted in connection with the central lobe in the herring and sprat is not easy to distinguish.

It will be interesting now to review all the above facts which associate the surface-feeding carps with the herring family. The general appearance of the former has given rise to certain names which show that early observers had been struck by the similarity of certain members of the two families as regards their form ; for example Engraulicypris can be translated into the English language as the anchovy carp, and Isaac Walton gives as an alternative name for the bleak, the fresh-water sprat. We have described the small easily detached scales and the abdominal keel as being present in these fish and that the eyes are large. It is very instructive to be able to point out the similarity in the brain pattern in the fourth group of carps and the Clupeoids.

We have described the large central acoustic lobe or area and its association with a small type of facial lobe which in both families does not appear on external observation. The optic lobes are also well developed. The vagal lobes are also feebly developed. We have here a striking example of the correspondence of general form and habits of feeding with the pattern of the brain. Another point also seems to be worth mentioning, namely, that the relative size of the central acoustic area varies inversely with the relative size of the facial lobes. In a later chapter we shall be able to show that the central acoustic lobe appears to be well developed in other families of fish in which the faculty of hearing is of considerable importance in their life history.

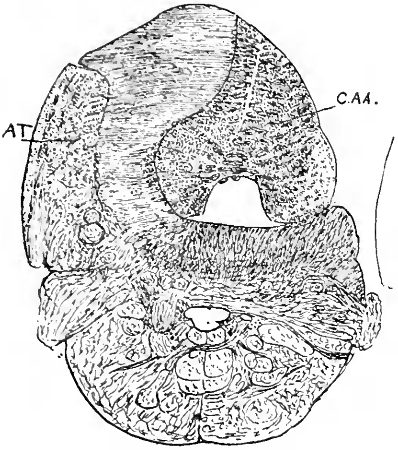


FIG. viiA.

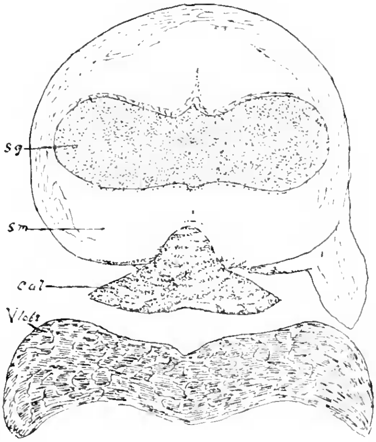


FIG. viiB.

FIG. viiA.—The central acoustic lobe of the sprat. It has been cut rather obliquely. This lobe occupies a large area of the cerebellum. The acoustic tubercles are prominent and the lateral line nerve is seen externally passing into it. The eighth nerve is also seen.

FIG. viiB.—Transverse section of cerebellum of Pilchard to shew central acoustic lobe, c.e.l. s.g. and s.m.—Strata granulosa and moleculare of cerebellum. V lobe.—Somatic sensory lobe.

If the dominant fresh-water fishes of the British Isles had been the Mormyridæ instead of the carps, the attitude of the scientist and of the fishermen towards the question of hearing in fish would not have been so sceptical, and we should have heard fewer dogmatic denials of its existence. The explanation of this statement is that this family possesses such an obvious ear and auditory apparatus that there could be no doubt of its acoustic function. Bearing this in mind, when the icthyologist came to examine the ear of a cyprinoid, he would have at once recognised that the Weberian ossicles were an integral part of an organ of hearing, connecting the swim-bladder with the internal ear; the whole subject of hearing in fishes would not have remained in such confusion as it has until recent times; and we would not have had to wait for a correct solution of the problem until the beginning of the twentieth century. But this family has many other claims to attention from the naturalist, and historically we read how it was venerated by the Egyptians; and the Mormyrs of the Nile are said to have been frequently represented on mural paintings and hieroglyphics. The reason for this distinction is the quaint and unusual features of the animal.

A prominent nose always seems to attract attention, and Mormyrus has been provided with a snout that even an elephant might envy. The front of the head in most of the species is prolonged and tends to curve downwards, while in some it is prolonged into a regular trunk, and the lower lip in some is continued into a fleshy appendage, no doubt of use in searching for food. In most, the mouth is small and the teeth are small and few. The eyes are small and may be covered over by a skin. Whether the mouth and lips are provided with taste-buds is not stated. The shape of the trunk varies from that of a torpedo to that of an eel; and in this connection it is interesting to note that its near relation, the Albula, has a larval form, through which the young pass, analogous to that of the eels. The most eel-like of the Mormyrids is Gymnarchus, which propels itself entirely by means of its dorsal fin, and moves with equal ease either forwards or backwards, nosing its way backwards by using the tip of its tail as a feeler. This fish also makes a floating nest which is jealously guarded by the male.

To add to this tale of eccentricities, the fish is provided with an electric organ situate in the caudal region and derived from the muscular system. There is a strange analogy between Gymnarchus and Gymnotus electrophorus; both fish are specially adapted so as to be eel-like in form, and in both the auditory organ is specialised; in both there is an electric organ caudally situated and derived from the muscular system; but the communication of the swim-bladder with the ear remains throughout life in Gymnotus, though indirectly through the pneumatic bulb, but becomes vestigial in Gymnarchus.

The conformation of the brain in the Mormyrids has been, and still remains, a wonder to the naturalist, and a puzzle to the biologist and neurologist, so that the literature on the subject is large and diffuse; according to the Cambridge Natural History, the brain is so large as to attain a weight which equals one-fifty-second to one-eighty second of the total weight of the fish, and this great increase of size is due almost entirely to the hypertrophy of what is known as the "valvula cerebelli."

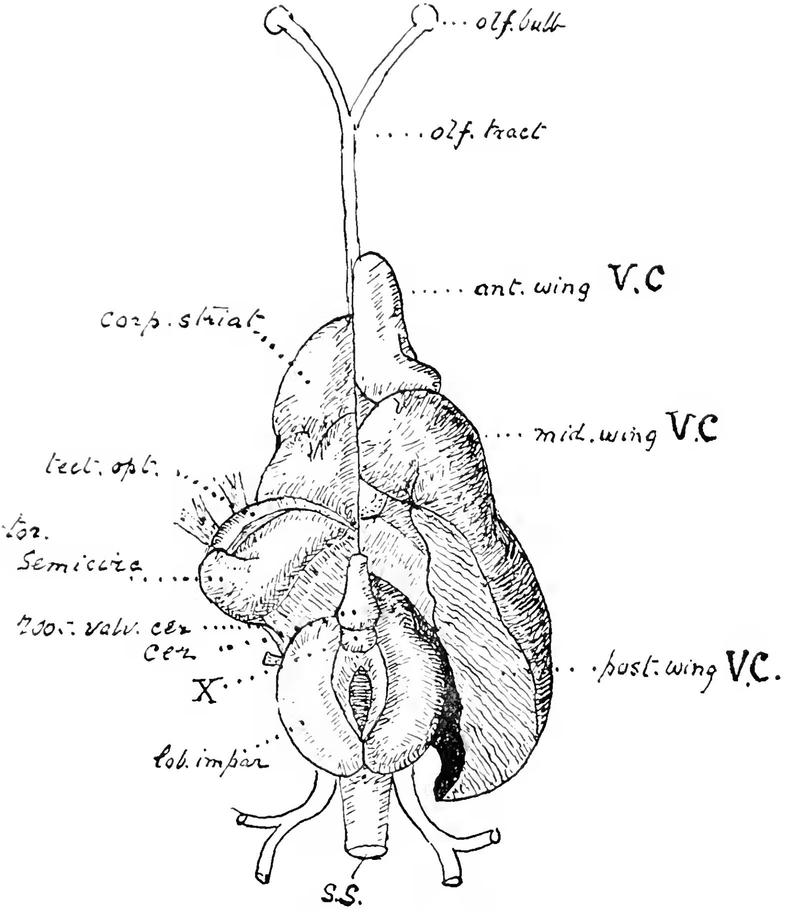


Fig. viii.—Brain of Mormyrus kannume after Burne.
V.C.—Valvula cerebelli. lob.impar. = lob. acustico-lateralis.

We have drawn attention already to this unfortunate terminology "*valvula*." It is a valve only in the sense that it separates the two halves of the tecta optica, and it does so particularly in those fish that grub in the mud and search between stones, such as the barbel and gudgeon among the Cyprinoids. The valvula is thus a forward tongue starting from the anterior aspect of the base of the cerebellum. It is this that has burgeoned forth, one might almost say, bubbled over so as to make a thick cap that covers the whole brain just as the cerebral hemispheres do in the human brain.

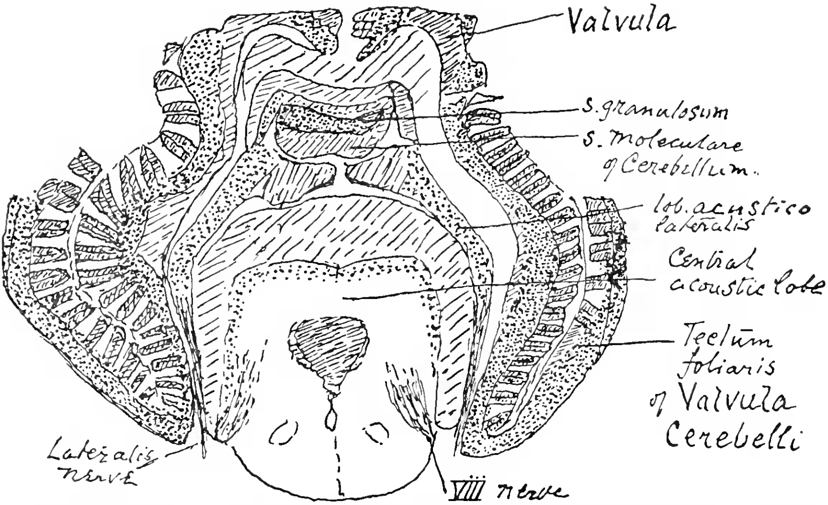
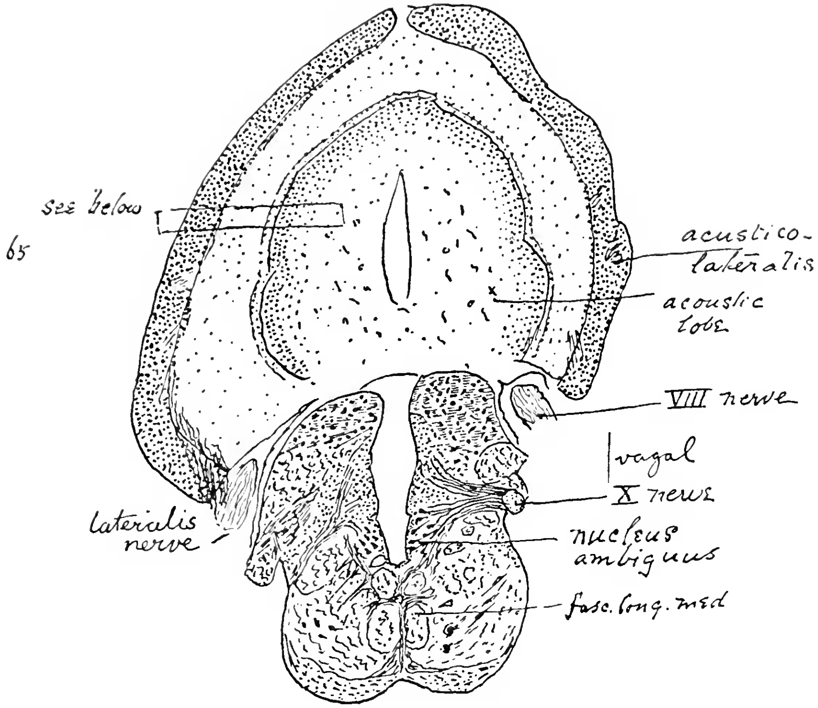
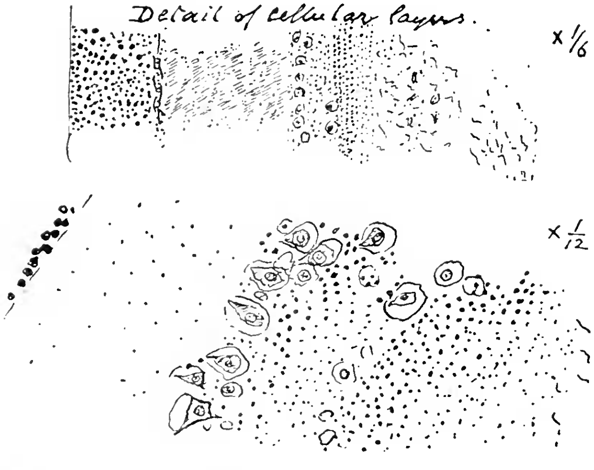


Fig. ix.—Section of brain of Mormyrus.—Semi-diagrammatic to show cerebellum acoustic and lateralis lobes enveloped by valvula cerebelli.

To make this description clear we reproduce a sketch (Fig. viii), redrawn from R. H. Burne; this has been also figured by Herrick, who does not agree with the identification of the two ovoid masses that form the medulla as the "lobus impar" as shown in Burne's lettering. I have had the opportunity through the kindness of Dr. Tate Regan, and more recently Dr. Norman, of examining three species of Mormyridæ, and have examined them both by the naked eye and by serial sections. After making a number of serial drawings and studying the literature of the microscopic structure of the medulla and cerbellum, I have become convinced that the so-called lobus impar consists of a central acoustic area and the acustico lateral lobe. I shall show two drawings of my sections across these lobes, and it will be seen that the eighth nerve passes to the central acoustic lobe and that more anteriorly the lateralis nerve enters the

PLATE 12.





Medulla oblongata of Mormyrus and acoustic lobe seen in transverse section. The oblong area outlined in the upper of the three drawings is shown enlarged under higher powers in the lower drawings.

granular layer of the acustico-lateralis lobe ; this section also shows the cerebellum lying more dorsally and the stratum granulosum joining the above-mentioned granular area. The details of the facial lobe are not very clear in my sections but the motor nucleus of the vagal is well marked. The section also shows the leaf-like structure of the calvula which seems to be almost unique in the neurological world and one is left in wonder at the artistic beauty of the design and the inner hidden meaning of its elaborate architecture.

From the point of view of my argument, we have here a clear relation of the very definite auditory organ with a central acoustic lobe ; as regards the functional significance of the valvula one can only throw out the suggestion that this is a central correlation organ associated with the acoustic, lateralis and olfactory lobes, which appear to be the most important sense organs in the hunting equipment of this fish.

As regards the feeding of Mormyrus there is very little said by the various authorities. But Mr. Michael Graham tells me that Mormyrus kannume on Lake Victoria apparently feeds entirely on insect larvæ of 45/45 stomachs containing any food, thirty-three contained blood-worms and there was one record oligochaete ; and one caddis. Its habitat surprisingly included rock and stony bottoms. It is interesting to note that Worthington's observations in Lake Albert and Kioga and elsewhere are similar to those of Graham.

CHAPTER VIII

THE SILENCE OF THE SEA AND THE VOICE OF FISHES

In the preceding pages a number of references to hearing have been made and the auditory organs of fish have been described. It may well be asked what are the sounds to be heard in the sea, and also in rivers and inland waters.

Although sounds are badly conducted from air to water, yet sound is well conducted in water. During the Great War the localisation of sounds produced by submarines was of outstanding importance to our Navy, and a committee was set up to enquire into the matter. I have heard it whispered that the scientists, which included physicists and biologists, did not see eye to eye, or rather ear to ear, in all the discussions that took place ; nevertheless, the hydrophone was invented, and the experiments in the detection of sounds in water were very successful and provided valuable aid to the Admiralty in their efforts to combat the submarine menace.

It is difficult for man, not being an aquatic animal, to project his mind into the brain of a fish, nevertheless, by means of the physiological methods, known as "conditioned reflexes," initiated by Pavlov and applied by Bull to experiments on hearing in fish, the subject has been put on a scientific basis. The ordinary man can readily prove for himself how well sounds are conducted in water by immersing himself in a bath and listening to the ticking of a clock or an electric buzzer placed under the water.

To those who are unfamiliar with the subject, from the point of view of a physicist, the simplest method of obtaining an outline of the subject is to read the Christmas lectures, given at the Royal Institution by Sir William Bragg, on the "World of Sound."

Carlyle in another connection made use of the phrase "the deep sea of Nescience," and it is a fact that the depths of the sea are very silent. In the deep sea there is very little movement of water, near the shore there is the flow of the tides, and where waves break there is noise because of the churning of the water into foam.

The movements of fish are noiseless and even when sea-birds dive and dart about under water no sound is audible, as experiments have proved. Noise is made when for some reason or other bubbles are formed, and when an animal dives into the water after its prey, it leaves no air cavity to make a noise. However, when a body moves so quickly through the water that it does leave a cavity behind it, the water rushes into the vacuum with all the suddenness of an explosion and is the cause of the noise made by moving steamers. This effect, called cavitation, is well known to naval engineers, as it has often a destructive effect on ships' propellers.

A fish moves with little fuss and very fast because it leaves no whirls behind it. This is simply due to its lines, as a naval architect would express it. There is a fisherman's saying that a cod's head and mackerel tail make for speed. The writer was the happy possessor of a small yacht designed on these principles, and it is a constant source of surprise to his guests, how quietly she sails with no wave or fuss with a fresh beam wind. The design of a modern air liner which recently appeared in the press, recalled the form of a gurnard, even to the downward slope of the prow-like head, and showed that the body had been designed for the least air resistance.

A fish has, therefore, the right shape for moving through the water without noise and without unnecessary effort. Sir William Bragg concludes, " that as animals that move under water can do so with such little noise, it is to be expected that they cannot or do not listen for sounds." However, there is other evidence that can be brought forward that suggests that this conclusion is open to adverse criticism. Dr. Beatty, of the Department of Scientific Research and Experiment under the Admiralty, also writes on the silence of the sea. He says, " the noises that at rare intervals float upwards from the hydrophone are of a somewhat bizarre character ; in the vicinity of an oyster-bed, a continuous rattle is heard from the closing shells ; whales produce, by some mechanism as yet unknown, a noise like the tinkling of a spoon on a plate ; and there is the phenomenon of the drumming fishes. In the surface layers there are the splashes due to leaping fish ; there is the roar of " breakers " and the " brabble " of the beach along the coast, and at river mouths, and the swirl and rip of off-shore conflicting currents.

Some degree of hearing power for such sounds may be advantageous. When herrings swim, that is, come to the surface, they discharge bubbles from their swim-bladder and these bubbles bursting must produce some sound and it is significant that herrings have an accessory organ of hearing. The question of drumming must now be discussed fully, and we will deal in the first place with the Maigre " Sciaena aquila," an inhabitant of the Mediterranean Sea. This fish is well known to possess a voice, the production of which, by a special mechanism, is well established. The drumming sound is supposed to have given rise to the Greek legend of the the song of the Sirens, which beguiled Ulysses. The voice is the voice of a troubador, so is heard mainly in the breeding season. In this family there is a special sound-producing muscle, which is not directly attached to the swim-bladder, but leads to a tendon that lies above this organ. The muscle contracts in a series of vibrations 24 per second, and these cause the air-bladder to vibrate ; when the bladder is removed or deflated the sound ceases, but it can be produced again if an artificial bladder of indiarubber is introduced. The sound is described as of a continuous booming character. All Sciaenidæ do not drum, but it has been found that the otoliths or earstones in the saccule of the ear are larger in the drummers than those that are dumb, so that a relation exists between voice and hearing in this family.

Dr. Beatty also describes the grunt fishes, which include the sea-robin (Prionotus) and the toadfish (Opsanus). "Here the operating muscles are intrinsically connected with the air-bladder, so that the bladder can be removed and caused to grunt by electric stimulation of the muscles. These fishes have been a source of considerable inconvenience to hydrographers engaged in charting the floor of the Atlantic by the method of echo depth sounding."

Coming to home waters we find that the familiar family of Gurnards are known to utter obscure grunting sounds, when taken out of the sea, and that they continue them at intervals as long as they are alive. The common English name gurnard is derived from O.F. "gornart" akin to the French "grogner," to grunt. Several popular names of members of the family doubtless refer to the sounds produced : the piper (Trygla lyra) and the grey gurnard or crooner are examples. To croon means, in Scotland, to make a dull croaking sound. According to Couch, "the grey gurnards, commonly keep together in companies, and in fine weather assemble in large numbers and mount to the surface over the deep water and, when thus aloft, they move along at a slow pace, rising and sinking in the water for short distances, and uttering a short grunt as if in self-gratification."

The personal experience of the writer of the article on sound production is described in the work, "Reptiles, Amphibians and Fishes." edited by Cunningham : "the sapphirine gurnard (Trigla hirundo) emits distinct sounds which may be described as a succession of short grunts. The sounds are produced in the air-bladder, which is divided by a transverse diaphragm perforated by a hole in the centre." The diaphragm contains radiating and circular muscle fibres and the bladder has thick strong external muscles supplied by two large nerves from the anterior part of the spinal cord.

According to Moreau, the diaphragm is thrown into vibrations by air being forced from one compartment to the other. In these fishes, it has been shown that the sound is produced by intrinsic muscles in the wall of the air-bladder, and a grunt is caused by a single contraction of these muscles : it can be called forth by electric stimulation even in a bladder which has been removed from the fish. The sound was not produced when the bladder was empty, but returned when a rubber bladder was put inside the natural one ; this proves that a diaphragm is not essential for the production of the grunt. The grey gurnard is a fish of considerable interest apart from its grunting, there is the strange development of its pectoral fin rays into fingers, and the pearl-like enlargements of its spinal cord, associated with this special adaptation. The maigre shows by its large otoliths the connection of voice with hearing. It is found, when the brain of the grey gurnard is examined, that it has a highly developed central acoustic lobe very similar to that found in the pilchard. This can apparently be associated with hearing, as most fish with closed swim-bladders and a bottom-feeding habitat do not show a central acoustic lobe, but only a rudimentary acoustic area.

It will have been noticed, that in the two families, the Sciaenidæ and Triglidæ, the production of sound is dependent on the air-bladder, and that the vibrations originate in connection with a gaseous medium, and are produced by the organ which is homologous with the lung, by which the voice of terresterial vertebrates is produced. There are other methods of sound production in aquatic animals, as example, the stridulating organs of members of the Siluroid family, as seen in certain Indian species. The writer of the above-mentioned article, to whom we are indebted for many of our facts, describes the production of sound by a trigger-fish " Balistes," which is abundant round the Island of Ascension. He observed " behind the pectoral fin an area of skin, resembling a drum, a portion of the air-bladder lying just beneath it. When the drumming sound was produced the pectoral fin was moved rapidly to and fro and the membrane could be seen to vibrate. No sound was produced when the fin was held stationary."

Hitherto, we have mentioned mostly dwellers in the sea that produce sounds, but we must not forget to mention that the air-bladder functions as a sound producing organ in many fresh-water fishes. The blind fish of the Mammoth Cave of Kentucky calls to its fellows by sounds, and the blind fish (Lucifuga) that lives in the subterranean waters of Cuba, communicates with its companions in the same way. Doras and several other South American cat-fishes have a special adaptation for the production of sound, known as the elastic spring mechanism by which the wall of the swim-bladder is made to vibrate. Muscles pass from the skull to the springs which are attached to the bladder and the contraction of these muscles causes the springs and the walls of the bladder to vibrate and to produce sound. There are other sounds of a very different nature produced by certain fresh-water fishes. These are the breathing sounds or " bruits de souffle," as described by Dufosse, and are said to occur in the eels, the carp, several species of loach, and the European cat-fish Silurus glanis.

According to Dufosse, quoted in the Cambridge Natural History, " these sounds originate in some cases from the expulsion of gas from the air-bladder through the pneumatic duct and mouth, and in others as in the loach Misgurnus fossilis, they are produced by the rapid expulsion through the anus of bubbles of air previously taken in at the mouth.

In conclusion, we must add that it is believed that both the cod and the haddock produce sounds through the medium of the swim-bladder. This is certainly true of the rock-haddock as we shall see later. The above examples of noises made by fishes clearly prove that the silence of the sea is not complete, and also give good grounds for attributing a sense of hearing to many fish hitherto considered to be deaf. But there is other evidence pointing to the susceptibility of fishes to noises, but the conditions in this case are artificial. We allude to certain methods adopted by fishermen designed to drive the fish into their nets; the first example to be given is a method, not well known, of catching herring. It has been described to the writer by one of the most experienced and observant of the skippers of steam-drifters fishing out of Lowestoft.

Observations on the reaction of the herring to loud noises prove that the immediate response is to dive. The Whitby and Scarborough fishermen employ a purely local method of fishing called " beating for herrings." In August the fish are found some ten miles from the shore in thirteen fathoms of water; late in the evening the fishermen put out to sea and, keeping a close watch, they wait till they see the surface of the water alter in colour and character as the mass of herring gradually " swim " or rise to the surface. They at once steam or row into the midst of this area, and shoot their nets; as they so do every bucket, tin can, or shovel available, is used to make a din by beating against the sides of the vessel, accompanied by shouts and yells.

It would appear that the vibrations of the screw and the disturbance produced by the oars is not sufficient to frighten the fish, but the noise produced by " beating " is so alarming that the fish dive to the bottom and are then enmeshed in the nets, which extend some seven fathoms down below the three fathom level, at which the net commences ; the reaction of the fish to loud noises is to make them dive ; if they did not dive they would swim safely above the net. Nature does not visualise that the danger is below, and in swimming from the noise they become entrapped in a danger in the depths. Another Clupeoid, the pilchard, is readily alarmed by noises ; and the firing of a heavy gun at a distance of twenty miles has, according to Couch, been known to cause the fish to sink.

Another example of noise being used in fishing is in the method of seining for grey mullet that has been practised in Chichester harbour from time immemorial ; this fish is very difficult to catch with a net ; when surrounded by the net, they endeavour to leap the cork line, to obtain their freedom. The fishermen, to prevent the fish leaping, beat the water frantically with an oar ; others wade waist deep making the welkin ring with shouts and oaths ; here again the fish fail to reach safety and dive to destruction.

This method of fishing for mullet is not confined to the fishermen of our south coasts. We have been told by one of the naturalists of the Ministry of Agriculture and Fishery, R. S. Winpenny, of the fishing for mullet in Egypt in which similar methods are employed

As a result of the above observations an examination of the brain of the grey mullet was undertaken and the size and structure of the acoustic tubercles and central acoustic area examined. Here is a fish which has well defined reactions to noises, and it was to be expected that this area of the brain would show some specialisation in connection with the function of audition. It was, therefore, not surprising to find that this fish has a very well-developed central acoustic lobe.

CHAPTER IX

FLAT-FISHES

The size and abundance of flat-fishes and the flavour of their flesh makes this family very familiar and useful to man. Flat-fishes are so-called from their strongly compressed, high and flat body. They are unable to maintain their body in a vertical position and rest and swim on one side of the body only. The side turned towards the bottom is sometimes the left and sometimes the right, colourless and termed the "blind" side; that turned towards the light is pigmented and frequently has adaptive patterns. Both eyes are on the coloured side, and this is the most marked sign of the asymmetry of this family. In the larval stage these fish appear to be symmetrical and the change in the position of the eyes has always aroused great interest and also the expression of conflicting views.

In pursuit of our study of the relation of hunting and feeding habits to the form and pattern of the brain, it would appear probable that this asymmetry would seriously interfere with the study; however, the only parts of the brain that show any distortion are the olfactory lobes and, of course, the optic nerves. The optic lobes, the cerebellum, and the medulla oblongata are practically symmetrical. It will be of interest to enquire how this has happened, and to study the history of the migrating eye. According to Norman in his recently published monograph on Heterosomata, "in the early stages of the development of the larva, before the bones of the skull have become ossified, there is a supraorbital bar, as it is called, which lies in the way of the migrating eye; this disappears or is absorbed and the eye passes through the gap, until it reaches the supraorbital bar of the other side. This bar of the ocular side becomes twisted over towards that side of the head by the movement of the two eyes into their final position. The supraorbital of the ocular side is finally absorbed, and as soon as the shifting of the eyes has been completed the frontal bones appear."

There is a genus of flat-fishes known as Psettodes which has retained a more symmetrical form and in which the eyes are as often found on the right side as on the left side. It is said to swim, not infrequently, in a vertical position, and there are good reasons for regarding this fish as the least specialised member of the flat-fishes (Heterosomata), and to have Percoid affinities. The usual explanation of the origin of flat-fish is that at some time in the distant past their ancestors acquired the habit of resting on their side on the bottom, and even sleeping in that position. It has been observed that Wrasses still have that habit. The view is held that some particularly lazy or drowsy fish adopted this attitude as a pleasant way of passing the time, and incidentally discovered that by lying on the bottom it was less molested by enemies. But the chief effect that resulted, was that either the sand was apt to get into the bottom eye, or that a permanent squint developed.

However, the process of adaptation caused the bottom eye to migrate to a dorsal position by passing through the front of the head in the manner we have described above ; another effect of this recumbent position was the loss of pigment on the bottom side, which is apparently due to the absence of light, as young flounders kept in a tank with a glass bottom on which light was projected, in the course of time, have been found to form pigment on the white side. Flat-fishes have a remarkable power of making the skin pattern on their dorsal side conform to their surroundings and as vision was necessary to review the background against which they lay, a further adaptation occurred. A sac-like protusion of the membranous wall of the orbit developed, which like the cavity of the orbit is filled with fluid. This enables the eye to be protruded above the surface of the head to a great extent, and allows free movement. It is significant that this protrusion is very marked in the plaice, a fish richly endowed with pigment cells, some of a brilliant colour, and that the optic lobes are remarkably well-developed and almost bi-lobed in shape.

Flat-fishes or Heterosomata have recently been the subject of a valuable monograph by Norman. In it he discusses the different views as to the origin of flat-fishes, whether they have been derived from a single stock of either the cod type, dory type, or perch type, or from a number of stocks. Norman regards the theory that they have arisen from a generalised percoid stock as the most probable. He considers Psettodes to be the least specialised member of the order, and that the soles and Cynoglossidæ may have arisen from another part of the percoid stem. After studying this monograph, the last volume of the Journal of the Marine Biological Association reached my hands, and it was with some interest that in an article by Ford on the vertebrae of Teleostean fishes, the similarity of the backbone of Psettodes with that of the generalised percoid type was pointed out.

The following table shows the position of the fishes according to the latest classification :

Family	*Sub-family*	*Species*
1. *Pleuronectidæ*	*Pleuronectinæ*	*Hippoglossus.* Halibut.
		Pleuronectes limanda. Dab.
		,, *Platessa.* Plaice.
		,, *Microcephalus.* Lemon sole.
		,, *Cynoglossus.* Witch.
		,, *Flesus.* Flounder.
2. *Bothidæ*	*Scophthalminæ*	*Rhombus maximus.* Turbot.
		,, *laevis.* Brill.
		Lepidorhombus whiffiagonis. Megrim.
3. *Soleidæ*		*Solea solea.* Sole.

We now propose to study the brain pattern of the Heterosomata and we shall find that the members of this family fall into groups, which, it is interesting to note, closely correspond with the four main groups of British flat-fish, as described by Cunningham. We shall take these groups in the following order :

Group I.—Species with eyes on the right side. Teeth only on the blind side. A " beard " on the lower side of head. Example, the sole, *Solea vulgaris.*

Group II.—Species with the eyes on the right side. Teeth most developed on blind side. Examples, the plaice, the lemon sole, the witch, the dab and the flounder.

Group III.—Species with eyes on the right side. Mouth large. Jaws similar on two sides. Example, the halibut.

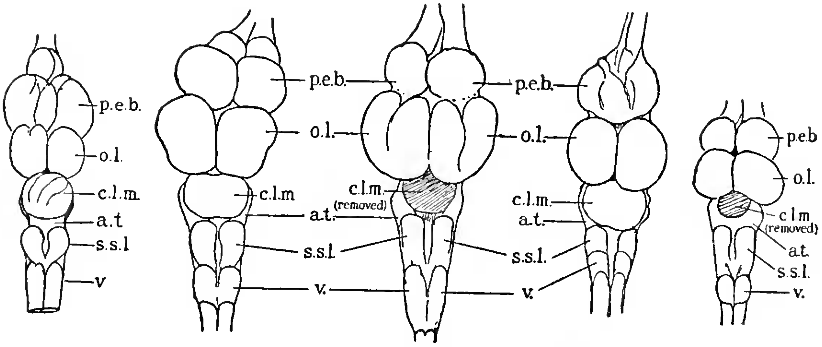
Group IV.—Species with the eyes on the left side. Teeth and jaws equal on both sides. Examples, the turbot, brill and megrim.

The examples mentioned are those fish which we have had the opportunity of examining both in the fresh state and by the study of serial sections. The asymmetry of the head, the upward aspect of the eyes and the crossing of the optic nerves have been fully discussed by many authorities : but, as for practical purposes, those parts of the brain, which concern us, are nearly symmetrical, we do not propose to make any further reference to these characteristic features.

THE SOLE

In Plate 13 is an outline drawing of the brain of the sole seen from above. The olfactory lobes are large and show some asymmetry, the left overlapping the right ; the primitive end-brain is very large and considerably larger than the optic lobes which are definitely small. The somatic-sensory lobes are large, and viewed from above their outline has the appearance of two clubs with the narrower ends tapering posteriorly and meeting in the middle line. The cerebellum is of moderate size. Posterior to the somatic-sensory lobes the vagal lobes are seen to be narrow and elongated. There is no sign of a facial lobe, although it does exist, but is very small and completely hidden by other structures.

PLATE 13.

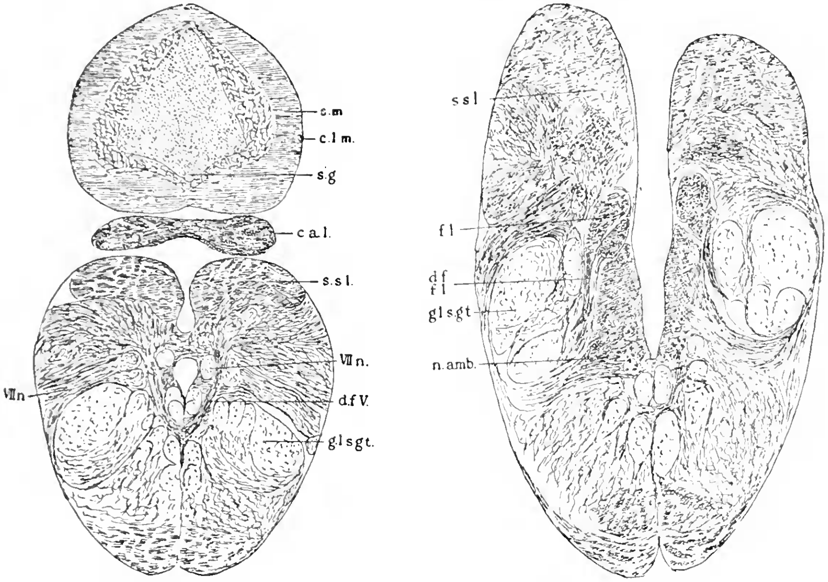


Sole. Lemon-dab. Plaice. Witch. Dab.

p.e.b.—Primitive end-brain. o.l.—Optic lobes. c.l.m.—Cerebellum. a.t.—Acoustic tubercles. s.s.l.—somatic-sensory lobes. v.—Vagal lobes.

When serial sections of the brain of a sole are examined it is found that certain conclusions as to the significance of the lobes, as would appear to be justified by naked-eye examination are not confirmed. The medulla has been described as very long, and having a pair of very prominent lobes (facial) upon its dorsal surface. These are not facial lobes. Anterior to the vagal lobes, which are narrow and not prominent, the facial lobes appear as small rounded areas resting on the dorsal extremity of the vagals ; more anteriorly fibres are seen passing ventrally and outwards from the facial lobes into the gustatory tracts in the typical manner ; these lobes are limited in extent both laterally and in an antero-posterior direction. The facial nerves are small and do not enter the medulla until the tip of the cerebellum appears in section, when they pass tranversely towards the middle line, and turning caudally run parallel to the ventricle before entering the facial lobe, the identity of which is thus established. The somatic-sensory lobes completely envelop the facials and are readily recognised by their histological structure ; they extend far in a cephalic direction and increase in size so as to form two prominent bulges which appear in the naked eye view.

PLATE 14.—Two Sections of Brain of Sole.



VII.—Facial nerve. c.l.m.—Cerebellum. c.a.l.—Central acoustic lobe. s.s.l.—Somatic-sensory lobe. f.l.—Facial lobe. n.amb.—Nucleus ambiguus. g.l.s.g.t.—Great longitudinal secondary gustatory tracts. d.f.f.l.—Descending fibres of facial lobe.

The acoustic tubercles are large. At the base of the cerebellum and at first separate from it is a broad band of tissue roofing the ventricle on the inferior margin of which are to be seen groups of round cells with tranversely running fibres dividing them ; this is similar to the areas which have been described in the cyprinoid brain and which we have associated with an auditory function. This central acoustic lobe has been seen in the herring and mormyrus, both of which have an elaborate auditory organ ; it is well-marked in surface feeding cyprinoids, but is rudimentary in bottom feeding species. How are we to account for its presence in such a typical bottom-feeder as the sole which, moreover, has no sound producing organ.

We must now mention the existence of a special organ, the well-known papillary area on the lower or left side of the head, an area covered with a number of villi. Bateson has stated that " contrary to expectation these villi do not bear sense organs of the nature of taste-buds," and my own observations confirm this conclusion, although it has been denied by Cunningham ; but it accords with the evidence given above, that the facial lobes are minute. The presence of these villi explain the large size of the somatic-sensory lobes which receive the tactile sensations from these sensory filaments.

" When searching for food the presence of which it recognises by smell, the sole glides gently about over the sand, tapping with the lower side of the head, in order to bring this sensory area in play. The sole is one of the flat-fishes most addicted to burying themselves in the sand or mud, leaving only the eyes exposed."

It is commonly held by fishermen in the North Sea that soles not only cover themselves when light is directed upon them but bury themselves during periods of intense cold. Russell states that they take no notice of a worm dangled above them : but Bateson observed " that they perceive objects approaching them, for they will bury themselves if a stroke is made with a landing net," but this might also be explained by vibrations produced by the rapid motion of the net. But soles, eels, and rocklings have a clear appreciation of light and darkness, always being buried during the day and swimming about in their tank at night.

The olfactory system is highly developed in the sole, as will be described later, and the eyes of the sole are small. Not only are the eyes of the sole small but their optic lobes are small in marked contrast with the large optic lobes of the plaice. When we review the above facts it seems possible to formulate a probable theory of the significance of the central acoustic area in the sole. As a general rule a central acoustic area is well-marked when the facial lobe is small and vice versa, and there is a large amount of evidence available in support of the view that it is associated with an auditory function. How can we explain its presence in the sole ? We suggest that an auditory centre would be of value to the sole, and at least it is a reasonable assumption that this centre is associated with the perception of vibrations.

The tapping of the sand so characteristic of the sole's method of hunting, reminds one of the thrush feeding on our lawns, tapping and listening for the hidden worm. Sea-birds, such as certain gulls and the sheldrake, tap for worms, in the same way, on our shores and in estuaries.

If this conclusion is accepted it would appear that the sole feeds by smell, touch, and hearing, represented centrally in olfactory, somatic-sensory, and central acoustic lobes, all of which are remarkably developed.

We have noted the very small facial lobes of the sole and the slight development of the gustatory system. The olfactory organ must now be described in detail. The striking similarity of the olfactory organ of the sole to those of the conger and the eel has been described by Bateson, " the plates are arranged in two rows on each side of a central raphé upon which the two rows are folded longitudinally, so as to form a lining to the olfactory tube. The raphé in the sole is depressed so as to form a groove from which the plates rise up."

Associated with this similarity we find that the olfactory bulbs and lobes of the conger, eel, and sole present a very similar pattern. " In front of the medulla of the eel, Anguilla vulgaris, the several regions of the brain are of approximately the same size and each is more or less clearly bilobed, the brain appears to consist of four pairs of rounded equal-sized nodules. The anterior pair (olfactory bulbs) are slightly pointed in front, and give off two large olfactory nerves. The thalamencephalon is remarkably long for a teleostean forming a narrow neck between the cerebrum and the optic lobes, a description which applies almost equally to the condition found in the sole." The diet of the sole must now be referred to and its relation to its brain pattern considered. The sole is nocturnal in its habits and is caught more frequently at night than by day : and in the daytime more frequently when the water is cloudy than when it is clea The sole seeks its food more by sense of smell and touch than by sight and in the Irish Sea prefers worms (nereids) to any other form of diet. (Jenkins, 1925.) According to Cunningham, " the sole is a distinctly shoal-water fish. The stomachs of 36 soles were examined and in 18 the food consisted of marine worms. Small fragments of the shells of bivalves were found, but these seemed to be, in most cases, to have been attached to the tubes of tube-building worms, although small bivalves were sometimes found entire. The throat-teeth are pointed and slender and cannot serve for crushing shells as do those of a plaice.

" Twenty-five per cent. of the stomachs contained echinoderms, mostly sand-stars, Crustacea were found in two per cent. In soles caught off the west coast of Ireland it was found that worms were most frequent, then echinoderms, then molluscs, then crustaceans, and lastly fish in a few cases. The echinoderms were mostly brittle-stars or sand-stars : among the molluscs were small specimens of the razor-shell ; the crustaceans were small specimens of sand-hoppers and shrimps ; the fish small sand-eels."

The above details of the diet of this family may be tedious and seem trivial, but they serve to emphasise the peculiar epicurean diet of the sole, which among a large concourse of bottom-feeding fish chooses to specialise in worms and despises shell-fish. It is interesting to speculate on the causes of this discrimination and to see if any of the facts we have noted may help to solve the problem.

In the first place, the presence of a central acoustic lobe suggests that the ancestors of the sole were surface feeders and, the absence of a marked gustatory system, that they were not bottom-feeders ; while the large somatic-sensory lobes remind one of the similar lobes of the whiting or ling and point to an inherited predacious habit of feeding. But there is other evidence pointing to their ancestors having been pelagic fish, namely, the presence of a rather large swim-bladder which is entirely wanting in the full-grown sole, but persists until it is half an inch long and until the left eye is very near the edge of the head, as is pictured in a drawing by Cunningham. The same observer notes the eggs of the sole when fertilised are buoyant and float in water. It is distinguished from the eggs of other fishes in British Seas by the fact that the outer layer of the yolk is divided into separate segments and that there is an immense number of minute oil-globules arranged in irregular patches at the surface of the yolk. These considerations suggest that the sole, originally a predacious fish, has at some time found itself in a shallow habitat and adapted itself to a diet of worms, and that its brain pattern has remained fairly constant in accordance with its sensory equipment and that its acoustic centre has become of advantage in its new habitat, and its habit of tapping the sand.

The conclusion that can be drawn from this study of the brain-pattern of the sole can now be reviewed. If it is assumed that the sensory activities of a hunting fish depend, as a rule, on three dominant senses, these in the sole appear to be : I.—Olfactory, as indicated by an elaborate olfactory organ and large olfactory lobes ; II.—Auditory as suggested by the large central acoustic lobe ; and III.—Tactile as is evidenced by the large somatic-sensory lobes ; so that smell, hearing, and touch are the dominant senses ; while on the other hand, sight and taste are poorly developed as indicated by the small optic lobes, and the minute facial lobes, by which all gustatory impressions are received.

As regards the central acoustic lobe, it will be remembered that the bleak, a surface feeding cyprinoid, the pilchard, a plankton-feeding clupeoid, the gurnard and the mullet, all have a central acoustic lobe of the same type. It has also been noted that the surface-feeding fishes have small facial lobes. It has been suggested by some writers that a large central acoustic lobe may be associated with the regulation of the gaseous pressure in the swim-bladder, but inasmuch as the sole has no swim-bladder in the adult this theory receives no support in its case. Moreover, the gurnard, a bottom-feeding fish with a closed swim-bladder, does not need any special control of the pressure in this organ.

Evidence has been given associating the large central acoustic lobe in both the gurnard and mullet with the reception of sounds, the former with noises produced by the fish, and the latter with noises from external sources. The large somatic-sensory lobes, similar to those seen in the turbot, and the presence of a large swim-bladder in the larval stage of the sole suggest that originally the sole had pelagic habits at an early evolutionary stage, and that the bottom habitat is a recent acquisition.

CHAPTER X

FLAT-FISHES—*Continued*

In this chapter the other groups of the flat-fishes (Heretosomata) will be considered in relation to their feeding habits and their brain pattern; it will be found that these groups conform to the recent classification of Norman and are supported by the work of Ford on the vertebral column.

The second of our groups consists of certain species of the family Pleuronectidæ and are as follows:

The plaice, Pleuronectes platessa; the flounder, P. flesus; the sand dab, Hippoglossoides; the lemon sole, P. microcephalus; the witch, P. cynoglossus.

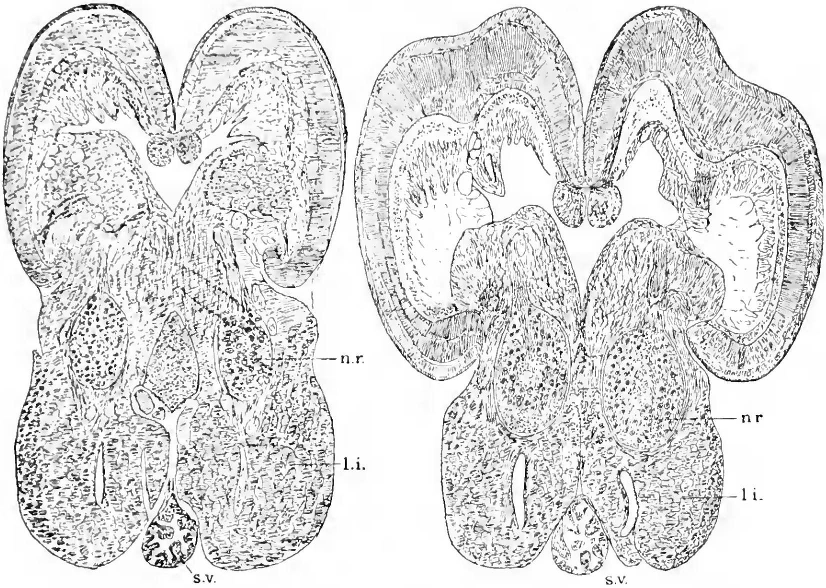
Plate 13, Figs. 2-5 contains outline drawings of the naked-eye appearance of the brain of lemon sole, plaice, witch, and dab. The characters of this group are best exemplified by the plaice. When the drawing of the plaice is compared with that of the sole, the most striking difference to be noted is the large size of optic lobes each of which is bi-lobed in an antero-posterior plane. The primitive end-brain is, on the other hand, much smaller. The somatic-sensory lobes, instead of having an anterior bulge, and appearing like two semi-colons facing each other, as in the sole, are narrow and elongated, and separated by a deep cleft.

It is now necessary to see what is the evidence relating to the acoustic and gustatory functions in the plaice. This can be furnished by an examination of serial sections; but before doing so the sections of the optic lobes should be examined and compared with similar sections of the sole.

The two large scale drawings of sections across the middle of the optic lobes show the very great prominence of the tectum opticum of the plaice compared with that of the sole; these drawings also show the details of the lobi inferiores to which we shall refer later.

In the plaice the facial nerves are of considerable size and pass transversely inwards before turning caudally. The facial lobes are large, and form a slight projection into the walls of the ventricle; they are capped by the fifth lobes and do not appear in a naked-eye view; their descending fibres form a strong band and pass ventrally and outwards into the great lateral secondary gustatory tracts. More caudally the motor nucleus of the tenth nerve or the nucleus ambiguus appears, but the vagal lobes are of a very moderate size. The great difference in size between the facial lobes of the plaice and those of the sole is no doubt to be associated with the presence of taste-buds in the plaice, which are numerous, as their description by Bateson makes clear.

PLATE 15.



Transverse sections across the optic lobes of (left) Sole, and (right) Plaice. Note the greater size of the tecta optica in the Plaice and its convoluted form. l.i.—Lobus inferior. n.r.—Nucleus rotundus. s.v.—Saccus vasculosus.

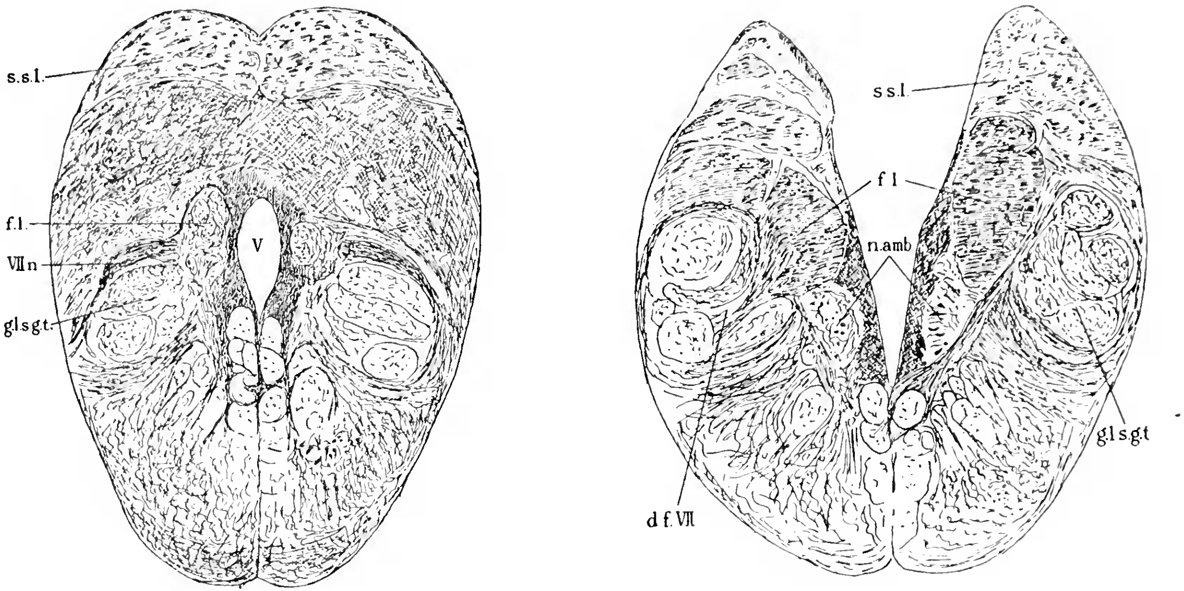
There is no central acoustic lobe or area. Bateson, in writing on the olfactory organ of Pleuronectes, states that the plaice, flounder, lemon sole, and dab, as well as the halibut, " have only one row of olfactory plates arranged in a single series in a direction parallel to the long axis of the body and not transversely to it." This is in sharp contrast with the condition that is found in the sole.

The lemon sole has a brain of similar external appearance to that of the plaice. The primitive end-brain is rather larger than in the plaice and the optic lobes are large ; they do not, however, possess the bi-lobed character of those of the plaice, nevertheless, there is a distinct lateral bulge anteriorly on either side. The cerebellum is moderate in size. The somatic-sensory lobes are more prominent than in the plaice, in fact they approach the form described in the sole. The vagal lobes are small. In the witch, the primitive end-brain is slightly twisted, and the optic lobes are smaller than in the plaice and lemon sole. The somatic-sensory lobes and vagals are similar to those of the plaice, but sections show that the former project more dorsally: the facial lobes are very similar to those of the plaice, but are smaller and produce no bulge into the wall of the rhomboid fossa. The optic lobes are well developed.

The brain of the dab is like that of the witch but smaller. The most striking feature of the brain pattern of this group is the size of the optic lobes. These, in the plaice and lemon sole, have also their peculiar characters. This is no doubt due to the importance of sight in the hunting habits of these fishes. But it must be remembered that this group is well known for its mastery of the art of camouflage. It is true that the protective coloration in fish is controlled by vision, which acts on the pigment cells, called chromatophores, through the medium of the network of nerve fibres that surround these cells. Flat-fishes have also the power of protruding their eyes to a remarkable extent, particularly is this the case in the fish we are now considering. It is assumed that it is necessary for the fish to survey the ground before it can be able to simulate its colour and pattern. Flat-fishes are peculiar in possessing an accesory organ the recessus orbitalis, the function of which is to make the protrusion possible.

The second feature to be discussed in Group II is the presence of a well-marked facial lobe which is associated with the presence of taste-buds on the lips and, therefore, indicates an important gustatory mechanism. At the same time it must be noticed that there is no central acoustic area in those fishes of the group that we have examined by serial sections. We are now in a position to learn what are the dominant special senses that make the hunting equipment of the group. They are, I, sight; II, taste or gustation; and lastly, smell. Audition takes no part. The marked difference of this picture from that of the sole is striking and it is not surprising that the sole is placed by systematists in a different genus. But there are other differences that may be mentioned namely, the character of the eggs. The eggs of the great majority of flat-fishes are buoyant and pelagic. Those of the sole have a number of small oil-globules at the surface of the yolk, but in all the members of the families, Bothidæ and Pleuronectidæ, the oil-globule is either single or absent altogether, while the plaice has an undivided yolk without

PLATE 16.



Two sections across the medulla oblongata of the Plaice at the level of the facial lobe. To the left is seen the ventricle and to the right it opens out into the rhomboid fossa. The facial nerve (left) is seen passing in a transverse direction towards a small facial lobe which becomes more prominent in the section on the right. s.s.l.—Somatic sensory lobe. f.l.—Facial lobe. VIIn.—Facial nerve. d.f.VII.—Descending fibres of facial lobe. n.amb.—Nucleus ambiguus. G.l.s.g.t.—Great secondary lateral gustatory tract.

an oil-globule. It should be remarked that the dentition of the plaice is well adapted for crushing shellfish : this is in great contrast with the teeth of the sole.

Writing on the bottom fauna and food of fishes, Stevens describes the feeding behaviour of the lemon sole, which depends on eyesight to discover its prey, and forages principally by day. At Plymouth its diet is solely marine worms and annelids, " Tubiculous annelids, unless hunted discreetly, disappear to safety down their holes. The lemon sole is always on the move. It comes to rest in a characteristic attitude with the head and fore part of the body raised well off the bottom. Remaining perfectly still in this position, it scans the ground with its very prominent and movable eyes. Should it then spy a worm, cautiously emerging from its burrow, it pounces upon it with a kind of forward leap, bringing its mouth down almost vertically upon its victim by a strong arching of the anterior part of the body." The plaice and dab behave in a similar manner when searching for food, but they do not raise the head quite so high before they pounce.

The plaice feeds chiefly on bi valve shell-fish, whose shell it is easily able to crush by means of the strong blunt teeth in its throat, but it also eats sea-worms. In the Firth of Forth, the most common food was a small species of bivalve called Scrobicularia, and next in frequency was the razor shell, Solen ; cockles and clams were also present. Of the worms all kinds were devoured, sea-mouse, lugworms, rag-worms and tube-worms. Sand stars were sometimes eaten, and an occasional shrimp, but fish very rarely. The witch favours marine worms ; they were present in 72 per cent. of the stomachs examined ; crustacea, 30 per cent. ; molluscs in 14 per cent. and echinoderms in only 3 per cent. Dabs feed mostly on crustacea. These occurred in 48 per cent. of the stomachs. Next in abundance were echinoderms, namely, sand-stars and brittle stars, which amounted to 21 per cent. Molluscs were less common and worms occurred in only 16 per cent. of the specimens ; sand-eels and small herrings in only 5 per cent.

The members of this group are, therefore, bottom-feeders, and their type of brain accords with their mode of hunting. The olfactory lobes are but moderately developed, but the optic lobes are large as also the facial lobes, the somatic-sensory lobes are less prominent as one would expect in fish which are not predacious.

The third group of flat-fishes belong to the family known as the Scophthalminæ, according to Norman's classification, and the common British flat-fishes belonging to this family, that will now be described, are three, two belong to the genus Scophthalmus, namely, the turbot, Scophthalmus maximus, and the brill, S. rhombus, and one to the genus Lepidorhombus the Megrim or sail-fluke, Lepidorhombus whiff-iagonis, hitherto known as Pleuronectes megastoma. This new terminology is rather harassing as it was a useful memoria technica to associate "meg" with megrim and megastoma, the latter word reminding one of the characteristic large mouth of this fish. These species have the following characters, eyes on the left side of the head, mouth large, and teeth and jaws equal on both sides.

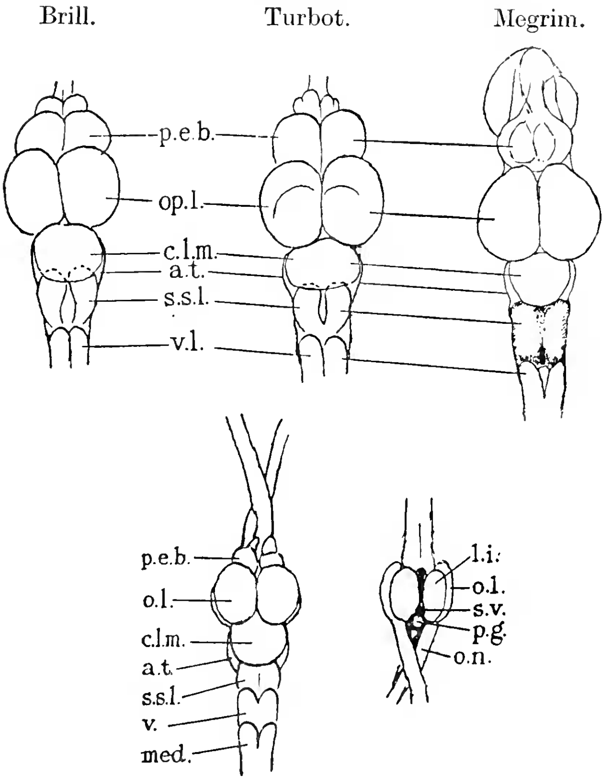
In describing the various species of fish, the brain pattern of which has been discussed, our attention has been drawn only to bottom-feeding fish, and those which feed on the surface. We have not, hitherto, encountered predacious fish, although the chub almost deserves that description.

It will not be unexpected, if it be found that fish with predacious habits present a very different type of brain pattern. This pattern is well exemplified in the cod family as we shall have occasion to describe in the following chapter, and it is also well shown in this third group of flat-fishes. Before going into details, it may be stated at once how different are the habits of feeding of this group from those of the groups above described; Group I feeds solely on worms, and Group II feeds on worms and shell-fish, while Group III has almost exclusively a fish diet. The characteristic pattern of a predacious fish is the large size of the optic lobes and the somatic-sensory lobes, the small size of the facial lobes and the absence of a central acoustic area or lobe.

The turbot, brill and megrim are bottom-feeding fish, and do not as a rule frequent depths greater than twenty fathoms. The swim-bladder is found in the post-larval stages and remains quite late in this transitional stage in the turbot, and specimens have been described as large as an inch long, in which it is still present. The transitional stages of flounder, plaice, and dab have been obtained near the bottom, and as they have no swim-bladder, they can only swim up from the bottom by active movements of the fins. But the young turbot has a neutral buoyancy and can rise or sink in the water without any active swimming. Cunningham has pointed out the advantage to the young fish of this power and habit of swimming at the surface. Even at these early stages the turbot and brill feed on other fishes, smaller than themselves; and in summer time the young of all kinds of fishes are more plentiful on the surface than near the bottom.

We will now describe the brain of the turbot, which may be regarded as the type of Group III, and the Plate 17 will enable the reader to contrast the pattern of the three members of this group. The medulla of the turbot is remarkably broad anteriorly, and this feature is particularly evident in the serial sections ; the somatic-sensory lobes are large and project more prominently as one passes caudally when they become separated from each other and round a somewhat quadrilateral rhomboid fossa ; the lateral margins of which bulge somewhat through the inward projection of the small facial lobes. The motor nuclei of the vagal or the nuclei ambigui are very well-developed. When the lining of the ventricles is closely examined the epithelium is seen to be much thickened and the lower angle of the ventricle is V-shaped and occupied by a fan-

PLATE 17.



Halibut.

p.e.b.—Primitive end-brain. op.l.—Optic lobe. c.l.m.—Cerebellum. a.t.—Acoustic tubercle. s.s.l.—Somatic-sensory lobe. v.l.—Vagal lobe. l.i.—Lobus inferior. s.v. — Saccus vasculosus. p.g. — Pituitary gland. o.n. — Optic nerves, decussating.

shaped area of tissue, the free edge of which is lined with ciliated epithelium beneath which are small pear-shaped cells, and from these fibres pass downwards to enter a fine nervous meshwork.

The acoustic tubercles are not prominent and there is no central acoustic area.

The cerebellum is characterized by the great extent of the stratum granulosum which leaves only a small area of stratum moleculare. When we compare the similar sections of the megrim, we note that the medulla is not so broad, but this is compensated by its greater depth. It has well-marked somatic-sensory lobes and small facial lobes which do not project so much into the wall of the rhomboid fossa: there are small acoustic tubercles and no central acoustic area. The cerebellum is of the same type as that of the turbot, with a very large area occupied by the stratum granulosum. If we compare this picture with that of the second group it is seen that the somatic-sensory lobes are more developed and that the facial lobes are much smaller while the vagal lobes are more prominent.

The food of the turbot, according to Cunningham, "consists almost entirely of other fish. It is a predacious creature; on the west coast of Ireland the principal fish found in turbots stomachs were sprats and sand-eels; occasionally a dab, a sole, or a pout." On the trawling grounds of the south-west of England he found "in the turbots stomachs the boar-fish known as the cuckoo, pilchards, whiting, sea-bream and pout, never anything besides fish."

The diet of the megrim, as of the turbot and brill, is fish, namely, sprats, sand-eels, whiting, gobies, etc. We find here a group of predacious fish, and the pattern of the brain is just what would be expected. The optic lobes are large, the sensory-somatic lobes very prominent and the facial lobes small—a condition comparable to that found in the pollack, with this difference, that the facial lobe is not apparent on a superficial examination, as they are completely concealed by the overlapping of the somatic-sensory lobes.

THE HALIBUT, *Hippoglossus*.

Although the halibut belongs to the family Pleuronectidæ and has its eyes on the right side of the head, it is of a very different build from the plaice, and has a very different habitat and diet. Just as we have seen in the carps, that fish, though belonging to the same family, may present a great variety of brain pattern, so in the Pleuronectidæ we shall find great differences in the pattern of the medulla oblongata, according to their methods of feeding. This is well shown when we contrast the brains of the halibut and plaice.

The halibut grows to a very large size and has small smooth scales. The eyes are separated by a fairly wide space. The mouth is large with strong jaws, and pointed teeth equally developed on both sides of the head. There is no air bladder. The upper side is of an olive brown to black colour and the blind side is white. The body is both longer and plumper than the majority of flat-fish. On the other hand, the plaice has a shorter, deeper, and thinner body, with a small mouth twisted over towards the blind side, so that the jaws and teeth are more developed on that side, and the teeth are adapted for crushing.

We have already described the hunting methods of the plaice ; it is only to be expected that the form of the halibut would indicate a different mode of life, and we find, although it sometimes lies flat on the bottom in wait for its prey, it is a powerful swimmer and often goes in active pursuit of other fishes. It is a predacious fish, and is found in depths up to 200 fathoms. Its diet is principally fish, but also feeds on crabs and shellfish, and is often found to frequent grounds similar to those occupied by cod.

The halibut is remarkable in its power to adapt its coloration to its surroundings and for the rapidity with which the pigmentary changes take place. Norman states that the fish does not consciously imitate the surroundings, the whole process partaking of the nature of a series of reflex processes and accomplished in less than a second.

The pattern of the brain of the halibut can be readily surmised by a consideration of its predatory habits and its deep sea habit. The optic lobes are large, and the somatic sensory lobes very large ; while the facial are small and no central acoustic area can be demonstrated. The optic lobes are particularly enlarged in a dorsoventral direction, and appear to bulge ventrally so as to give it a bi-lobed shape ; this, as in the plaice, may be associated with its facility for protective coloration.

A more difficult problem for investigation is the cerebellum ; this is prominent and its lateral margins are extended ventrally so as to overlap the margins of the somatic sensory lobes for some distance posteriorly ; these lateral extensions are not only composed of the stratum moleculare, but the stratum granulosum extends downwards, so as to join the granular matter of the acustico-lateralis lobes, which are not very prominent ; where these two structures meet there is an accumulation of large cells, similar to those known as the cells of Purkinje. This unusual arrangement of stratum granulosum and acoustic tubercle may be explained by the deep-sea habitat ; we shall have occasion to describe the modifications that occur in the acoustic tubercles of such fish as the hake and the scabbard fishes in association with the great depths of the sea they inhabit; in the latter fish we shall note, in addition to the large size of the acoustic tubercles, that the granular portion extends inwards in the form of a pyramid (in section) and the apices of this extension consist of accumulations of large cells.

There is reason to connect this development with direction finding in the darkness of the depths where sight can be of little avail; we suggest that, as the halibut descends to two hundred fathoms, this modification of the acustico-lateral area may also be associated with its hunting in conditions where light does not penetrate.

CHAPTER XI

THE COD FAMILY

Before comparing the brain pattern of the different species of Gadoids it may be well to make a few general remarks about this family. As Cunningham has pointed out, like the flat-fish, all the members of this family are without spiny fin-rays and generally without spines or bony armour; they carry no weapons of offence or defence except their powerful jaws and teeth. Some, like the cod, are powerful swimmers and the form of their body makes for speed which has given rise to the fishermen's saying "a cod's head and a mackerel tail," in describing the best lines for a fast vessel.

The fin rays are soft and flexible and the scales are small, smooth, and thin and easily detachable. The dorsal and ventral fins extend a great part of the length of the body, the tail fin is separate. The eyes are large, except in the nocturnal feeders and in many kinds there are barbels on the lips and chin. The majority feed in the day time, hunting their prey by sight, and being voracious and rapacious fish have large mouths. Some, besides a fish diet, feed on crustacea and mollusca so that there is a great variety in dentition but all have powerful pharyngeal teeth.

The following is a classification after Cunningham of British species; but we include only those fish which have been studied in relation to their brain pattern.

I. Species with three dorsal fins and two ventral fins:

   i. *The cod.*—Grows to a large size; body not much elongated; colour greenish-yellow with numerous small black spots, lateral line, white, and there is a barbel on the chin.

   ii. *The haddock.*—Smaller, but similar, has a black blotch on the shoulder and a black lateral line. Barbel small.

   iii. *The whiting.*—Sides silvery, no barbel; body more slender and better fitted for active motion as seeking their prey in higher regions than do the two preceding.

   iv. *The coal-fish.*—Differs from the preceding in having a lower jaw longer than the upper. It has a small barbel. Colour dark slate blue, almost black on sides; lateral line white.

v. *The pollack.*—Like the preceding but with no barbel and the lower jaw longer. Colour a dark green.

II. Species with two dorsal fins, the hinder long, the front one short; one ventral fin:

vi. *The ling.*—A barbel on the chin. Body elongated, scales minute, fins narrow, very flexible.
vii. *The Mediterranean ling.*—Molva elongata, more elongate, and more eel-like than the common ling, molva vulgaris.
viii. *The burbot.*—Closely resembles the ling, but the body is broader behind, the head and the scales are larger and the fish is much smaller.
ix. *The forkbeard.*—A barbel on the chin. The pelvic fin forms a long filament extending behind the vent.

III. Species in which there is no separate first dorsal, but the front of the single dorsal is a narrow fringe kept vibrating during life:

x. *The three-bearded rockling.*
xi. *The five-bearded rockling.*

MERLUCCIIDAE

The **hake.**—This has been omitted from Cunningham's classification, as although it is in many ways like a gadoid, several features have made it clear that it belongs to a separate genus. Its external features are, no barbel, scales larger than the ling, fins broader and stiffer. Teeth larger and mouth black.

When we attempt to study the relationship of feeding-habits to the brain pattern in the cod family, we find some different features from those we have described in the Cyprinoids. In the latter family we were able to describe three groups, each with its characteristic brain pattern, and the third group could be further sub-divided into two sub-groups. In the cods or gadidæ we shall find that the different species can be graded into a greater number of groups, and that in the first of these groups further sub-divisions can be made according to their diet, whether this is mostly of crustacea and shell-fish, or is mostly fish; between these two extremes we find intermediate types, for example, a diet largely of crustacea but also fish or a diet mostly fish, but occasionally crustacea. When we examine the pattern of the medulla oblongata we find a gradation corresponding to the types which vary between the two extremes.

Some authorities have been unable to identify the facial lobe in the cod family. We have made a detailed study of the brain of the whiting and have clearly established its existence; in those fish that feed on crustacea and shell-fish it is well-developed; but in those fish of predatory habits these lobes are less well marked, but on the other hand the somatic-sensory lobes, or fifth lobes, are highly developed, and in some cases almost envelope the gustatory lobes.

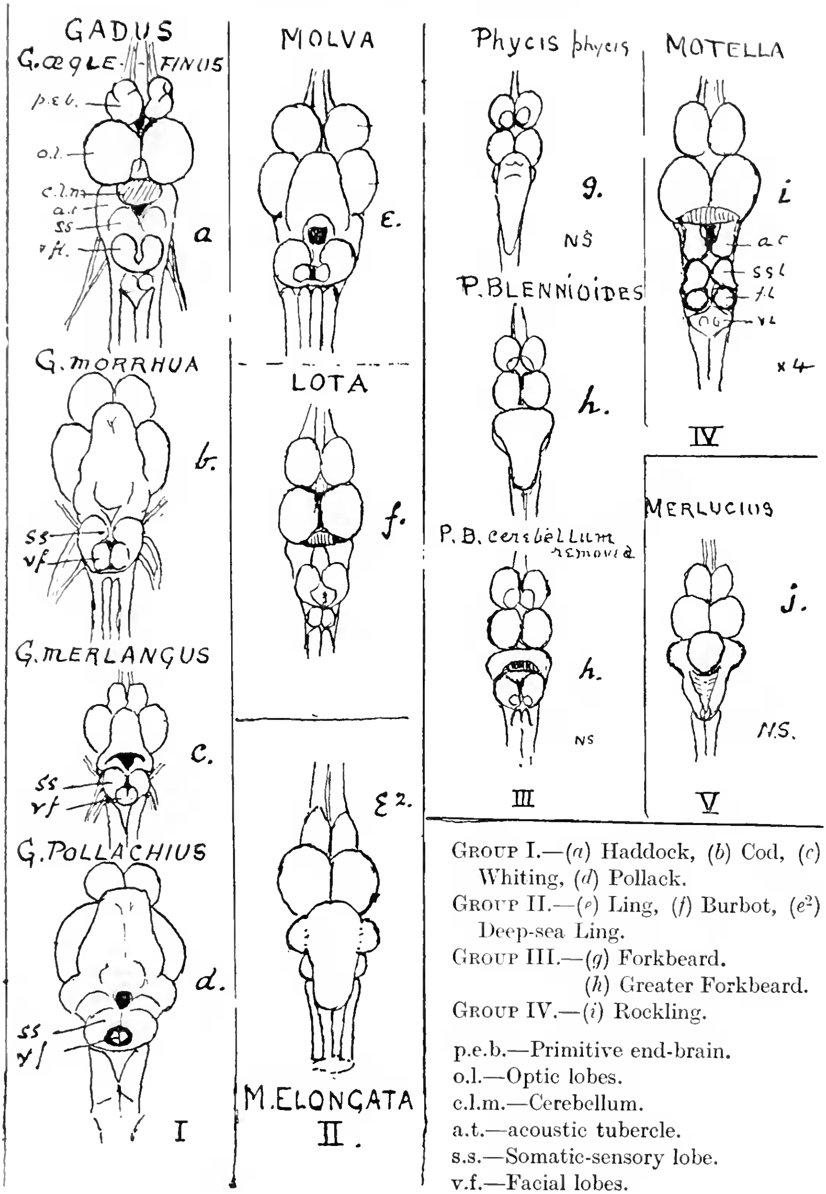
Plate 18 gives drawings of the dorsal aspect of the species of gadoids, all common and familiar fishes in British waters, except the forkbeards and the deep sea ling, Molva Elongata.

In the first figure *a*, which represents the dorsal aspect of the brain of the haddock or "shell-fish," as the Germans call it, the somatic-sensory lobe is of moderate size, but the facial or gustatory lobe, v.f.l., is large. The haddock is the type of a ground feeding gadoid with a diet of crustacea, molluscs, echinoderms and worms. If we now compare this drawing with Fig. *d*, which represents the brain of the pollack, a typical predatory fish, the somatic-sensory lobes are very prominent and spread backwards on either side so as to embrace the minute facial lobes which are completely surrounded by the tapering ends of the lobes which meet posteriorly in the middle line. The pollack is very predacious and its diet is fish and rarely anything else, when fully grown. Between these extremes we have the cod, whiting, and ling, and the size of the anterior (SS) somatic-sensory areas increases according to the importance of fish in their diet, and at the same time the size of the facial or gustatory lobes diminishes as the crustacean and shell-fish element in their diet figures to a less extent; so that we get a series, starting from the haddock, of the cod, feeding on crustacea mollusca and fish; the whiting, feeding on shrimps but mostly fish, and the ling, feeding almost entirely on fish. The hake has been purposely left out of the series; the reason for this omission will be clear from the drawing; the brain pattern is most "uncodlike."

The cerebellum of the hake is not tongue-shaped as in the gadidæ, but is sessile, and is prolonged laterally into the two large acoustic tubercles, from which lateral eminences extend backwards as narrow ridges which meet medially and enclose a tiny lobe, presumably representing the gustatory lobe. We gather from this description that the hake has no business to be included in the gadidæ, but should be placed in a separate family, the merluciidæ, as recent writers have already done. As both the life history of this fish and its brain pattern are unique we propose to discuss the many interesting facts that arise in a separate chapter. But there are two other features in the gadidæ which are of importance, the presence or absence of barbels and the relative size of the optic lobes.

PLATE 18.

The Cod family or Gadidæ.



Group I.—(*a*) Haddock, (*b*) Cod, (*c*) Whiting, (*d*) Pollack.

Group II.—(*e*) Ling, (*f*) Burbot, (e^2) Deep-sea Ling.

Group III.—(*g*) Forkbeard.
(*h*) Greater Forkbeard.

Group IV.—(*i*) Rockling.

p.e.b.—Primitive end-brain.
o.l.—Optic lobes.
c.l.m.—Cerebellum.
a.t.—acoustic tubercle.
s.s.—Somatic-sensory lobe.
v.f.—Facial lobes.

Taking the barbels first, we note that the haddock, cod, and ling, have barbels. But it will at once be asked why has the ling a barbel, when it is not a bottom-feeding fish, and has a minute gustatory lobe ; it can be readily understood that barbels are of use to the haddock and cod in search for food on the bottom. It has, we believe, been shown that the barbels of the ling do not have taste-buds, and are only tactile in function and the optic lobes give a further clue to the problem. The optic lobes of the ling are small while the optic lobes of the pollack and haddock are large, and associated with this condition, it is well known that the ling is a typical deep sea fish and, moreover, is a night feeder.

Another point can be made out by comparing the drawing of the brain of the ling with the pollack. The primitive end-brain of the ling is definitely larger than that of the pollack, and this is associated with an increased olfactory function doubtless of importance in hunting at night. There are several facts worth noting in the dentition of the fish we have been considering ; it would naturally be expected that those fish that feed on crustacea and shell-fish would be provided with crushing teeth, and this proves to be the case. We give in Plate 21 six drawings of the upper jaws of the fish under consideration. We do not propose to give a detailed account of the various dentitions, but just to point out the general characters presented in each species. The drawing of the haddock shows the lower jaw divided and held apart so as to expose the upper jaw ; this is seen to have a marginal area of small sessile teeth, 3 mm. in width in the middle line and a small toothed area on the vomer. There are similar small teeth on the edge of the lower jaw. These teeth are adapted for crushing.

The next drawing is of the upper jaw of the cod, a much more formidable organ. There are three rows of sharp teeth, the anterior row of teeth being the longest, and the widest central portion is 6 mm. deep ; within this area on the vomer, is a V-shaped area with a rough tuberculated surface. So that there is present an anterior dentition useful for hunting fish and also a crushing area for shell-fish, etc.

The drawing of the whiting is readily comparable with that of the haddock, as the lower jaw has been divided and separated in the same way. There is a single row of sharp pigmented teeth on the edge of the upper jaw, they are widely separated, and the longest may be 3 mm. in length. The lower jaw has similar teeth, but smaller. There is a V-shaped area on the vomer, as in the cod, but the teeth are small and sharp ; this dentition clearly indicates a predacious habit.

The ling has a very elaborate dentition, as is well shown in the drawing. There is a broad band of small teeth, three deep extending further back than in the cod and within this on the vomer is a raised horse-shoe shaped area bearing four teeth on either side, and a single median tooth ; these are conical in form, strong, and sharp. The dentition of the pollack is simpler ; there is a band of small teeth in two rows, but mesially in four rows ; there is a V-shaped area on the vomer with small sharp curved teeth in two rows. Both the dentary formula of ling and pollack point to a well-marked predatory habit of feeding. The dentition of the hake will be described later in the chapter devoted to this interesting fish.

Reviewing the above descriptions it is clear that the haddock, cod, whiting, and pollack have teeth suitable to their diet, and we note a more or less gradual change in type as the crustacean and shell-fish diet gives place to a purely fish diet. The ling has a unique dentition and this is most evident in the vomerine teeth. It may be that this dentition is of some particular value in its nocturnal habits of hunting, but what precise use the conical teeth are to the fish and why they have been evolved is difficult to imagine.

In the descriptive letterpress to the drawings of gadoid brains, there is given a short summary of the diet of each fish. We propose to amplify the facts there stated, as there has been a vast amount of research on the stomach contents in recent years by the naturalists of the Ministry of Agriculture and Fisheries. These reports we shall quote and also make free use of the textbooks of Cunningham and Travers Jenkins. Starting with the haddock, it is found that crustaceans and molluscs are found most frequently. The actual percentages vary, but if we pool the observations of all the observers they are present in about equal proportions. Polychaete worms and echinoderms are also found, but fishes rarely, and never more than three to five per cent. of the contents. Herring spawn may occur, whence the name, " spawny haddocks," applied to the fish at certain periods. The haddock is, therefore, with reason, called by the Germans " the shell-fish."

The cod, gadus morrhua, is the next in the series and is found to be not only a feeder on the bottom fauna, but is also predacious and hunts other fish. Like the fishermen who go to sea in a drifter-trawler, when herring are about, the pursuit of fish is the means of livelihood, and at other times the bottom of the sea provides the harvest. But further complications arise in the feeding habits of the cod, as with advancing size the diet of this fish changes, it might almost be said becomes reversed. The cod is a voracious feeder on other fish and also has a marked appetite for crustacea.

Their diet is of herring and whiting, also hermit crabs, various other crustaceans such as Norway lobster, molluscs and Aphrodite. But if the stomach contents of this fish are classified according to the size of the fish, it is found that those of 15 cm. have no fish in their stomachs, but when the length of 30-60 cm. is reached 50 to 67 per cent. of the contents consists of fish. But when we look at the records for crustacea it is found that the small fish contain crustacea up to 100 per cent. ; but as the size reaches 60 cm. the percentage falls to 63 per cent. The small number of polychætes and mollusca remains constant.

The whiting, the next in our series, has a diet which might appear to vary according to the observer ; but this is not really so, as when one studies the sites from which the specimens were caught, it will be found that stomach contents give very conflicting results. Some authorities say that the food of this fish is mainly whiting and herring, and shrimps in large quantities. Cunningham found that in the Firth of Forth their principle food was fish and crustacea, 65 per cent. of the former and 37 per cent. of the latter. On the other hand, Todd, in the report of the Food of Fishes (North Sea) gives crustacea 67 per cent. and fishes 40 per cent., which is the reverse of Cunningham's data. But if we analyse Todd's statistics, we will find that on certain banks as the Leman Ground, that fish were 91 per cent. and, if herring were about, 88 per cent.

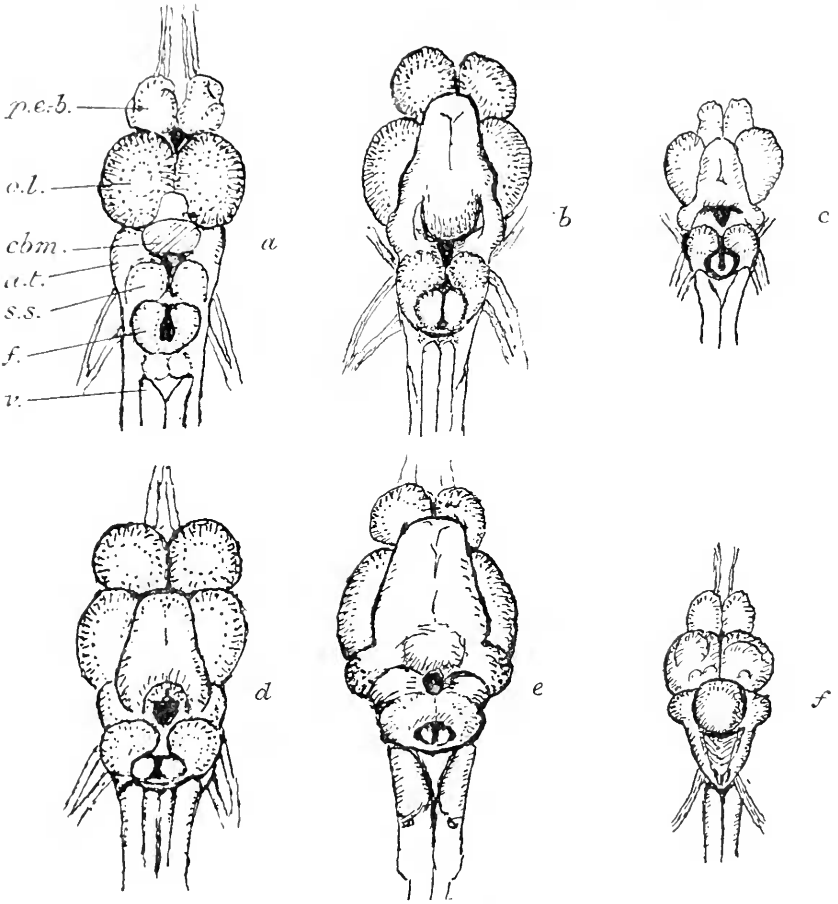
The ling is a voracious animal of prey, and devours all varieties of cod, whiting, mackerel, megrims, dabs and haddock. All writers agree that it lives almost entirely on other fish and is a nocturnal feeder.

The pollack is another voracious feeder on herring, sprats, pilchards and mackerel. It is purely a fish eater.

It has been suggested above, that the pattern of the medulla in the cods shows a gradual transformation as the species changes from a purely crustacean and molluscan diet to a purely fish diet. When we consider the facts, just described, it would seem more accurate to describe the gadoid brain as being of three types : I.—With well-marked facial lobes, as exemplified by the haddock ; II.—Facial lobes small, but large somatic-sensory lobes, as in the cod and whiting, which are both molluscan and crustacean in their diet and also fish eaters. III.—Large somatic-sensory lobes, embracing very small facial lobes, as in the ling and pollack ; and as we have seen, also in the turbot ; these are predacious fish, feeding solely on fish. In relation to its shell-fish tastes it may be mentioned that in both cod and pouting taste-buds have been described on the lips, barbel, pectoral fins and the body.

PLATE 19.

Drawings of the Brains of five Gadoids and of Merlucius.



Top row.—(a) Haddock. (b) Cod. (c) Whiting.

f.—Facial lobe diminishes in size from *a* to *c*. *s.s.*—Somatic-sensory increases from *a* to *c*. Diet of Haddock.—Crustacea mollusca and worms. Diet of Cod.—Crustacea Mollusca and fish. Diet of Whiting.—Mostly fish, also shrimps.

Bottom row.—(*d*) Ling. (*e*) Pollock. (*f*) Hake.

f.—Facial lobes very small in *d* to *e*. *s.s.*—Somatic-sensory large and embrace the facials especially in *e*. Hake atypical. Diet of Ling.—Fish almost entirely. Diet of Pollack.—Fish rarely anything else. Diet of Hake.—Fish only.

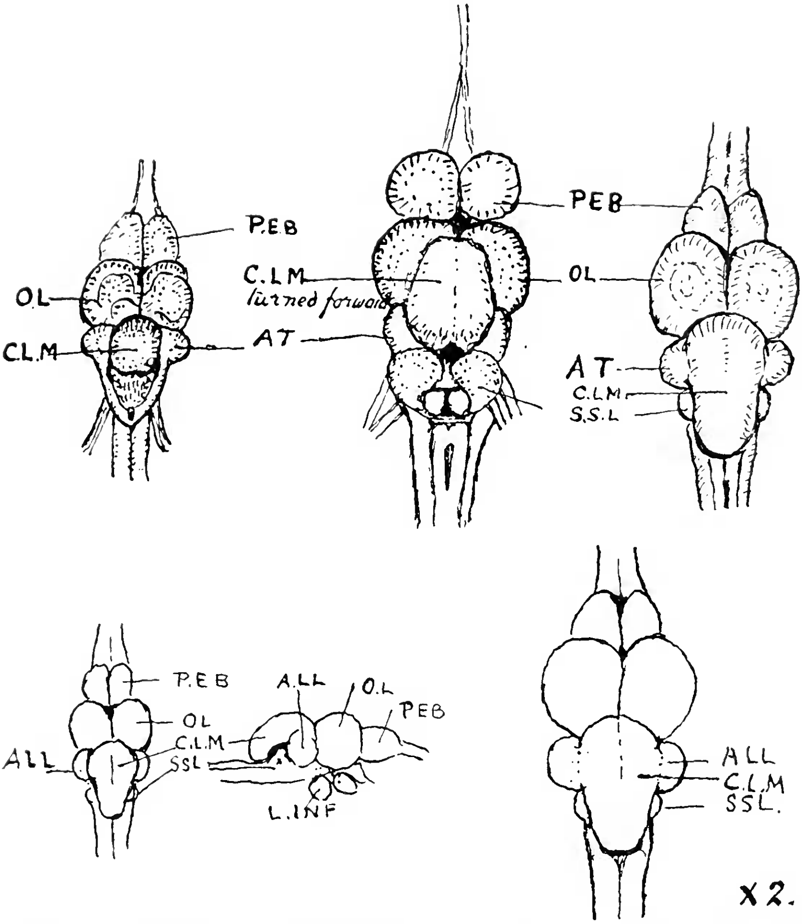
CHAPTER XII

THE COD FAMILY—*Continued*

In the previous chapter we have described the habits and brain structure of the fishes, the brains of which are figured in column I of Plate 18, and it may have been noticed, that with these fishes we included the ling, Molva molva or vulgaris, which stands at the top of Column II*e*. Its position there is due to the fact that it is typical of a group of gadidæ which have elongate bodies with small scales, and among these we include the blue and Mediterranean lings, and the only fresh-water cod, the burbot or eel-pout, Lota vulgaris. The Mediterranean ling or molva elongata is much more eel-like than the other lings, and is caught in deep water south-west of the British Isles. It is silvery in colour, but greyish towards the dorsum. The jaws are long and narrow with a protruding lower jaw. There are large teeth on the palate arranged in the form of a horseshoe, as we have seen in M. vulgaris, and the teeth of the lower jaw are sharp. The pectoral fin is prolonged into a long filament. There is a barbel on the chin and the first three rays of the ventral fin are elongated.

According to Hickling, the range in depth of this fish is 220-520 fathoms, and as they usually come to the surface with stomachs everted they probably feed in the lower layers. The eyes are large, the diameter of the orbit being approximately one inch. Another interesting feature is the large size of the swim-bladder, which is remarkable for the extent of its rete mirabile; this in a small specimen measured four inches in length. When we compare the pattern of the brain of molva elongata with that of the common ling we note that the cerebellum is in both of moderate size and the optic lobes are not large. The acoustic lobes are very much larger in M. elongata than in the common ling, and the somatic-sensory lobes are also very large and project beyond the margins of the cerebellum. The prominence of the somatic-sensory lobes is well shown in a lateral view, which depicts the cerebellum making a sickle-like curve over these lobes. The facts revealed by this examination, namely, the very prominent acoustico-lateral lobes, similar to those of the hake, and the large somatic-sensory lobes confirm the suggestion

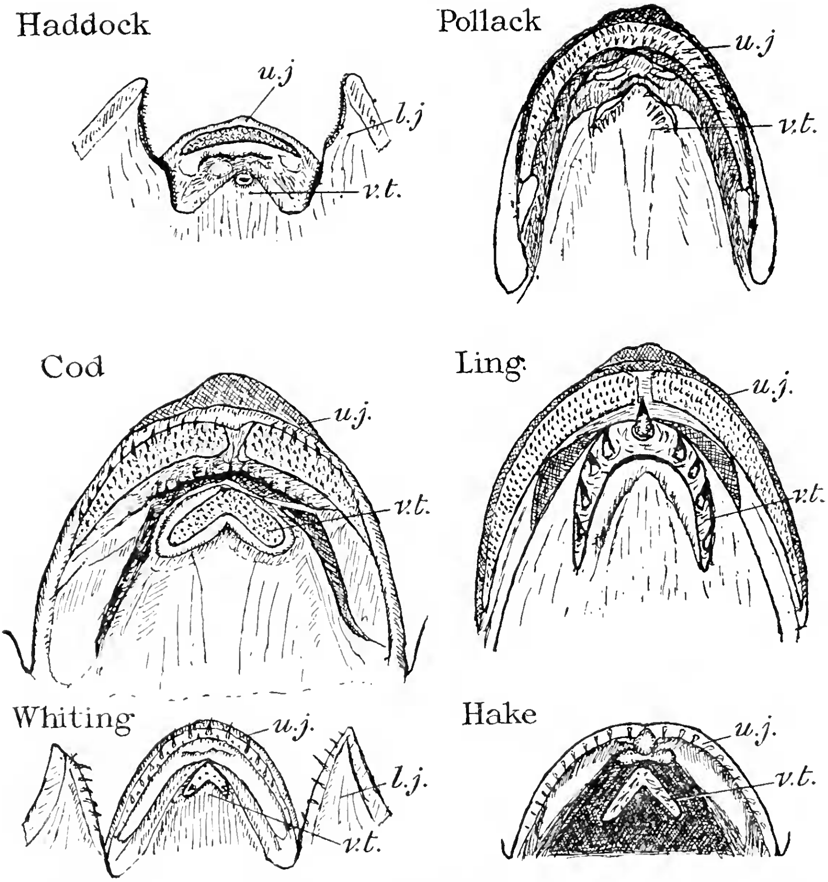
PLATE 20.



Top row.—The brains of three deep water fish, left to right—Hake, Ling, Molva elongata. Below.—Three drawings to scale of M. elongata. To left—Dorsal and lateral view natural size. To right.—Twice natural size. Note the very prominent acoustic tubercles in M. elongata. P.E.B.—Primitive end-brain. O.L.—Optic lobes. C.L.M.—Cerebellum. A.T.—Acoustic tubercles. S.S.L. —Somatic-sensory lobes. A.L.L.—Acustico-lateralis lobe. L.INF.—Lobus inferior.

that the former are highly developed in order to give some functional advantage to a predacious fish hunting in the depths which, in the case of the deep sea lings, must be associated with almost complete darkness.

PLATE 21.



Dentition of the Gadoids figured in Plate XX to show relation of teeth to feeding-habits. The drawings are of the upper jaw from below. *u.j.*—Upper jaw. *l.j.*—Lower jaw. *v.t.*—Vomerine teeth.

The drawing of the burbot (Plate 18, Fig. *f.*) in column II is on a bigger scale than the drawings of the two lings in the same column, and the cerebellum has been removed at its base to expose the medulla-oblongata. This fish is the only gadoid that has a fresh-water habitat. The burbot or eel-pout has, as its name suggests, some of the characteristics of an eel, as well as those of a cod. It is more or less cylindrical in shape with a flattened head. The scales are small and the body is covered with a thick slime. Its movements are sinuous, and, like an eel, it is nocturnal in its habits, and can live a long time out of water. In addition to the barbel on the chin, it has developed small barbels on each anterior nostril, which recalls a similar condition found in the eel. The dentition is very interesting on account of its similarity to that of the ling, which, as Travers Jenkins points out, is its nearest relative. According to Tate Regan, the mouth is wide with bands of small pointed teeth in the jaws, and a crescentic band of similar teeth on the vomer ; it may be added that the latter are longer than those on the jaws and are recurved and pigmented. This vomerine dentition corresponds very closely with the condition all ready described in the ling.

To quote Tate Regan once more, " the burbot is a gluttonous fish and eats great quantities of the eggs of other species. It is very destructive to other fish. In the daytime it pounces on small fish which come near its lurking place, whilst at night it goes in active pursuit of prey." The brain of the burbot is a very interesting example of brain-pattern giving a clue to the habits of a fish, and also its relationships. The medulla oblongata recalls at once that of the ling. The somatic-sensory lobes are large and globular and are prolonged posteriorly by two extensions which meet medially and enclose two small facial lobes which are deeply situated. The optic lobes are small, but the primitive end-brain is very prominent and the olfactory organs are large. The picture is, therefore, that of a night-feeder which hunts mostly by smell and its feelers ; its predatory nature is well shown by its large somatic-sensory lobes, as we have already noted in the common ling.

FORKBEARDS (*Phycis phycis*)

In the preceding pages we have considered the variations in the pattern of the medulla oblongata of those Gadoids which frequent the seas that surround the British Isles. A journey to the islands of sub-tropical seas enables the observer to examine species of different fish, which, we shall show, throw light on various problems which still puzzle the investigator ; moreover, such a journey provides further examples of the eccentric adaptations which occur in the cod family. Frequenting the shores of Madeira is a small member of the Gadidæ known locally as " Abrotia " among the Portuguese ; its scientific name is Phycis phycis ; there is another fish seen also on their markets bearing the same name, but this inhabits deep water. It is the former that is of considerable interest, as it shows how a shore habitat may contain members of the same family living on a very similar diet and yet presenting a very different method of hunting their prey. The general aspect of Phycis is that of a typical cod, and a further examination proves that it has the characteristics of this family in the details of its jaws and dentition, its fins, scales and so on.

Its dentition is very similar to that of gadus morrhua with a well-marked V-shaped area on the vomer and this indicates a shell-fish diet, so that it is not surprising that the German name for this fish is "shell-fish," which, it will be remembered, is also given to our haddock. The head is shorter and broader than that of the haddock and suggests that of a cat; this is due apparently to the large space occupied by the otoliths, which are exceptionally large. There is a small barbel under the chin, and on either side is a long finger-like feeler which is prolonged distally by two filaments; this is merely a modified fin-ray and does not bear any taste-buds. These also recall the cat and its whiskers. But when in the course of removing the roof of the skull to expose the brain, the firm grasp on the trunk caused the animal to purr, the name of cat-fish seemed most appropriate.

On opening the abdomen to investigate the cause of this strange noise, to my astonishment I found that the swim-bladder was not attached to the dorsal wall of the cavity as in most cods, but that there was a triple-expansion gas-bag loosely attached, except at its anterior end. The three compartments of the sac were separated by narrow constrictions; the posterior compartment was the largest, of the size of the posterior sac of a Cyprinoid of similar weight. It had a tough external coat and a thin internal coat. The middle division was smaller and lying in the front part its wall contained two small retia mirabilia, vascular bodies covered with a specialised epithelium, which enables the animal to secrete gas; the anterior sac was partially divided into two so as to produce two auricles on either side, which were capped by a thick mass of muscular tissue. At the base of each auricle there was also a small rete mirabile.

It was the pressure on this sac that presumably caused the queer noise which was heard when I pressed the body of the fish, and there can be little doubt that the contraction of the muscles of the auricles of the anterior chamber are able to produce sound by driving gas from one sac to the other; in fact, act as a kind of bag-pipe. How strange it seems to find a sound producing organ in a cod when the cod of our waters has only an air-bladder which divides anteriorly into a pair of caecal prolongations which extend forwards to the head and are often curiously coiled. This condition of the swim-bladder is associated with the auditory organ.

To quote the Cambridge Natural History "these caecal prolongations from the air-bladder have their extremities apposed to the outer surfaces of the fibrous membranes which close a pair of vacuities in the outer walls of the peri-otic capsules, the inner surfaces being bathed by the perilymph surrounding the auditory organs. It remains somewhat of a mystery or an unsolved problem why this sub-tropical species should possess a sound-producing organ.

In our waters, sound-production is known in few species, and the gurnards are the most familiar ; it is interesting that the gurnards are also characterised by the presence of tactile processes which are really specialised fin-rays. It is, however, a fact that in the warm waters of the Atlantic there is a host of sound-producing fishes, such as the maigre and other sciaenoids and roncadors. It would appear that Phycis has followed the local fashion. These remarks on the internal anatomy lead one to the description of a remarkable brain-pattern in the species Phycis. The large size of the anterior lobes of the brain is very noticeable as they are as large, if not somewhat larger, than the optic lobes. These anterior lobes are not simply due to the primitive end-brain. The primitive end-brain is represented by two small globular median lobes which are surrounded laterally and anteriorly by large olfactory lobes. The cerebellum is very long and tongue-shaped, longer and narrower than that of gadus morrhua which it otherwise resembles. The acoustic tubercles are small. When the cerebellum is lifted to expose the medulla the somatic-sensory lobes are seen to be of only moderate size and the facial lobes not clearly distinguishable.

It appears, therefore, that we have here a shell-fish eating fish, not unlike the haddock, which goes about its job of getting its dinner, not by gustatory organs but by smell and touch, as evidenced by its large olfactory organs and by its sensory tentacles and also by the size of the somatic-sensory lobes ; as we have already stated above, we have no theory as to the value to the animal of its elaborate swim-bladder, but it should be noted that its otoliths are of noticeable size and in this respect resemble the maigre.

When we contrast this brain with that of the haddock we notice that the optic lobes are much larger than the end brain in our haddock and that the cerebellum is not so long, and that the facial lobes are as prominent as the somatic-sensory.

The rock-haddock, Phycis blennioides, is said by Gunther to be an occasional visitor to the British Isles. To-day it is landed in large quantities at Milford Haven from the trawlers fishing out of that port. This species, together with Phycis phycis and P. Mediterranean, are characterised not only by their external features, and by their internal structure, but also by the pattern of their brains. It was fortunate that my acquaintance with P. phycis preceded my knowledge of P. blennioides, as several adaptations rudimentary in the latter are further specialised in the former. The head is larger in P. phycis and the eyes more prominent. In both species the pelvic fin is prolonged on either side by a long filamentous and bifid tentacle ; this seems to be longer in P. blennioides than in P. phycis. Couch describes this fish under the name Greater Forkbeard, or Hake's Dame. It would be interesting to know the origin of this quaint appellation. He says that "these tendrils from their structure may be judged to be endowed with lively powers of sensation ; they have joints along their course and are well supplied with nerves from what may be termed an axillary plexus, situate in the axilla of the fin, one branch of which passes along the course of the fin-rays and sends a branch to penetrate through it, while the other, which anastomoses with the first branch in the axilla, is carried along the posterior margin. Their special function is shown by their proceeding from the spinal cord to their termination, without communicating with any other nerve ;" this is another example of the careful meticulous detail of the old school of anatomists.

An interesting point that requires investigation is why the gurnard should have a paired series of globular swellings in that portion of the cord which receives the nerves from their sensitive filaments, and that the forkbeard has no similar enlargements in its spinal cord. P. blennioides has a range in depth of 200-500 fathoms and has been caught in 140 fathoms. According to Hickling it feeds on crustacea which almost certainly belong to a bottom-fauna, such as crabs, Geryon and Gonoplax, and the prawns, Munidia and Nephrops ; so that there is strong evidence of a bathypelagic habit in this deep-sea fish.

We have compared the brain of several specimens of P. blennioides landed at Milford Haven and compared them with those of P. phycis landed at Funchal. The type in both species is the same. The olfactory lobe and bulb are in close opposition and form a lobe about the same size as the optic lobes. The cerebellum is long but not so long as that of P. phycis : the medulla oblongata is smallish, and the general appearance is not unlike that of the ling and burbot. The acoustic tubercles are small ; this is of some interest as it suggests that the depth at which this fish lives has not been the cause of any great development of this lobe. We have seen a great enlargement in the acoustic lobes of the deep-sea ling, and it might be thought that its bathypelagic habitat was the cause of this adaptation; but the above observations of the forkbeards does not support this theory. The above type of brain, together with the known habits of feeding of P. blennioides, points to the importance of smell and tactile sensation in their hunting equipment. Sight seems to be of secondary importance and the small facial lobe does not point to a gustatory function of their tentacles. The diversity of form of the swim-bladders of the two forkbeards, we have studied, is remarkable.

We have already mentioned the tripartite bladder of P. phycis. The swim-bladder of P. blennioides is a thick-walled sac, the specimen that I have before me is 13 cm. in length, but the anterior lateral prolongations end in a tendon which adds another 1.5 cm. to the length. There are two slight constructions, suggesting a resemblance to the bladder of P. phycis, which divide it into an anterior portion 3 cm. in length, a middle division 4 cm. in length, and a posterior 6 cm. long. The diameters of the three divisions are 4 cm., 3½ cm. and 2½ cm. from behind forwards; there are retia mirabilia in the anterior and middle sections, but the unique feature is the row of appendages on either side about the size of a small pea, about 25 in all on each side. These communicate with the interior, and there are grooves crossing transversely from one to the other. The function of this adaptation of the bladder is unknown, but must obviously not be a sound-producing organ like that of its near relative, P. phycis.

The study of the lings and the forkbeards suggests an explanation of the function of the acustico-lateral areas. The deep-sea ling differs from M. vulgaris in the size of the acoustic tubercles. The deep-sea blenny shows no enlargement of these lobes. The deep-sea ling and vulgaris have large somatic-sensory lobes, but these in the P. blennioides are not large. We may argue from this that large acoustic tubercles are of some functional importance to a pelagic predacious fish hunting in the depths in darkness, but are of no value to the sedentary fish hunting by touch.

The rocklings are a very interesting group of gadoids and comprise three species, in which there is no separate first dorsal fin, but the front part of the single dorsal is a narrow fringe kept vibrating during life. There are three well-known species. The three-bearded rockling, the four-bearded rockling and the five-bearded rockling. Recently, a fourth species has been identified at the Plymouth Laboratory. As their name implies, the species are distinguished by the number of their barbels, three, four or five, situated on the chin and upper lip. In the five-bearded rockling there is one barbel on the chin, two on the upper lip, and two on the margin of the anterior nostril. These barbels have been described as possessing taste-buds.

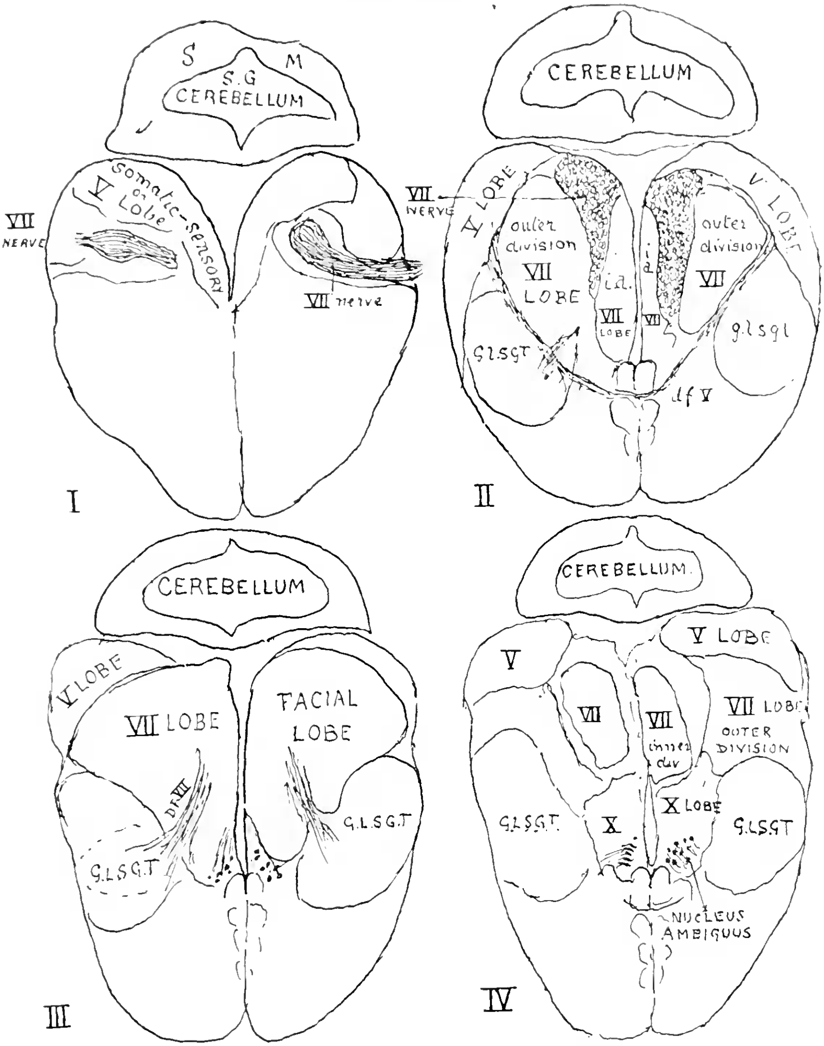
The most important and unique characteristic of this fish is the adaptation of the dorsal fin to subserve the function of taste. One cannot do better than quote an early writer on this organ, for instance Couch (1866) says, "the organ often represented as the first dorsal fin lies in a chink from which it projects when the fish is in the water. It is formed of a membrane from the edge of which rises a thickly placed row of threads, the foremost of which is the stoutest and most prominent. This organ is in continuous and rapid motion. It is well furnished with nerves which render it acutely sensible to impressions." (It is now known to be well provided with taste-buds.) "This dorsal organ is supplied by a special nerve which reaches it directly from the brain, a branch of this nerve also goes to the pectoral and ventral fins which are thus endowed with particular sensation (these are also provided with taste-buds), in addition to those of action, the last-named faculty being controlled by branches of the intercostal nerves."

We quote the above as showing the accurate anatomical observations of the older authors. The following description of the brain of a five-bearded rockling is from a specimen which had been specially hardened for the purpose of cutting serial sections.

We reproduce a drawing of the naked eye appearance (see Plate 18, Fig. iv) of the brain after the cerebellum had been removed to expose the medulla oblongata. The primitive end-brain, as in the burbot, is large, approaching the optic lobes in length. The optic lobes are of moderate size compared with those of other gadidæ. The acoustic tubercles are prominent and prolonged posteriorly into the somewhat globular somatic-sensory lobes. These are prolonged caudally by extensions which would be similar to those of the burbot, if they were not displaced and separated by the globular eminences of the enlarged facial lobes, which meet but do not fuse in the middle line. The vagal lobes are very prominent more caudally and join in the middle line.

The study of serial sections will show the dominance of the facial lobe in the sensory elements of the medulla. We give a series of sections of the medulla oblongata, which have been drawn under low power by means of a projector apparatus (Plate 22). The first drawing is a section of across the somatic-sensory lobes near the base of the cerebellum, and it cuts across both the facial nerves which have a transverse course just below the fifth lobes. These nerves are remarkable for their size, no doubt due to the branches of the

PLATE 22.



Four transverse sections of the medulla oblongata of the Rockling. I.—The most anterior shows the large facial nerves passing madially to enter (in II) the facial lobes which are separated thereby into inner and outer divisions; in III their descending fibres are seen entering the great lateral secondary gustatory tracts (G.L.S.G.T.). In IV the vagal lobes (X) appear and the nuclei ambigui.

facial, somatic in origin, from the fins and the barbels, and dorsal organ. As the sections are traced caudally the facial nerves turn sharply backwards and are seen as a thick trunk entering the facial lobes. This trunk at first lies superficial to each lobe, which seems to be divided into a mesial and lateral portion by some of the fibres of the nerve, the lateral portion being the larger.

As the nerve loses itself in the substance of the facial lobe this is seen to increase greatly in size, and each lobe, appears in section as a somewhat pear-shaped mass bulging laterally, and ventrally a stalk, composed of descending fibres from the lobe, passes downwards and outwards to enter the great longitudinal secondary gustatory tracts. More posterior still the large mass of the facial lobes appears to be again separated into two divisions, the internal portion extending further caudally than the lateral. In the more posterior sections the motor nuclei of the vagal lobes appear, and dorsal to this the sensory portion of this lobe is seen to pass upwards to occupy the site previously taken by the inner division of the facial lobe.

We see here a somewhat similar condition to that found in the gudgeon loach and barbel, a division of the facial lobe on either side, and also of the seventh nerve after it enters the brain, corresponding to the elaboration of the gustatory function which results from the varied stimuli received from the different groups of taste-buds. The course of the nerves supplying the dorsal organ have now been traced to the medulla, and it may be assumed to a specialised area of the facial lobe ; there can be little doubt that the vibratile membrane of the dorsal fin causes a stream of water to pass along the chink with its collection of taste-buds, and the taint of any prey or food would be recognised by these organs.

The rocklings are entirely nocturnal in their habits and remain under stones or in crevices among rocks except when they dart out to seize their prey, which they recognise by smell, but more particularly by taste and to a much less extent by sight. The large primitive end-brain points to a well-developed olfactory function and the small optic lobes are in keeping with their nocturnal habits.

CHAPTER XIII

THE HAKE, THE SCABBARD FISH, PROMETHEUS AND NESIARCHUS

Until quite recently the hake was considered to belong to the cod family, in more technical language it was classified among the gadidæ. In Cunningham's standard work on "Marketable Marine Fishes," the hake was included with the ling and the forkbeards, among the species with two dorsal fins, the hinder long and the front one short. But the hake has no barbel, which is present in the ling. The scales are larger than in the ling, and the fins broader and stiffer.

The term hake (Ger. hecht. pike) is now applied to several species constituting the genus Merluccius, allied to the cod, but now often made a separate family, Merluciidæ.

M. Merluccius is the common European form. In America, however, the term is applied to certain marine gadoid fish, having narrow filamentous pelvic fins, placed under the throat. It is important to remember this fact when consulting American authors. For example, Herrick notes that "in the gadoids, particularly the tom-cod and hake, the free filiform rays of the pelvic fin function in a similar fashion to the barblets of Ameiurus, and are likewise provided with end-organs of both touch and taste." Now the tom-cod (compare the French "tucaud," whiting pout) is a small gadoid which resembles the common cod-fish except in size, but the hake, described by Herrick, is not the same fish as that frequenting British waters, but is allied to the forkbeards.

In the course of a study from a comparative point of view of the brains of gadoids, the very great dissimilarity of the brain of the hake from the brains of other gadoids was very evident. Its brain pattern will, therefore, be described, and then its characteristics, habitat and diet.

The brain is rather smaller that the average brain of a gadoid, and the most obvious difference is to be seen in the cerebellum, which instead of being tongue-like and extending backwards so as to overlap the medulla oblongata is only a median globular eminence, which projects above two lateral lobes which are the very enlarged acoustic tubercles, as is demonstrated when serial sections are examined. These acoustic tubercles, or acustico-lateral lobes, extend backwards and diminish in size so as to form two lateral ridges, which border the rhomboid fossa and merge into the somatic-sensory lobes. These lobes do not produce any globular swellings as in the ordinary gadoid medulla, but they gradually approach the middle line posteriorly, so as to enclose a triangular area within the apex of which appears a minute lobe divided medially by a depression ; this our serial sections prove to be a small facial lobe.

To return to the acoustic lobes, it is found that their extent is not only great laterally but also in a dorso-ventral direction. It is also found when serial sections are examined, that the large-celled granular layer of the acoustic tubercles is both wide and deep, and that anteriorly it merges directly into the stratum granulosum of the cerebellum. There is no central acoustic area. The facial lobes are small and are completely overlapped by the somatic-sensory lobes, but the nucleus ambiguus, the motor root of the vagal lobe, is large and extends some distance in a caudo-cephalic direction. It is quite clear that this picture of the brain of the hake is quite atypical.

According to Gunther Merluccius has some striking features, " The neural spines of all the abdominal vertebræ are extremely strong, dilated, and wedged into one another. The parapophyses of the third to sixth vertebræ are slender whilst those of all the following abdominal vertebræ are very long and broad, convex on the upper and concave on the lower surface ; the two or three anterior pairs are as it were inflated. The whole forms a strong roof for the air-bladder and reminds us of a similar structure in Kurtus."

If any of my readers should be interested in the remarkable structural differences of the backbone and vertebral spines of Merluccius compared with the generalised type of the gadoids, they are referred to a recent account with beautiful illustrations in the *Journal of the Marine Biological Association*, 1937 (vol. XXII, No 1), by E. Ford.

Considering the great depths at which the hake is found, it would seem reasonable that this bony canopy has been evolved to give support to the swim-bladder which must be subject to great pressures. The hake is a deep-water fish, having been taken at depths of 400 fathoms, that is to say, approximately half a mile ; it is also oceanic, only approaching the coast occasionally. It is more abundant on the south coast of England and Ireland than on the other coasts of the British Isles. It is not caught on the east coast of England and the neighbouring parts of the North Sea.

The feeding habits of hake, and its life history, have been studied with great skill and perseverance by Hickling, and he has made the subject accessible to the general reader by an excellent small monograph in the Buckland series. The following are extracts from this work, "The food of large hake consists of fishes and fantails or cephalopods. The most important item is the blue or bastard whiting (gadus poutassou), then come small hake, horse-mackerel, mackerel, fantails and herring, in that order. During winter and spring, when most of the hake are living at depths of 90 to 300 fathoms or more, their food is almost entirely of blue whiting, smaller hake and fantails. When the hake move into shallower waters in summer and autumn they find themselves among herring, mackerel and horse-mackerel, and feed heavily on these fish, as well as on smaller hake. An interesting fact about the food of hake is that bottom-living fish are rarely eaten. All the fishes and fantails, i.e. small cephalopods, which form the main food of the hake, are creatures that live in the middle depths of the sea, such as the blue whiting, which can be caught near the surface in suitable nets in places where the depth is more than 1,000 fathoms, herrings and mackerel, which are usually caught in drift nets, and fast-swimming fantails whose relatives are the giant squids. Since the hake feeds so much on mid-water creatures, it must usually swim in mid-water to get its food. It must be, therefore, usually out of reach of the trawl. But the hake feeds mostly at night and lies quietly on or near the sea bottom during the day. Diminished catches of hake at night are as notable in very deep water (300 fathoms or more) as in shallower water ; it can scarcely, therefore, be a simple matter of light and darkness. When the hake are feeding at night they probably scatter about at all levels of depth in their hunt for food. When we study the food of hake a step farther back we find that all these fishes and the fantails feed on a group of small mid-water fishes and shrimps, of which easily the most important are the krill. Krill are shrimps specially adapted for swimming, and have a definite habit of swimming upwards towards the surface at night and sinking to the bottom by day."

The teeth of hake are sharp and spaced like the whiting, but they are movable with elastic hinges which bend back. They are pigmented and so also is the mouth ; there is a small V-shaped area of dentition on the vomer. Some fishermen say that the bite is poisonous. It is not wise to speculate too boldly, but we feel there is some ground for suggesting that the skeletal changes and the unusual conformation of the acoustic tubercles may be associated with the great range of depth which is so characteristic of its habitat.

THE ACOUSTIC TUBERCLES IN DEEP-WATER FISHES

In the previous pages the unusual pattern of the cerebellum and acoustic tubercles of the hake has been figured and described, and a tentative suggestion was made that the large development of the acoustic tubercles might be due to the great depths (300 to 400 fathoms) in which this fish has been found. An opportunity has since arisen of investigating the pattern of the brain of fishes which descend to great depths, even a mile down, and we propose to describe the remarkable confirmation of the theory that was advanced to explain the brain-pattern of the hake.

The warm waters of the Atlantic provide the Madeira fishermen with a rich harvest in the spring of " Espada," the black scabbard-fish (Aphanopus carbo), which is often so plentiful, that a fish several feet long can be bought for sixpence. Incidentally, it may be recorded that my ignorance was so great that I paid a shilling for a head, to the great joy of both merchant and my friends. This fish is caught at depths of 600 to 1,600 metres, and always is brought to the surface dead.

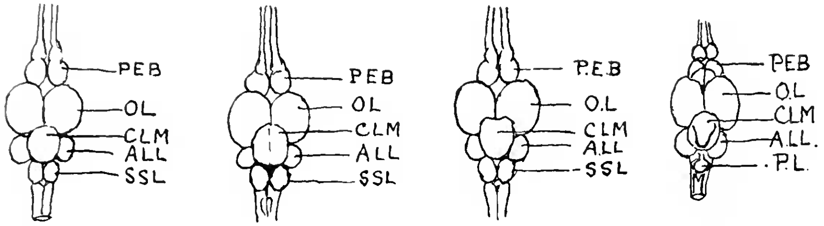
Lying on the slabs of the fish-market these fish appear sheathed in a skin of black patent leather, shiny and without scales, elongated like an eel, with the body compressed rather than round ; the dorsal fin extends as a continuous fringe from head to tail, the eyes are very large, as big in circumference as a half-a-crown, while a fearsome looking head gives support to large and long jaws, both upper and lower of which bear large and prominent teeth. A bite from these fish is accompanied with very severe bleeding, and the blood from the gills is said to produce inflammation, so that the after-results are marked on the fisherman's disfigured hands.

The caudal fin is very small, and there is a narrow constriction separating this diminutive forked tail from the body. The penalty for its large eyes and small tail, is for its dead body to be carried home with the tail threaded through the empty sockets, according to the cook's technique with the whiting. Both fish are very good eating.

This fish, and the others I shall shortly mention, belong to the cutlass-fishes or hair-tails (Family: Trichiuridæ), and curiously enough are distantly related to the mackerel and tunny, the forked tail being the only superficial resemblance that is left. But it is interesting to note that on the same day, in the same market, are to be seen large numbers of tunny and mackerel, and also horse-mackerel and other carangidæ, together with rows and rows of Espada.

On removing the roof of the bony cranium, it is found that the brain is well supported by a thick tenacious mucus, so that it is advisable to harden the brain, before endeavouring to separate it from the enveloping mucus. The brains of all the Trichiuridæ hitherto examined, Plate 23, which include the white scabbard fish, the rabbit-fish (Promethicthys prometheus), and Nesiarchus nasutus, conform to the same type, and recall the type seen in the hake. The optic lobes are relatively not large, the cerebellum small, and not tongue-shaped, bearing on its lateral margins globular projections, which are the acoustic tubercles, more prominent than in the hake. The somatic-sensory lobes are well-marked, but the medulla oblongata does not show any differentiation into lobes posterior to these prominences.

PLATE 23.



Aphanopus carbo. Lepidopus caudatus. Promethichthys prometheus. Nesiarchus nasutus.

PEB—Primitive end-brain. OL—Optic lobe. CLM—Cerebellum.
ALL—Acoustico-lateral lobe. SSL—Somatic-sensory lobe.

The primitive end-brain is globular, of moderate size, and is prolonged anteriorly into smaller olfactory bulbs. Another deep sea fish which I was able to examine was the sea-bream, Brama raii, which also belongs to the Scombriformes, a stout fish with a deep body which descends to over 200 fathoms. On removing its brain it was at once evident that further confirmation of the view was present, that excessive prominence of the acoustic tubercle was associated with a deep water habitat.

The brain of this fish is characterised by a larger optic lobe, and a larger cerebellum than in the scabbard fishes, while the acoustic tubercles though prominent are not so globular. Brama is a pelagic and predatory fish and is often to be seen in the Maderia fish market.

The white-scabbard fish is of similar shape as the black, but is remarkable for its uniform silvery appearance ; it may grow to a length of six feet. According to Norman this is a surface fish, but my informant, Mr. Gunther Mohl, the curator of the Museum at Funchal, told me that it is sometimes caught at 100 fathoms, and

Gunther describes it as a deep-water fish ; it seems probable that this fish has a wide range of movement just as the hake. The teeth are smaller than those of the black scabbard fish, but it has three or four large teeth at the anterior end of the upper jaw. This fish is also known in the seas around New Zealand, and it is very sensitive to cold ; it sometimes swims ashore in its thousands on frosty nights, apparently "in a state of temporary insanity" (Norman). This view does not commend itself to the writer, to whom it suggests some movement very similar to the mass immolations of lemmings and springbok.

The coelho or rabbit fish (Promethicthys prometheus) differs from the preceding, by having a large forked tail like a mackerel ; it is silvery on the dorsal part of the body, while below the lateral line, which is very curved, the tint is greyish ; the dorsal fin has spinous rays and is black in colour. The head is not so elongated as in the two scabbard fishes and the jaws are shorter, but the canine teeth of the upper jaw are curved and prominent. The depth to which this fish is known to descend is from 100 to 300 or 400 fathoms.

It will be wise to consider in some detail the lateral line organs which are supplied by the lateralis nerve ; this, together with the acoustic or eighth nerve ends in the acoustic tubercles or acustico-lateralis lobes. They are pits developed in the skin and run along a line on the sides of the fish ; each has a sensory organ of the same type as is present in the ampullæ of the semi-circular canals of man. The linings of these pits are more sensitive than other parts of the body to effects produced by the flow of water or any change of pressure. They can detect pressure produced by their own movements and, though a fish does not produce vibrations rapid enough to cause sound, yet it cannot move without causing movements of water, and when water moves the pressure changes from place to place and time to time. Special changes occur when it is passed by another fish.

Fish are, therefore, sensitive to both pressure and to impulses from outside. They must also be sensitive to the pressure of the column of water, which in the fishes which we are now considering, must be very great. The effect of great pressure on physical phenomena must be very difficult to estimate ; but we know from the experience obtained in diving operations that talking in compressed air gives the voice a high pitch and sounds squeaky.

There are many other physical facts to be considered in relation to the waves produced by the movement of a body in water and these can be investigated in a ripple tank. To quote an article by Sir William Bragg, "If the water in such a tank is touched circular ripples spread away and the ripples fade away as the circles become wider. If two places are touched at the same time two sets of interlacing ripples start out. Each set goes on its own way right through the other set, as if it were not there." A little imagination will make one realise how important these facts are when we endeavour to understand the function of the organs of the lateral line.

In a discussion on the significance of the enlarged acousticolateralis lobes of Aphanopus carbo there are several interesting facts pointing to a correct interpretation. If we compare the brain of the hake with that of a pollack, both predacious fishes, we note the smallness of the optic lobes in the former (see drawing) ; if sight is of so little importance to the hake in hunting, some other special sense will probably be found to take its place.

Can the lateral line organs take the place of eyes, and of sight ? Hickling is of opinion that the lateral line organs are direction finders, that is to say, are able to interpret the position of a moving object, producing waves at a distance, as these waves would affect differently a lateral organ situate in the front of the body, from one situate posteriorly. Incidentally, it may be noticed that the hake is elongated and, therefore, there is a greater length of lateral line and a longer base for recording waves. This may be expressed in another, more nautical, way, by saying the lateral line organs are able to take cross bearings of a distant fish, from which undulations of water replace the vibrations of light or the waves of photons. The function of these organs have recently been investigated by Dr. Sands at Plymouth ; he has shown that the effect of movements of water in the lateral canals, when recorded by the electric variations in an isolated nerve fibre prove that the lateral line organs are receptors of vibrations.

These researches by Dr. A. Sand, published in the Proceedings of the Royal Society, have been summarised in the Report of the Council of the Marine Biological Association. His method of investigation has shown the great sensitivity of the sense organs to movement of fluid in the canal, and has established the exact proportionality between the rate of flow and the frequency of impulse discharge. The behaviour of the sensory system with reference to displacement of fluid in the lateral line canals proves that they record and perceive vibrations coming from a distance ; and the way in which the impulse discharges follow the frequency of low tones produced in the neighbourhood of the fish justifies the description of the lateral-line system as a form of auditory organ. We have already shown how the experiments of Bragg prove that waves of low frequency are produced by the movements of a fish, but that they are not of sufficient frequency to produce sound. These waves are, therefore, perceived by the lateral line organs and as they are distributed along a long base the wave would be received in varying intensity by organs situated at a distance from each other. In this way a series of observations made by a predatory fish of the waves produced by its prey would enable its position to be plotted, in the central area of the brain, which we have given reasons to suggest, is the acustico-lateralis lobe.

These facts relating to the hake are of still greater importance in the hunting equipment of the scabbard fish and of other deep sea fish ; it is true that these fish have very large eyes but the optic lobes are comparatively small ; however, the acoustic tubercles are very large. The eyes are large in order to obtain the maximum of light in the darkness of the deep, and the optic lobes are of little use until the last act of the drama and the seizing of the prey. The lateral line organs may, therefore, be the means of guiding the attacking fish in pursuit of prey, and this accounts for the functional enlargement of the acoustic tubercles. It must also be noted that the scabbard fish is of great length, and this gives it a long base for their observations and increases the efficiency of the lateral line organs.

CHAPTER XIV

THE EEL. ANGUILLA VULGARIS

IN this chapter we propose to consider the feeding habits of the common eel and its brain pattern, without any reference to the other species which spend their entire life in the sea, such as the conger and the Moray or Muraena; although we shall make some reference to the olfactory lobe and organ of the conger. There is a good description of the brain of the common eel by Burne in the Catalogue of the Museum of the Royal College of Surgeons, from which we quote. Looking at the brain from the dorsal aspect we notice that " in front of the medulla the several regions of the brain are approximately of the same size, and as each is more or less clearly bilobed, the brain appears to consist of four pairs of rounded equal-sized nodules, situated one behind the other. The anterior pair (olfactory bulbs) are slightly pointed in front, and give off two large olfactory nerves. The optic lobes and cerebellum are divided down the middle by a shallow groove. The cerebellum is considerably broader than long. The medulla is small and much shortened." But if the cerebellum is removed, it will be seen that acoustic tubercles are not prominent and that they pass obliquely into two elongated and narrow lobes which are the somatic-sensory lobes; these are continued caudally into the narrow vagal lobes. There is no sign externally of any facial lobes.

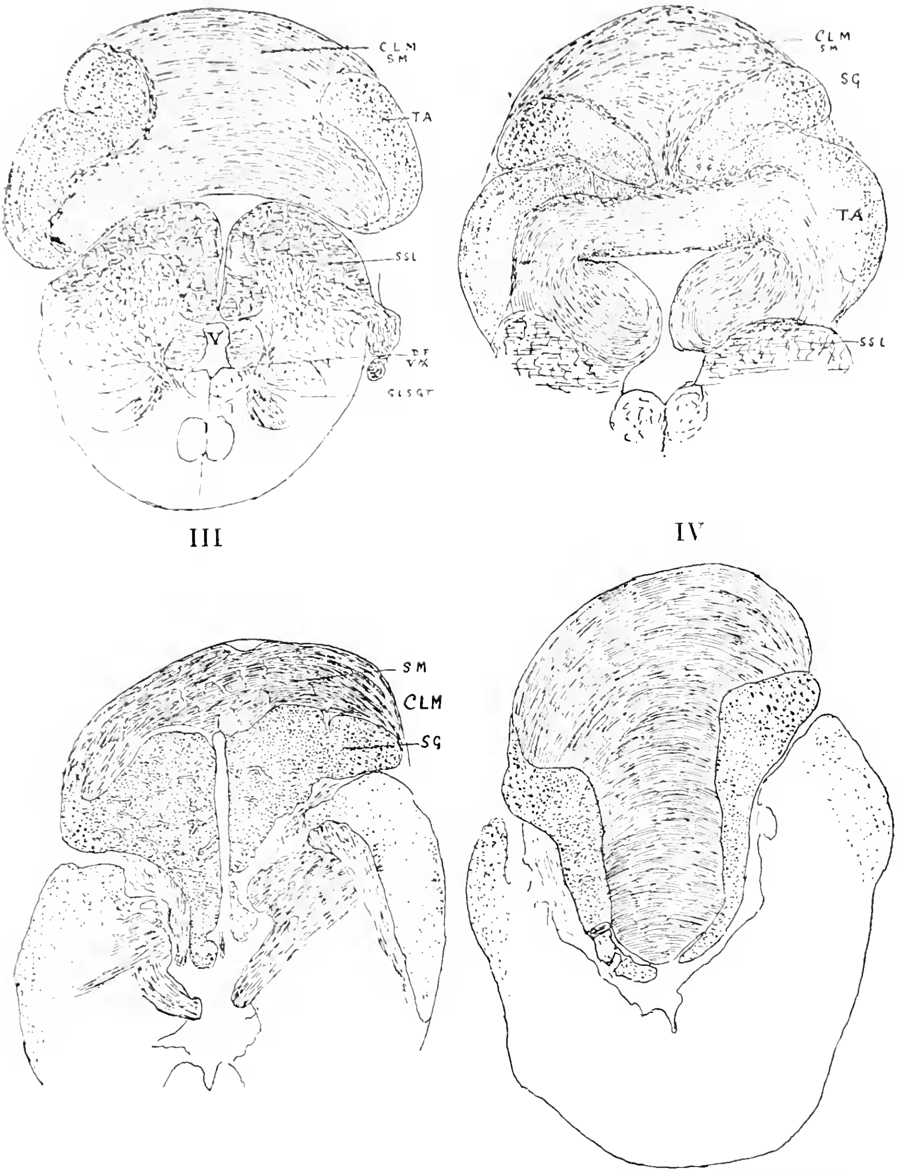
We must now refer to the same writer's description of the brain of the conger, " it is remarkable for the large size of its olfactory centres. It shows a decided right-handed rotation of its anterior lobe. The olfactory bulbs are of great size. The right bulb lies partly below the left, much as in the sole. The thalamencephalon is remarkably long for a teleostean, forming a narrow neck between the cerebrum and the moderately developed optic lobes," a description which applies almost equally well to the condition found in the sole.

We must make a diversion for a moment to point out that not only are the olfactory bulbs of great size, but the olfactory organs themselves are highly specialised. These have been described by Bateson as follows, " the olfactory plates lying within the organ are arranged in two rows on each side of a central raphé, upon which the two rows are folded longitudinally so as to form a lining to the olfactory tube." It is interesting to note when we consider the important part the olfactory system plays in the feeding habits of both eels and soles, that the sole has a similar arrangement of its olfactory plates, but the raphé in the sole is depressed so as to form a groove from which the plates rise up. It will be noted how intimate the functions of smell and taste are in the eels.

In anguilla, taste-buds are present on the tongue and lips and on the skin of the anterior tubular nostril. A section across the medulla of the eel will show that the large facial nerve passes in a transverse direction to end in a large facial lobe on either side, and this oval-shaped area makes a slight bulge into the rhomboid fossa ; however, it does not appear on the surface, being completely covered by the overlying somatic-sensory lobes. Nevertheless, the facial lobes extend a considerable distance in an antero-posterior direction.

It may be recalled that the sole has a minute facial lobe and that taste-buds are absent ; but there is a well-marked central acoustic lobe. In describing the complex cerebellum of the eel, we shall have occasion to refer to its acoustic area. As an earlier study of the cerebellum of the eel disclosed several interesting and suggestive details in connection with its relations to the acoustico-lateralis lobes, I have re-examined the serial sections and made a series of drawings under low power by the help of a Leitz projector. Plate 24 is a section across the commencement of the acoustic tubercles, and the cerebellum is seen overhanging the prominent fifth lobes of the medulla. Fig. ii is a section across the most prominent portion of the acoustic tubercles which are here both broad and deep ; the superior extremity of the large-celled area on either side curves medially and merges with the stratum granulosum of the cerebellum, which does not extend across the middle of the cerebellum as is usual among the teleosteans, but is divided medially ; the result is that two sigmoid areas are formed, facing each other, and formed by the large-celled tissue of acoustic tubercles and the stratum granulosum of the cerebellum. The stratum granulosum extends right up to the lateral margins of the cerebellum and in the middle line there is a narrow band of stratum moleculare separating the two sigmoid areas. In this section there can be seen a small group of cells on either side representing the central acoustic area of other fish ; it is necessary to note this, as it is said by some observers that an eel can grunt, and therefore we would expect some indication of an acoustic area. Fig. iii is a section still further forward where the acoustic tubercles have ceased to be

PLATE 24.



Four transverse sections of the cerebellum and acoustic tubercles of the eel Anguilla vulgaris. Fig. I.—The most posterior shows the large acoustic tubercles T.A. on either side of the stratum moleculare of the cerebellum. S.S.L.—The Somatic-sensory lobes give off descending fibres and between these and the ventricle V is seen the beginning of the facial lobes. G.L.S.G.T.—Great lateral secondary gustatory tracts. Fig. II.—More anterior. The acoustic tubercles form a sigmoid curve with the strata granulosa. Fig. III.—The next in an anterior direction shows the large divided strata granulosa and Fig. IV the stratum moleculare dips down between them so as to produce an inverted pear-shaped section.

joined with the cerebellum. The stratum granulosum occupies the greater part of the ventral portion of the lobe extending from one lateral margin to the other but divided in the middle line by an extension of the ventricle, so that the cerebellum would be divided into two, it if were not for a narrow area of stratum moleculare which unites it dorsally. The acoustic tubercles are still present in this section.

In the last figure (iv) the cerebellum has become considerably narrower and it is no longer divided medially. The stratum granulosum now occupies the lateral margins of the ventral portion of the lobe, while the greater part of the lobe is formed by a central area of stratum moleculare which expands dorsally into a hemispherical prominence. This description may seem tedious but we shall now suggest the possible functional significance of this unusual type of cerebellum.

We are now in a position to review the relative importance of the various sense-organs represented in the brain of the eel, and certain conclusions seem to be clearly indicated. The olfactory system is obviously very important, as shown by the size of the olfactory bulbs and the complexity of the olfactory organ. The insignificant size of the optic lobes reflects the secondary importance of sight in the feeding habits of a nocturnal animal. It is true that the eyes of the silver eel become enlarged, previous to the trans-atlantic migration, but this phenomenon is probably due to the obscurity of the depths into which it will enter. The gustatory system is next in importance, as shown by the large size of the facial lobes, which receive all the afferent fibres from the taste-buds of the lips, tongue, and the marginal barblet of the nostrils. This picture is in marked contrast to the condition found in another nocturnal feeder, the sole, which has poorly developed facial lobes but a highly developed central acoustic lobe ; we have just seen how poorly developed the central acoustic area is in the eel ; this seems to be but another example of the fact that the facial lobe varies inversely in size with the acoustic lobe and vice versa.

The question which presents some difficulty is the significance of the large size of the acoustic tubercles and their relations with the cerebellum. Here there are three points to be considered, first, the width and depth of the large-celled tissue of the acoustic tubercles, secondly, the fusion of this tissue with the mesially divided stratum granulosum of the cerebellum, and thirdly, the division of the cerebellum into halves, connected only by a dorsal band of the stratum moleculare. The only fish that we have had an opportunity to examine that has an equally large acoustic tubercle is the hake and the scabbard fish; these fish are known to frequent depths of over 400 fathoms. During its migration the eel swims at great depths, and it is difficult to say what depth it descends when it enters the final stages of its reproductive activity. The division of the cerebellum and the union of the tissue of the acoustic tubercles with the divided stratum granulosum must be considered together. It would seem almost inevitable that the acoustic-lateralis area should join up with the inner ends of the stratum granulosum as this tissue extends peripherally to the lateral margins of the cerebellum; so that this condition may be said to be the result of the divided cerebellum; further this division might reasonably be expected to be of some value in direction finding, and the direction-memory that sets the course to the Atlantic abyss and tropical trysting place may be helped and furthered by this adaptation.

The diet of the eel varies very much with its age and the old eels are not only predatory but almost omnivorous. According to Tata Regan, the diet of the yellow eel is chiefly worms, small fish, crayfish, etc. Like the sole it is a nocturnal feeder. As is well known the eel ceases to feed when about to undertake its migration to its breeding ground. There are other interesting facts which affect the brain, in association with this phenomenon, but we must defer describing them until we have mentioned some recent observations on the pituitary gland in fish generally.

CHAPTER XV

THE ANATOMY OF GUSTATION

G. H. Parker, of Harvard, in his monograph on smell, taste, and allied senses, says: "there are no separate gustatory nerves in the vertebrates as there are olfactory nerves and optic nerves. Gustatory fibres occur in several cranial nerves and it is by means of these that the taste-buds of various regions are provided with those nervous connections that have been described." The result of our study of the distribution of the taste-buds in a large number of fish of different species makes it clear that taste-buds, although as regards their microscopic anatomy they are apparently similar, yet have functions that vary according to their central representation in the medulla oblongata. Taste-buds supplied by the facial nerve have a true gustatory function; those supplied by the glossopharyngeal nerves on the soft palate, etc., have a sentinel function, connected with swallowing, and those supplied by the vagus have a sentinel function designed to protect the lungs from food-stuffs, a directional function.

Taste, like smell, is a chemical sense, and the gustatory organs enable the animal to recognise sweet, sour, salty, and bitter substances. Fish living entirely in a fluid medium must necessarily be furnished with an extensive gustatory system and so we find that certain families not only possess taste-buds over the whole surface of the body, but have a peculiar comb-like organ with ridges covered with taste-buds in the mouth known as the palatal organ.

Recently the late Prof. A. E. Boycott, when examining the orifice of the pneumatic duct which leads from the swim-bladder into the gullet, noticed that there was a ring of taste-buds, and that these guarded the entrance to an enlargement of the duct of an unusual structure. This is known as the pneumatic bulb.

This observation has been confirmed and described by myself in the tench, and the significance of the existence of taste-buds in this situation pointed out. Recent experiments by Damant and Evans have proved conclusively that under normal conditions fish with a pneumatic duct, opening into the gullet, fill their swim-bladder by coming to the surface and swallowing air, which is pumped into the bladder by the pneumatic bulb. The taste-buds, it would appear, act as sentinels and discriminate between the food and the swallowed froth, which can be observed lying at the orifice of the pneumatic duct. When it is borne in mind that in man taste-buds are known to be present not only on the tongue but also on the anterior pillars of the fauces, the under surface of the palate, the pharynx, and the epiglottis, it becomes clear that in man also these organs must at times have a function other than true taste and can also be regarded as sentinels, particularly those situated on the epiglottis, which is an important part of the mechanism which prevents food "going the wrong way."

The barbels of fish are usually well supplied with taste-buds and they have been described on the margin of the anterior nostril ; but perhaps the most unusual position in which they have been found is in the site of the dorsal fin in the rockling.

It is clear from the facts above, given as to the site of taste-buds, that these organs can perform different functions, and we can give, as an example, the exercise of these functions as they occur in a carp. In the process of feeding the fish first of all recognise the presence of food by smell, which may be called a distance receptor ; the food is then examined by the gustatory organs, the taste-buds on the lips and barbels, and, if considered satisfactory, it is passed on to the palatal organ which, in mud feeding fish, separates the inorganic particles from the proteins and carbohydrates present in the mud before passing the nutrient material into the gullet ; the innervation of the first stage of taste is by the facial nerve, and the central connection in the brain is the facial lobe ; the innervation of the second stage is by the vagal nerve and the central connection is the vagal lobes. Again, when the carp swallows air, the air must pass the taste-buds in the lips and after being swallowed passes with a certain amount of mucus into the gullet and thus reaches the orifice of the pneumatic duct where it is recognised by the taste-buds there present ; the pneumatic bulb then sucks in the air bubbles and drives the gas into the swim-bladder. The innervation of these taste-buds is also by means of the vagal nerve and the central connection is the vagal lobes.

It would appear, therefore, that the facial lobe is concerned with purely gustatory sensations, whereas, the vagal lobes have a discriminatory function allied to taste which enables the animal to sort and sift, retain or reject, by means of the palatal organ and also to separate air bubbles from solid matter by means of the sentinel ring of taste-buds guarding the orifice of the pneumatic duct. These considerations have also their counterpart in the gustatory mechanism in man ; here the anterior part of the tongue is supplied by the chorda tympani, which represents the branch of the facial nerve passing along the inner surface of the mandible in fish and the taste-buds have a true gustatory function.

The anatomy of fish and its nomenclature is very much obscured by the fact that the detailed knowledge of human anatomy supplies the terms which are used in describing simpler, but similar, structures in a lower vertebrate, such as a fish. We propose to approach our problem in the reverse direction and follow the simple nervous structure of a fish upwards to the higher vertebrates. If we take the facial lobe of a carp, a typical teleostean fish, we note that the facial lobe lies anteriorly to the vagals, and can be looked upon as a forward extension of the latter, although in this fish the bilobed character of the facial is lost. It receives all the gustatory fibres by the VIIth or facial nerve from the lips, tongue, barbels and body. This nerve, the VIIth, or as it is called by T. H. Huxley, the portio dura, has been described by this great anatomist, in the pike. "The portio dura of the pike, which leaves the skull by a special foramen in the pro-otic bone, traverses the hyomandibular bone and then divides into two branches, one of which runs backwards to the hyoidean arch, while the other is directed forwards and downwards and passes to the inner surface of the lower jaw, along which it runs to the extremity of the ramus." This last branch is represented in Man by the chorda tympani. But, as has already been stated, the facial muscles so important and largely developed in man are not represented at all in fish. Hence, in the latter we might expect to find, only mandibular, and hyoidean branches of the portio dura corresponding with the chorda tympani on the one hand, and the stylo-hyoidean and digastric branches on the other in man. And this is really the case, as the following pages will show.

The facial nerve in man at once raises the picture of a lop-sided face, due to Bell's paralysis, which is caused by disease affecting this nerve. Sir Charles Bell, the first neurologist, insists that this nerve is the respiratory nerve of the face and points out its diminished importance in fish as being due to the absence of facial muscles in these animals. The correctness of this assumption is borne out by the study of the facial lobe in Teleosts, which we have seen is an anterior extension of the vagal lobe. Huxley helps us to understand the change in the function of this nerve. He points out that the portio dura of the seventh nerve in man perforates the petrous bone, and after skirting the inner wall of the tympanum leaves the skull by the stylo-mastoid foramen. Before it does so it gives off a recurrent branch, the chorda tympani, which takes a very singular course, entering the tympanum, crossing the auditory ossicles, to make its way out at the front wall of the tympanum, then uniting with the gustatory division of the trigeminal, or Vth nerve, and, passing along the inner side of the ramus of the mandible with it, until eventually it leaves it to become connected with the submaxillary ganglion. The principal portion of the portia dura, on the other hand, makes its way out by the stylo-mastoid foramen and is distributed to the facial muscles, some comparatively insignificant branches only being furnished to the levators of the hyoid and depressors of the lower jaw.

We can now refer to the studies of Cushing and others which prove that the Vth nerve takes no part in the innervation of taste-buds in man. According to the diagram after Cushing, the taste-buds of the tongue are innervated by the IX or glossopharyngeal nerve and fibres pass along the lingual nerve which are continuous with the chorda tympani and end in the geniculate ganglion. It is established, therefore, that the true courses of the nerves of the taste-buds of the tongue are through the VII and IX nerves.

An interesting and difficult problem arises. How are we to explain the fact that a taste-bud seems to be associated with a particular function according to its situation, and that there is no anatomical difference in its structure wherever it may be situated. It would seem that taste-buds have varying functions, or rather that the afferent impulses from a taste-bud have a different effect according to the part of the brain, in fish a lobe, which receives the stimulus. If we assume that the facial lobe receives impressions recognised as of a true gustatory type and the vagal lobe receives impressions recognised as of a warning type we explain the varying functions of the taste-buds as due to their central nervous representation.

The facts remain clear, however, that the facial nerve in fish is primarily a sensory nerve carrying gustatory stimuli and has only a small motor element. The facial in man is an important motor nerve supplying the face muscles and also has a stylohyoid and digastric branch ; its small sensory element appears as the chorda tympani and this is the nerve that carries true gustatory stimuli from the anterior part of the tongue and the circumvallate papillæ. The warning and discriminatory impulses in fish are carried by the glossopharyngeal and vagal nerves from the branchial region and palatal organ to the vagal and glossopharyngeal lobes and the vagal receives also sentinel impulses from the taste-buds surrounding the orifice of the pneumatic duct.

In man the taste-buds of the palate and pillars of the fauces are innervated by the glossopharyngeal nerve and here food is prevented from passing into the post-nasal space ; the sentinel taste-buds of epiglottis and pharynx are innervated by the vagus and thereby a mechanism is called into play that prevents food entering the glottis. It would appear that the central connections in the brain interpret the sensations received in accordance with the area from which the afferent impulses arise.

In concluding these details of the facial lobe, it is necessary to mention the large lateral nerve that conveys the gustatory impression from the skin. The facial nerve has a ganglion called the facial or geniculate ganglion ; into this the lateralis portion of the facial enters ; it has the following branches each of which may have a ganglion at its root a superficial opthalmic, a buccal and an external mandibular branch.

As regards the names of the prominent lobes of the medulla it may be well to mention that the large bilateral lobes have been called the lobus posterior and the pneumogastric lobe, while the central lobe or anterior have been called the mediam lobe of Baudelot or the " lobule mediane du Bulbe." The terms now in common use are, the vagal lobe for the former and the facial lobe for the latter. Herrick has made a detailed examination of the skin of a small cat-fish and has prepared a diagram reproduced in many textbooks of the distribution of the taste-buds over the external surface and of the cuteneous branches of the seventh nerve which supply them. A broad summary of the above facts relating to the lobes of the medulla can be made in Herrick's words, " The vagal lobes for mouth-tasting and facial lobes for skin-tasting are local enlargements of the visceral sensory brain as is illustrated in the dog-fish. All the taste-buds in the pharynx and back part of the mouth are supplied by the vagal and glossopharyngeal nerves—those in front of the mouth lips and outer skin from a root of the facial nerve which apparently corresponds with the portio intermedia of human anatomy."

The whole matter is best summed in the words of Sir Charles Bell, " an animal may have a particular organ developed and with the external apparatus there is a corresponding or adjusted condition of the appropriated nerve."

APPENDIX I

THE IX NERVE

In our description of the vagal lobes and facial lobes in fish, we have, hitherto, made little reference to the glossopharyngeal lobe and nerve. This lobe lies just anterior to the vagal lobe and is only to be defined by the study of serial sections. The ninth or glossopharyngeal nerve is, according to the Cambridge Natural History (Fishes), perhaps the most typical of all the branchial nerves ; it has a pre- and post-branchial branch which enclose the hyo-branchial cleft. It has a palatine branch which extends forwards and anastomoses with the corresponding branch of the seventh.

The latest authoritative description of the taste-buds in the adult human being says that " they have been identified on the dorsal surface of the tongue except the mid-dorsal region on both the anterior and posterior surfaces of the epiglottis on the inner surface of the arytænoid process of the larynx on the soft palate above the uvula, on the anterior pillars of the fauces, and on the posterior wall of the pharynx. In fishes the taste-buds of the gill region are supplied by the vagus and the glossopharyngeal. In man certain parts of the vagus are distributed to the larynx and to the epiglottis as well as to the most posterior part of the tongue and innervate the taste-buds of these regions.

The glossopharyngeal supplies the posterior third of the tongue, including the foliate and vallate papillæ and adjacent part. The anterior part of the tongue is supplied by the chorda tympani of the facial as we have seen above. The view that each area of taste-buds has a different function according to the central connections of the nerve which carries the afferent impulses to the brain is strongly supported by these anatomical details. It would appear that, in man, there are three areas to be considered, the true taste area supplied by the facial nerve, an area on the anterior pillars of the fauces and uvula supplied by the glossopharyngeal nerve which controls the act of swallowing and prevents food entering the posterior nares and an area presided over by the vagus on the posterior wall of the pharynx and epiglottis which prevents food entering the windpipe.

CHAPTER XVI

HEARING, EQUILIBRIUM AND THE CEREBELLAR FUNCTIONS

It has been the aim of this comparative study of the cerebellum and acoustic tubercles, or more correctly the acoustico-lateralis lobes, to disentangle the various functions of the nervous components of this complex area.

If it is found that certain areas in the cerebellum and acoustic tubercles are enlarged in a particular fish, endowed with certain habits or mode of life, and diminished in a fish that has not these habits or mode of life; it seems reasonable to associate this area with a certain function, to which the habit or habitat gives the clue.

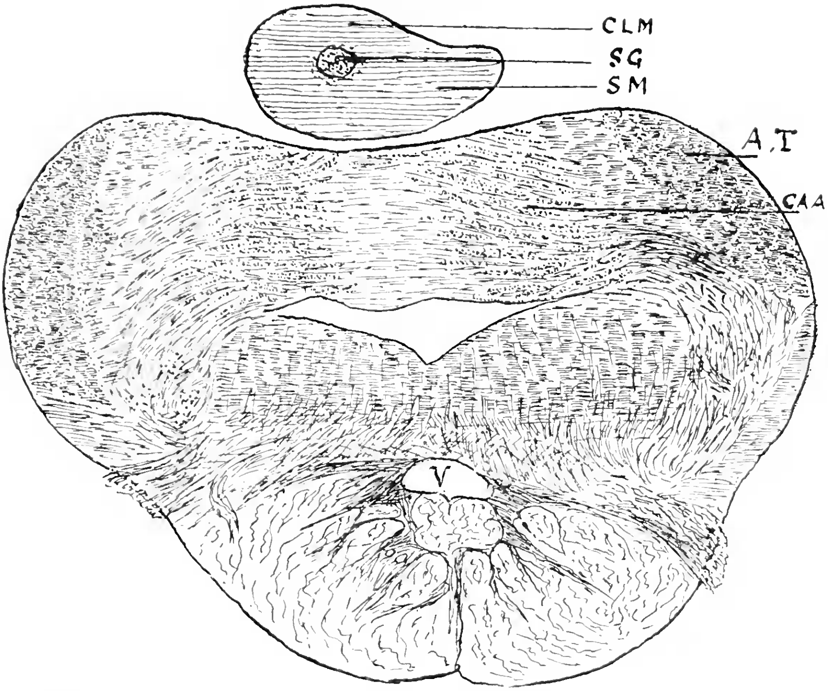
For instance, if it is found that a surface-feeding fish has an accessory air-breathing organ, and that this fish has an enlarged area at the base of the cerebellum which is rudimentary or absent in other members of the same family of fish, it is reasonable to associate these two facts with a common factor, namely, the atmosphere, in the one case the air is the medium for supplying oxygen and in the other the vehicle for the perception of vibrations or sound; in other words respiration and audition; and this is the case in certain Indian fishes, as has been shown by Bhimachar, in which the central acoustic lobe is well marked in proportion to the development of an accessory air-breathing organ. When we examine these facts closer we find that in plankton-feeding animals such as the herring, bleak, etc., there is a similar development of the central acoustic area which in some fishes becomes a separate lobe.

But before we proceed with this discussion of the acoustic area, we propose to describe the microscopic structure of the acoustic tubercles of the scabbard fish, a bathysmal fish, living at a depth of 600 to 1,600 metres; the naked eye appearance of these tubercles has already been described, and they are typical of all the bathysmal fishes we have had an opportunity to examine.

If a section across the most prominent part of the large acoustic tubercles be examined (Plate 26), it will be seen that the lateral convexities consist of the typical small-celled tissue, so characteristic of this area, in which the peripheral cells are found in small groups.

This greatly enlarged area appears to diminish gradually in extent towards the middle line, so as to give the appearance of a pyramid (in section), the apex of which nearly meets that of the opposite side. The small-celled tissue at the apex becomes gradually replaced by elongated pear-shaped cells, which bridge the intervening gap. The cerebellum in this section is completely separated from the acoustico-lateral areas, and has its typical conformation of strata granulosum and moleculare. But continuous and inferior to the small-celled area we have just described is a narrow area of transverse fibres interspersed with rows of small cells, which we recognise as similar to the central acoustic area we have described in the carps. The remaining portion of the lobe consists of a tissue similar to that of the stratum moleculare with a few large cells

PLATE 25.



A transverse section of the brain of the Black Scabbard fish (Aphanopus carbo) across the commencement of the acoustic. A.T.—tubercles and the cerebellum. The central acoustic area C.A.A. is well seen and fibres passing from it to the auditory nucleus. S.G.—Stratum granulosum and S.M.—Stratum moleculare of C.L.M.—Cerebellum.

scattered here and there. If we now examine a section posterior to the above (Plate 25), we find that the special tissue of the acoustic tubercle occupies but a small part of the periphery of the lobe and that the lobe is made up of tissues of the central-acoustic type, fibres which pass downwards and outwards to enter a gangloinic mass of cells before joining the fibres of the eighth nerve. At this level the tip only of the cerebellum appears, while below the somatic sensory lobes are seen to meet in the middle line, although anteriorly these lobes are separated, and form a widening of the rhomboid fossa.

The importance of this special adaptation of the acoustic tubercles must be emphasised. Here we find a typical section of a cerebellum, separated from a highly differentated acoustic tubercle, the granular areas of which meet medially and are joined up by a group of large nerve cells.

This area is again completely separated posteriorly from a central acoustic area, in which there is no intermingling of lateralis nerve fibres. These three areas differing so markedly in structure must clearly be endowed with separate functions, and their relation to function can only be assessed by comparison with other teleostean types.

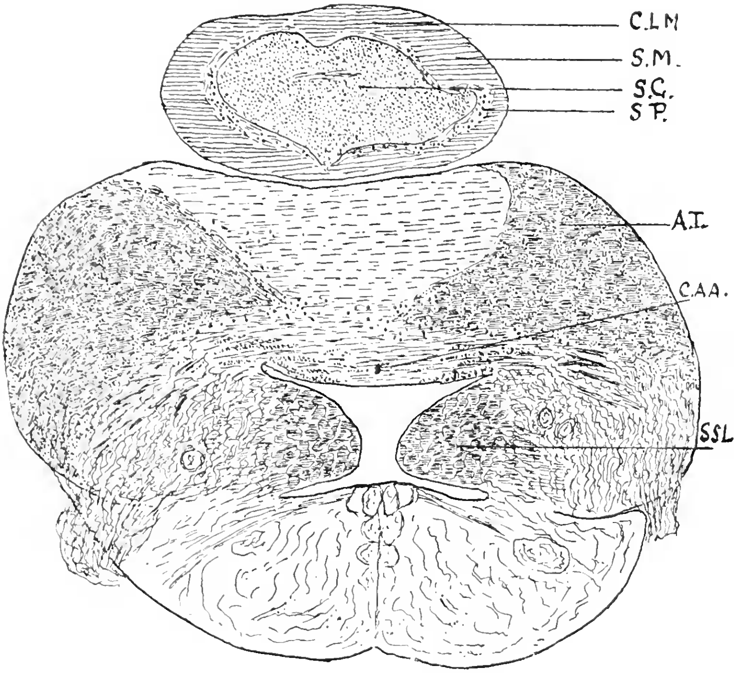
If we refer to the drawing of the brain of the herring, we see that the central acoustic lobe forms a definite projection mesially and that some fibres from it pass outwards to the acoustic tubercles, but most of the fibres pass downwards and outwards to a ganglionic mass before joining the eighth nerve ; in this family the central acoustic lobe is the largest and most differentiated element in the acustico-lateralis complex. If we now consider the minnow a fish, which in the laboratory of Prof. von Frisch has revealed a nacute perception of sounds, by means of a modified Pavlov technique of conditioned reflexes, we find that it has a well-developed central acoustic area, in which both cells and nerve fibres form a characteristic pattern ; this we look upon as the central representation of the auditory function.

It may be noted in passing that the gurnard, a fish with a sound-producing mechanism, has a similar central acoustic area to that of the minnow. Von Frisch has also shown experimentally that the saccule in the minnow is the peripheral sense organ for the perception of sound waves. We must, therefore, associate the similar area in the scabbard fish with audition.

The work of certain Japanese investigators seem to confirm the usually accepted view that the cerebellum proper is concerned with equilibration. By a process of exclusion, therefore, we reach the conclusion that the enlarged lateralis area in the scabbard fish must be associated with the organs of the lateral line which as Dr. Sands has shown are the organs for the reception of waves of low frequency.

According to Sand, Hoagland was the first to discover the spontaneous activity of the lateral-line receptors and the former has shown that the lateral-line system is exceedingly sensitive to low-frequency vibrations. " Direct mechanical stimulation of the lateral line, as well as vibrations propagated from a distance, are effective in exciting the reception, on account of the movements they cause to occur in the endolymph of the canals." Let us consider what theoretical advantage to a deep-sea fish there would be in the increased development of the acoustic tubercles.

PLATE 26.



A transverse section a little anterior to that shown in the previous Plate. The cerebellum is larger. The acoustic tubercles are very prominent and have a triangular shape in section with a curved base. Where the apices approach each other the round celled tissue is replaced by scattered large cells. A small area of central acoustic tissue is still seen. S.P.—Cells of Purkinje. S.S.L.—Somatic-sensory lobes.

It must be remembered that the lateral line of the black scabbard fish may extend for from four to five feet or more and, therefore, a vibration reaching the fish when in an oblique position as regards the object, from which the disturbance proceeds, would excite the anterior sense organs with a vibration of greater amplitude than that which would reach the organs situated at the posterior extremity. This, it is clear, would enable the lateral line to be used as a direction finder. When the fish becomes directly head on to the object producing the waves, the lateral organs of either side would receive an equal stimulation. The fish would now go all out in the direction of equal stimulation and on sighting the prey, when almost on top of it, would open its capacious mouth, and the final stage of the tragedy would end in the capture and swallowing of the victim. It is difficult to conceive any other system of direction finding than a series of observation points situated along a base of several feet, and the proved capability of the lateral line organs to receive such vibrations, as would be made by a moving object, makes this explanation seem most probable.

When we add to these considerations the facts of the great enlargement of the acoustic tubercles in those bathysmal fishes, which can find no use for sight in hunting for their daily bread, and also recall the fact that the eyes of these fish, though large, are associated with quite small optic lobes, there seems no doubt that this explanation of their methods of hunting is highly probable.

We have mentioned the more recent work on the function of the lateral-line organs, but have not described the work of G. H. Parker, who cut the nerves of the lateral line and also the fifth and seventh nerves supplying the similar organs on the head of fish ; he then compared the behaviour of fishes so treated with normal specimens. The result of these experiments was to suggest that the chief use of the lateral-line organs is to perceive the movements of other fish in the water.

Cunningham, in commenting on Parker's work, says, " we do not know at present to what distance vibrations due to such movements would extend, but it is evident that if a fish is affected by a body falling in the water, it must also perceive the movement of another fish or animal in the water. The above account of the various methods of hunting that are employed by fishes has proved that some fish hunt by sight, some by smell, and some by taste, but experiments have so far not been made to ascertain how far a fish without sight or hearing would be able to preceive an enemy in its neighbourhood or detect the exact position of the fish it preys upon.

In conclusion, we must refer to the observations in a previous chapter, on the acoustico-lateralis lobes of the eel. It will be remembered that these lobes were very developed and had an unusual relation to the stratum granulosum of the cerebellum; we are inclined to think that this adaptation may be the result of its deep-sea habitat in the later stages of its life journey.

CHAPTER XVII

VALVULA CEREBELLI

We purpose in this chapter to refer in a little more detail to the valvula cerebelli, which has been mentioned on several occasions in connection with mormyrus and the barbel. The anatomical position of this organ does not render it accessible to experimental biological research ; if efforts were made to ablate this organ in the living animal it would be necessary after exposing the tecta optica of the optic lobes to remove them and then to dissect out the valvula from its posterior attachment to the body of the cerebellum. This might be possible in a hardened brain in the dead animal, but it would involve very serious damage to other parts if attempted in the living animal, and the results of such an ablation, as shown by the behaviour of the fish, would be open to justifiably adverse criticism. This being the case it seems that an attempt at understanding the physiology of the valvula might be undertaken by a series of anatomical observations on groups of fish closely related, but yet differing in a marked way in their habits and behaviour.

There has been very little done in this direction, but it may be of some value if the facts already known about this organ be mentioned, and they may suggest an attack on this problem by other workers. In the cod, Gadus morrhua, the hinder part of the optic ventricle is occupied by a forwardly projecting process of the cerebellum, the valvula. " This structure is formed by the invagination of the anterior parts of the cerebellum into the cavity of the midbrain, and thus in sagittal section shows two super-imposed layers—the lower one continuous behind with the cerebellum, and passing in front by reduplication into the dorsal layer. The latter is closely applied to the first and is continuous posteriorly with the hinder margin of the tectum opticum." This description is taken from the physiological catalogue of the Royal College of Surgeons and, accompanying this, are drawings which demonstrate the relations very clearly (page 19).

If we dissect the brain of a mackerel we find a very different picture. The valvula cerebelli occupies the major part of the cavity of the optic lobes and causes them to appear very large.

There is a central portion continuous with the cerebellum and two lateral sausage-like lobes which are bent backwards on each other so that their terminations turn inwards towards their attachments to the central lobe. The Trichiuridæ which include the scabbard fishes are nearly related to the Scombriformes so it is not surprising that they have also a special development of the valvula, as we have demonstrated in serial sections of the Black scabbard fish. When we come to the carps we find that in the ground-feeding members of the family the tecta optica are more or less widely separated by the protrusion of a large valvula, so that the optic lobes are superficially very large and this is most marked in the Barbel.

As we have already noticed, Mormyrus has a brain remarkable for the immense development of the valvula which bursts through the tectum opticum and forms a canopy over the whole brain. To quote the R.C.S. catalogue, " this unusual relation of the valvula cerebelli to the tectum opticum appears to be a further extension of some such process as that seen in the carp, in which the lateral parts of the tectum are divaricated and the central area much thinned out, but without extrusion of the valvula. The wings of the valvula are called anterior lateral and posterior. Their deep surface is occupied by a layer of small cells (nuclear layer) covered over superficially by a number of parallel ridges, each composed of molecular, nuclear, intermediate, and fibrous layers." The result is of a very beautiful design.

We will now mention a fact of great importance, as will be seen later, that the valvula is connected by tracts to the lobi inferiores, a structure which will be the subject of the next part of this chapter. As to the function of the lobi inferiores, we have the authority of Herrick for the statement that "the ascending secondary gustatory tract of both facial and vagal lobes terminate in the superior secondary gustatory nucleus, situate in the lateral wall of the isthmus. The third chief gustatory tract arises from the cortical layers of the above ; this tract is somewhat obscure, but it has been proved that fibres pass from it ventrally to the lateral lobule of the lobus inferior." He also gives a diagram showing the relations of the olfactory and gustatory paths in teleosts in which an olfactory conduction path terminates in the lobus inferior, " this is the chief centre of correlation of olfactory and other higher senses."

THE LOBI INFERIORES, SACCUS VASCULOSUS AND INFUNDIBULUM

There is an area of the brain that receives in teleostean fish even less consideration than the cerebellum does in human anatomy —we refer to the ventral surface of the brain which lies beneath the optic lobes, posterior to the crossing of the optic nerves, and anterior to the medulla oblongata. This area is illustrated in the drawing of the brain of the halibut. In the right hand figure the lobi inferiores appear partially obscuring the large optic lobes. They are large bean-shaped bodies with their median surfaces in apposition. In the middle line in front of these is the spherical pituitary body. The apposition of the pituitary body and lobi inferiores is not complete, and a triangular space is left, by which there emerges, on the ventral surface of the brain, the red thin-walled saccus vasculosus.

Anterior to the lobi inferiores, the most prominent area of grey matter is the lobus infundibuli. From the third ventricle, which lies in front of the level of the optic lobes, there passes a hollow passage in the body of the lobus infundibuli. This passage is prolonged downwards and somewhat backwards and communicates ventrally with the cavity of the pituitary body. Whereas the ventricle is lined with ciliary epithelium the infundibulum has a lining of ependyma, which in part consists of large multipolar nerve cells. Before terminating in the cavity of the pituitary, that is to say more dorsally, the infundibulum communicates with large cavities within the lobi inferiores, and finally it is prolonged into the saccus vasculosus ; this is a thin-walled glandular sac and is very vascular ; its function would appear to supply the ventricles with their fluid content. If the drawing of the transverse section of the optic lobes of the plaice be referred to the saccus vasculus will be seen and its communication with the infundibulum.

The ventricles of the lobi inferiores are also to be seen, and dorsal to them on either side are two very characteristic oval areas of nerve cells, these are the nuclei rotundi. The minute anatomy of these nuclei is as follows : a number of round or oval islets of grey matter lie in a granular matrix interspersed with nerve fibres. Nerve fibres pass from the ventral part of the lobi inferiores into the nuclei and some surround it. Dorsally, a large strand of nerve fibres passes from the nucleus to the thalamus.

Before considering the very important subject of the pituitary body, we propose to mention the relations of the lobus infundibuli to the lobi inferiores. We have made a special study of the course of the nerve connections in the Megrim as well as the sole, plaice, and other flatfish. If we examine sections of the lobus infundibuli, we note that anteriorly beyond the attachment of the pituitary body, fibres pass ventrally from either side of the infundibulum, and unite to form a median bundle of nerve fibres ; a little further caudally, a meshwork of fibres appears on the lateral margins of the mesencephalon, and the median bundle becomes dumb-bell shaped. Further back still the median bundle divides into two trunks which move dorsally. The pituitary is here attached to the margins of the infundibulum, and a ganglion appears on either side of the attachment, from which fibres pass dorsally along the margin to the meshwork before mentioned. Finally nerve fibres pass from this meshwork to join the fibres of the nervus infundibuli, and the combined trunk enters the ventral end of the nuclei rotundi. It thus appears that the lobi inferiores are the co-ordinating centres, not only for the olfactory and hypothalmic impulses but also for the optic and gustatory nerves, and that the nuclei rotundi also receive fibres from the infundibulum and from the lateral nuclei at the attachment of the pituitary body. As we have already seen fibres pass to these lobes from the valvula cerebelli, so that there is every reason on anatomical grounds to consider the lobi inferiores are an important organ for regulating the various messages received from both sensory organs and hormone producing organs as the pituitary body and possibly also the pineal gland.

CHAPTER XVIII

THE PITUITARY BODY

The late Professor Haldane once said that anatomy, if studied with intelligence, can be as important as physiology in the investigation of function. In this chapter I hope to be able to convince my readers that this is possible ; if the pituitary body is studied with a definite object in view, results can be obtained without the aid of experimental biology, which are quite as convincing as many physiological experiments. The only drawback to this method is the length of time involved to get the required answer to the problem set before the observer. Before describing the pituitary body of the eel, which is the fish we have chosen to study, we may state that it is known that in vertebrates, this gland produces hormones (chemical messengers) that have a great influence on the generative organs, and these are known as gonadotropic hormones ; it is further known that certain changes take place in the gland, as shown by the staining reactions of certain cells, when these hormones are producing their effect.

Now the eel, as is well known, puts on its wedding dress, which is evident when it changes from the yellow eel to the silver eel, and its eyes become larger and its flesh becomes firmer, when it is about to migrate and start on its marvellous journey to its breeding ground. These changes do not take place in the British Isles as a rule until the end of the summer or the beginning of autumn. Now it occurred to the writer, as the result of certain findings as to the appearance of the gland when sections were examined, which did not tally with textbook descriptions, that the differences noted might be due to the different periods of the year, at which the fish had been taken. This proved to be the case and it was decided to make a systematic series of examinations of the pituitary of the eel, commencing in the spring and going on month by month until the end of October, or the beginning of November. These observations were carried out during a period of two years, and it was very definitely shown that marked changes took place in the microscopic appearance of the gland in September and October ; and it was further shown that these changes took place before the ovaries and sperm began to develop and could be clearly recognised. The conclusion drawn was that we had demonstrated a connection between the hormonic activity of the gland and the physiological urge to migrate.

The pituitary body of fish is a small body resting just in front of the lobi inferiores and is attached to the ventral walls of the infundibulum either directly or by a stalk. In the eel it is ovoid in shape, and when divided sagittally in the middle line, it is somewhat kidney-shaped, with the hilum facing the infundibulum. The pituitary body in the eel consists of two lobes anterior and posterior; they are entirely different, both in their structure and development. The posterior lobe is developed as a hollow downgrowth of the part of the embryonic brain which afterwards becomes the third ventricle. In fishes the cells which compose its walls become converted into nerve-cells and fibres, and, as the lobus infundibuli, become an integral part of the brain. The anterior lobe is developed as a tubular prolongation from the epiblast of the lining epithelium of the cavity of the mouth, with which it is therefore originally in connection. In the adult it is constituted of a large number of tubules or alveoli like those of a secreting gland, and in like manner lined by epithelium. It is very vascular and has a number of sinusoidal spaces. Vesicles are sometimes present, and these may be filled with a colloid substance similar to that found in the thyroid vesicles.

The posterior lobe of the eel consists of two parts, closely related, the pars intermedia and pars nervosa. In comparison with a mammalian gland, the pars nervosa takes a very small share in the make-up; a number of nerve fibres spread out fan-like and loose themselves in pockets of the pars intermedia. This consists of a large number of acini, the peripheral part of which is, in the resting stage, composed of three or four layers of cells, while in the centre is a circle of ependyma cells connected with the neuroglia of the pars nervosa. In the active stage, that is to say towards the autumn, a very different picture is seen. The peripheral cells are almost entirely replaced by a yellow-staining secretion. In the centre the lumen is surrounded by empty ovoid cells. In some acini the granular secretion is converted into an ovoid refractile mass of brown colloid.

Surrounding each alveolus is a meshwork of fine capillaries, and within them can be clearly seen small masses of brown colloid, together with a few red blood corpuscles. The blood vessels arise from small peripheral arteries which can be seen passing inwards to end in the capillary anastomosis.

The capillaries from the acini converge to form three groups from which large vessels arise, two lateral and one central, and these unite towards the hilum to form one main trunk which passes backwards and enters the substance of the lobus infundibuli. The evidence as to the direction of the circulation in this system, which appears to start from the fine capillaries, is as follows: there can be seen in the course of the branching nerve fibres of the pars nervosa, as it enters the pockets of the pars intermedia, a number of small round globules of colloid which are homogeneous and refractile. It will also be noted that the hollows into which the nerves dip are bordered by blood vessels, from which it seems that the globules have escaped. These globules have been described in the mammalian pituitary by Miss Una Fielding, who has looked over my sections and given me much help in reference to the voluminous literature on the subject. She points out that the direction of the blood flow can be gauged by their colloid accompaniment. As colloid (whatever it may be) is formed in the pituitary, and not in the brain, its association with vessels may be taken as indicating that the direction of the flow is certainly hypophysio-hypothalmic (that is from the pituitary to the part of the brain known as the hypothalamus).

Sometimes the colloid globules occur in the lumen of the vessels and sometimes in the inter-vascular tissue of the neural portion of the stalk. Our very definite observation of the colloid material in the network of capillaries that surround the acini seems to confirm the suggestion of de Beer that products other than those of the anterior lobe may be blood borne.

It has been established by Hogben that the normal rhythm of colour change in amphibia is controlled by the secretion of the pituitary gland. He points out that "the pituitary gland is a specifically vertebrate structure, from which no active substance has been isolated in pure form. Extracts of the pituitary of mammals, birds, reptiles, and fishes (teleostean and elasmobranch) have a powerful excitatory action on the mammalian uterus and upon mammary secretion. Extracts of all classes of Amniota, Amphibia, and Teleostei exert a pressure diuretic action on the mammal. In fact the posterior lobe of the mammal while the storehouse of probably several substances of very great activity has not yet been proved conclusively to have any functional significance." There is, on the other hand, the clearest evidence for regarding the pituitary secretion as the main factor in co-ordinating the pigmentary responses of amphibia to the changing conditions of its environment.

The pigmentary changes in the eel when about to migrate are well known. Before the beginning of puberty, the eels, male and female alike, have a green and yellow coloration, dark brownish green on the back, and bright yellow on the belly. These colours now change; the green takes on a shade of purple and the yellow of the belly fades away and becomes a pearly white. There is also noted an apparent increase in the size of the eyes, they protrude more, in fact there is a condition allied to exophthalmos. Associated with these external appearances we have noted a great increase in size of the posterior lobe and also a gradual replacement of the peripheral cells of the alveoli by yellow colloid secretion which also appears in the surrounding capillaries. It seems, therefore, that the theory that these colour changes are connected with the increased size of the lobe and the secretory activity receives some support from the analogy of the pigmentary reponse in amphibia as described by Hogben. Before referring in detail to other changes in the pituitary gland at the time of approaching migration it will be necessary to say something about the microscopic appearances of the anterior lobe.

Compared to the posterior lobe, the anterior is very vascular. It consists of groups and columns of epithelial cells with dilated sinusoids. The cells are either chromophil or chromophobe. The chromophil are either acidophil or basophil. The acidophil cells are granular and stain pink with eosin, while the basophil cells stain with haematoxylin and are larger than the eosin-staining, though their granules are smaller. The sinusoids vary much in size, and in that part of the anterior lobe, which faces the opening of the infundibulum, there is a wide depression occupied by what appears to be a stringy secretion, and deep pits dip into the epithelial portion of the gland. Anterior to the infundibulum the stalk of the pituitary descends from the margin of the lobus infundibuli. In addition to the secretion above mentioned it is important to notice the small globular refractile bodies described in the mammalian pituitary by Poppa and Fielding. These globules are seen to be present in considerable numbers in the hilum facing the infundibulum and I have counted twenty globules of various sizes in two consecutive serial sections and in a neighbouring section, two vessels have been cut in a longitudinal direction containing numerous globules which give the appearance of a string of beads and others are seen lying free.

These vessels communicate with the capillaries of the pia mater clothing, the ventral margin of the lobus infundibuli and from these vessels ascending branches supply the tissues of the stalk. The above is the appearance of a section of the gland in the autumn, in which there is very marked enlargement and a great increase of eosinophil cells. Newton in Evans's Advances in Physiology says, "In spite of the presence of only three types of cell in the anterior pituitary it is nevertheless the birthplace of a number of hormones. These act on the general bodily growth, the gonads, the mammary glands, the thyroid and carbohydrate metabolism, and other tissues and glands." What is of interest to us in the study of the eel is obviously not the mammary glands. But bodily growth, the gonads, the thyroid, and general metabolism all enter into the picture of the complicated functions of the anterior pituitary. The earliest knowledge of the functions of the pituitary were connected with growth in certain pathological conditions. In mammals the anterior lobe secretes a growth hormone which produces, if in excess, gigantism in children, and in adults acromegaly.

The relationship between the gonads and the anterior pituitary is based on accurate observation. The secretions of the ovary are dependent on the pituitary and occur in a cyclic fashion. These functions of the gonads are not automatic, for removal of the pituitary in immature animals prevents their appearance, and in mature animals leads to their arrest. Implantation of anterior pituitary substance, or the injection of suitable extracts before puberty, causes precocious sexual maturity. It is not surprising, therefore, to find in the eel about to migrate a great enlargement of the anterior pituitary. It has already been stated that the source of the gonadotropic hormones is in doubt, but the anterior pituitary is increased in nearly all species during pregnancy. This, in mammals, is said to be due to chromophobe cells, but in man some eosinophile cells are produced and are known as pregnancy cells. It is clear that so far as my observations are concerned, which extend over a period of over two years, that the enlargement of the anterior pituitary in the eel is due to a great increase of acidophile cells. It is interesting to refer to some earlier work on the stimulus for a breeding migration, especially in the eel.

Walter Heape suggested that the immediate stimulus came from the periodic increase of the internal secretions, elaborated by the gonads. John Hammond (1925) explains his observations on growth and reproduction, by assuming that the anterior pituitary hormone is responsible at different times for stimulating both processes, its physiological effect being transferred from one function to the other in the process of individual life. Heape was very definite in his view that the impulse to migrate is induced by changes in the functional activity of certain organs included in the reproductive system, and suggests "that the details of the problem must be left in the hands of the student of the reproductive system."

Reading Heape's work carefully leaves us with the impression that he recognised the switching off of the endocrines from a growth producing function to a gonadotropic function: but the work of Parkes and others on the gonadotropic function of the anterior lobe of the pituitary was after his time. Nevertheless, on the eel he says, "comparison with a great variety of other animals and especially of fish induces me to hold a strong opinion that development of the reproductive glands and cells is due to a switching off of energy which was previously engaged in those metabolic processes which result in growth."

Our earliest knowledge of the functions of the pituitary were connected with growth in certain pathological conditions, and it is now known that in mammals the anterior lobe secretes a growth hormone which produces, if in excess, gigantism in children, and in adults acromegaly. Extracts of the pars distalis in mammals causes growth to take place when it has ceased as the result of the removal of the pituitary.

It is interesting to note the condition analogous to gigantism in those eels that have been prevented from making the gametic migration. To quote Roule, "not all the eels set out on this hazardous journey. Some at the period of puberty cannot from the nature of the locality leave the lake or the pool in which they are too closely imprisoned. Like the sterile trout of the deep lakes, and for the same reason, their ovaries, for these eels are usually females, change and atrophy. Rendered sterile and naturally castrated like pullets they grow fat in the same way, but go on living and growing larger. Eunuch eels of this sort have been kept in captivity for twenty or thirty years."

I am informed from a keen and scientific fisherman that he has seen eels of this kind in New Zealand three feet or more in length with the girth of a man's thigh. We have made arrangements so that at the earliest opportunity, the pituitary of a "eunuch" eel will be examined, and we look forward to some interesting findings.

It is now possible to review the colour and other changes that precede the migration of the eel in relation to the activity of the pituitary body. The colour changes have been shown to occur some time before the actual migration and at the same time the posterior lobe enters on a stage of activity as shown by the increase of colloid secretion.

The anterior lobe may be the cause of the exophthalmos, as it is known to cause an increase of thyroid activity; we have more direct evidence of the effect of the anterior lobe on migration as the increase in size, the increase of the acidophile cells immediately precedes migration, the onset of which coincides with the appearance of both ova and sperm. We hope that another year of monthly examinations may add further confirmation of these observations and conclusions.

CHAPTER XIX

THE PROBLEM OF PAIN IN FISHES

Do fish feel pain ? This is not an easy question to answer. For obvious reasons we can have no real knowledge of a fish's feelings or sensations, and there is only the answer obtained by analogy, by anatomy, and by the reactions of fish to certain stimuli or their behaviour. I suppose we all instinctively recoil when we see a fisherman skin a sole alive, and shudder at the living shambles in the fish-markets of many Continental countries, and most of us prefer to knock a caught fish on the head rather than allow it to prolong its death agonies by flapping on the floor of the boat. But we cannot estimate the pain or sufferings of a fish by its facial expression as it has no facial muscles, and though certain fish, as the gurnard, grunt when taken out of the sea we cannot say whether these sounds indicate pain or discomfort.

There is often some confusion of thought when we use the term cold-blooded ; the original meaning of cold-blooded is having cold blood, and is used in relation to those vertebrates whose body temperature varies with that of the water in which they live ; but it is also used in a figurative sense as lacking in sensibility of feeling, and thus the conclusion is reached, quite unjustifiably, that a fish is devoid of feeling. Some light can be thrown on the question if we approach the subject from an anatomical standpoint.

An analysis has been made in man of cutaneous sensibility by certain scientists, who have allowed themselves to become their own laboratory animals, and have studied the various sensory functions, and their recovery after experimental division of their cutaneous nerves. According to some, all forms of cutaneous sensibility, touch, temperature and pain, are grouped in two series, one, known as protopathic sensibility, subserves general diffuse sensibility of a primitive form. The sense organs are arranged in definite spots, yet the spot stimulated cannot be accurately localised. There are separate spots for touch, heat and cold, and be it noted "pain spots." The other series known as epicritic sensibility is more discriminatory and is probably of a later evolutionary origin.

We need not discuss the latter further as pain sensibility is not included in this type, pain being wholly protopathic. Some physiologists state that there are definite nerve-endings for pain, while others regard pain as a quality which may be present in any sense and not as itself a true sensation.

The free nerve-endings among the cells of the epidermis are probably the pain receptors, because these endings alone are present in some parts of the body where susceptibility to pain is the only sense quality usually present, such as the dentine and pulp of the teeth and the cornea of the eye. A section of the tooth of a fish shows the outer layer of dentine and fine nerve terminals entering the cavity, and ending free.

Again in a section of the cornea there are various plexuses in the connective tissue and sub-epithelial layers which end in an intra-epithelial plexus terminating in naked fibrils, often varicose, amongst the superficial cells. Similar endings are found throughout the epidermis. Skin-pain is, therefore, probably received by free nerve endings lying between the superficial cells and is wholly of the protopathic type. But it must be borne in mind that excessive stimulation of other sense organs may give rise to pain, although in such cases the pain is accompanied by the usual sensation of the particular organ. For example, a very loud noise may cause acute pain, but it retains, nevertheless, the character of sound.

The epidermis of fish is, of course, characterised by its scales, which is in sharp contrast to the appendages of the human skin, hairs and their sebaceous glands, and the sweat glands. Before mentioning the special types of sense organs peculiar to the epidermis of fish we must refer to the end-organs of chemical sensibility found in man only on moist epithelial surfaces, but in fishes they may be present over the entire surface of the body. But the most characteristic of the sensory organs of fish are taste-buds and the organs of the lateral line. The former are composed of cells arranged like the segments of an orange which are enclosed in a sheath which leads to the surface by a pore so as to allow access to the tips of the sensory cells. They are most in number on the lips and barbels, but are found all over the body and on the fins.

These important sense organs are also associated with tactile sensation, as such fishes as the barbel, gudgeon, and loach have prominent barbels, which they use in hunting for food in gravel and stony bottoms, and it is noteworthy that in these fish the nerves divide within the brain, so as to lead to special areas of the facial lobe, suggesting a differentiation of function. Pit-organs is the term applied to a type of sensory organ found either isolated or in a long connected linear tube, called the lateral line, often clearly defined by pigment, as in the haddock. These organs are very similar to the sense organs in the ampullae of the semi-circular canals of the fish's ear and their function is to register waves of low frequency.

Finally we come to an organ peculiar to fish, the function of which has been investigated recently by Dr. Sands at the Plymouth Marine Laboratory; by means of an oscillograph he has made tracings of the action currents in these mucus canals, named from their discoverer, Lorenzini's ampullae, and finds that they record changes of temperature. To review the functions of the epidermis of fish we find Touch, Chemical Sense, Taste, Vibrations and Temperature all represented; we have no means of recognising pain-spots, but we may assume their existence as they are a primitive form, and even if they do not exist we have seen that excessive stimulation of any sense organ can produce a painful sensation.

There is one more piece of evidence pointing to the perception of pain in fish. Many fish are provided with poisonous spines, and the most marked effect of the puncture by these spines is acute pain, in man of an excruciating nature: these organs were not evolved for protection against man. Fish have been seen to attack small fry with these spines, and experimental observations show that acute symptoms follow the subcutaneous injection of the venom of these organs. In conclusion we may say that there is no evidence that fish do not feel pain, and there is no reason to suppose that they are devoid of a protective mechanism common to most vertebrates.

CHAPTER XX

RETROSPECT AND CONCLUSIONS

The interesting connections of brain pattern with the diet and habitat of fish can now be reviewed.

In cyprinoids the association of diet with brain pattern is very clearly seen in the enlarged vagal lobes and facial lobes of the bottom feeding fish, and the differences of size of these lobes according to the habit of extracting nutriet material from mud, or groping and grubbing on stony or gravelly bottoms. There is reason to believe that the enlargement of the vagals is due to the palatal organ, which is an adaptation for sorting, sifting, retaining, or rejecting food particles ; there is also strong evidence that the enlargement of the facial lobes is due to the presence of barbels which are supplied with taste-buds, as the facial nerve divides within the brain into two branches leading to anterior and posterior areas of the lobe of varying size, according the importance of the barbels : when we come to the next group which are surface feeders we find that sight is a very important sense in hunting and therefore the optic lobes are prominent, while the vagals and facials are small. But in the highly specialised plankton feeders, like the bleak and engraulicypris, the naked eye appearance of the brain is remarkably altered in type, as the facial lobes do not appear on the surface and can only be demonstrated in serial sections, when it is found to be completely overlapped by the somatic-sensory lobes ; and, further, a special area at the base of the cerebellum becomes very prominent, and being associated with audition we have ventured to call it the central acoustic lobe. This lobe is present to a lesser extent in the fish belonging to Group II, but in the purely ground feeders it is rudimentary. Bhimachar has also shown that cyprionodont fish, living at the surface of the water, have the medulla oblongata narrow, without prominent vagal and facial lobes, and that there has been developed a conspicuous central acoustic area.

THE BRAIN PATTERN IN GADOIDS

In this family the relationship of brain pattern to diet and habitat is more complex. In the first group, according my classification, there is a great similarity of brain pattern, but the relative size of the somatic-sensory and facial or vago-facial lobes varies as the diet passes from a shell-fish diet, through a mixed diet, to a purely fish diet.

A division of this group may be made by separating the night feeders, the ling and burbot, from haddock, cod, and so on, as in these fish the olfactory lobes become prominent, and the optic lobes less so in accordance with the predominance of smell in their search for food. The third division includes two species of an interesting genus physics, or the forkbeards, phycis from the shallow waters of the bays of Madeira, and phycis blennioides landed at Milford Haven.

The brain of both fish differs from the usual gadoid type in the largeness of the primitive end-brain and the smallness of the optic lobes; the former has also a characteristic division. The cerebellum is narrow and very elongated, and the medulla small, with fairly large somatic-sensory lobes. This bottom feeding animal which inhabits rocky ground has its ventral fin on either side converted into a long bifid feeler, and it also has a barbel. Smell and touch would appear to be its chief hunting equipment. Phycis is known as the "schellfisch" by the Germans, and so also is the haddock and phycis blennioides is also known as the rock haddock; this is no doubt due to the similarity of diet, but the habitat seems to have given rise to a different adaptation in the forkbeards, as the true haddock, hunts through its taste-buds, and phycis by olfaction and touch, probably as a result of their rocky habitat; therefore diet has been over-ridden by habitat in determining the method of hunting and brain pattern.

This seems a favourable opportunity to mention other variations in the primitive end-brain of gadoids; this lobe is always closely connected with the olfactory lobe and varies in size with the importance of smell in the hunting equipment; the ling and burbot emphasise this fact; when we compare their brains with other gadoids such as the pollack and cod we notice that these lobes in the ling are large and almost hemispherical, approaching the optic lobes in size; the burbot shows the same relative size of these lobes, as is seen in the ling; it has been described above that these fish are both night feeders. The primitive end-brain in flat-fish also shows well-marked variations in size. This has been noted in the sole, and the drawing of the brain of this fish shows that it exceeds the optic lobe in diameter and gives rise to olfactory bulbs, which tend to overlap. But the members of the groups of flat-fish II and III, in my classification, show throughout a very definite similarity in size of their primitive end-brains, thus in Group II, the end-brain of the lemon-dab, plaice, witch, and dab are larger than those of Group III, the brill, turbot, and megrim. If we compare the drawings of the lemon-dab and brill it will be seen that both olfactory bulbs and primitive end-brain are more developed in the former than the latter. As Group II are bottom feeders and feed largely by smell as well as taste, both elements of the anterior lobes are functionally well developed.

An examination of the plate giving the dorsal view of the three types of Cyprinoid brain will reveal the same information as to feeding habits as we have just noted in plaice and lemon-dab. The barbel, gudgeon, loach, and tench have an elongated primitive end-brain of considerable size, and these fish all feed largely by taste and no doubt also by smell. The sight-feeding group as typified by the roach have small end-brains, while the carp group have end-brains intermediate between the above groups.

Passing backwards we reach the mid-brain which superficially appears as the optic lobes. These lobes are not so simply constituted as would appear ; if the transverse section of the optic lobes of the plaice be referred to, it will be seen that there is a broad cellular layer of concentric bands of nerve tissue and fibres, which is known as the tectum opticum, and that this forms a roof to a cavity into which protrudes the base of the lobi inferiores and the nerves passing dorsally from the nuclei rotundi. The optic nerves passing from the internal surface of the tectum also occupy the anterior part of the cavity on its lateral aspects. But posteriorly as can be seen in the drawing of the brain of the cod there is another protrusion or rather insertion of another structure, the valvula cerebelli, which not infrequently causes a wide separation of the anterior ends of the tecta and exceptionally pushes its way right through and envelops the optic lobes as in Mormyrus.

We would recall in illustration of this condition, the optic lobes of the various groups of carps ; it has been shown that those that feed by sight have big optic lobes as the roach, but the barbel a ground feeder has also a large optic lobe, but the wide separation of the tecta optica by the valvula is the cause, as is very obvious in the drawing, which illustrates these types of cyprinoid brain. The loach is another good example of an apparently large optic lobe. Nevertheless the fact remains true that fish that hunt in the dark, as the sole, have small optic lobes, while those that hunt by day, as the plaice, have larger lobes. But large eyes do not necessarily mean that a fish will have well developed optic lobes. This fact is observed in certain fish that frequent great depths, as the Black

Scabbard fish, known as Espada, and the Rabbit fish or Promethichthys prometheus, which have eyes as large in circumference as a two-shilling piece, but yet have optic lobes of average size. At depths of 300 to 400 fathoms, approximately half a mile down, there can be very little light and the large eyes are adapted to receive as many photons as possible.

If the eyes of a plaice are removed they will be found to lie in a membranous covering, filled with fluid, and this communicates with another sac situated ventrally which also contains fluid. By means of a muscle external to the lower sac, the fluid is driven into the sac lining the orbit and thus the eyeball is protruded. It would appear that this accessory organ is evolved as an aid to the phenomenon of protective coloration. We can daily observe that in addition to the black and yellow chromatophores which produce the various markings in the plaice that there are bright red markings. The eyes of this fish are also well known for their marked prominence. It is a matter for thought and consideration whether the bi-lobed optic lobes of the plaice may not be associated with the function of protective coloration. It has been noted how that in the gudgeon, the development of barbels with their taste-buds has produced a division of the facial lobe into anterior and posterior lobes and that this anatomical condition is associated with the grubbing habits peculiar to the species. On the same principle there may have developed a special area in the tectum opticum connected with the power of self-concealment by colour changes; this would explain the bi-lobed character of the plaice's optic lobes, and also the bulge of the lemon sole's optic lobe.

The fact that these fishes feed by sight does not seem to explain the condition, as many sight feeding fishes exist which have large eyes and well developed optic lobes, but show no modifications of these lobes of a similar nature. If the eyes of a sole are dissected the minute size is very impressive and when the dissection is carried further it is difficult to make out any recessus orbitalis although there is a slight projection usually of the cavity of the orbit.

The more the phenomenon of protective coloration in flat-fishes is considered, the more complex and mysterious is the mechanism of its evolution.

The various physiological and anatomical devices that have been evolved, to perfect these fishes in adaptation to their surroundings, are very complex. To the naturalist that probes into the details of the modifications of structure, that complete the picture, a feeling of wonder at the results of random variation must arise.

The flat fishes have adopted a recumbent posture which gives them protection from enemies and concealment from their prey; at the same time this protection is dependent on adaptive coloration and conformity to their background. To enable the fish to do this, the background must be surveyed and, by some unfathomed optical reflex, the fish becomes more skilled than the leopard, and changes its spots, and thus produces the desired design. The great development of the eyes and optic lobes in the plaice have been described, but the higher centres, which presumably carry out the artistic effects, are unknown; but there must be some central nervous mechanism present to control the nerve plexuses that surround each pigment cell in the skin. The reflex artistry of the plaice, which with natural pigments reproduces on its own canvas a picture of its background, by what must, under the best of circumstances, be an oblique view is one of the astounding phenomena of nature.

The observations on the protrusion of the eyes and the recessus orbitalis are most remarkable. The migration of the eye, and the anatomical details that accompany this change of outlook, have been described; but a further adaptation became necessary after the eye had reached its comparatively exalted position, as the range of vision was not sufficiently extensive to obtain a view of the surrounding ground; this apparently was the case with the upper eye. It was necessary that some mechanism should be evolved to allow the eye to be protruded; so it appears that a hydraulic sac was developed in connection with the membranous wall of the orbit, and this allowed the eyeball to be protruded to a remarkable extent. Now the protective coloration ensures the survival of the fish, but before this protection could be obtained an extensive view of the surroundings was essential and this was not possible until this mechanism had been evolved; therefore the recessus orbitalis must have been formed before any protective colour change could have become efficient. It would seem that the greater the power of protrusion of the eye, the more efficient is the power of colour adaptation, as is exemplified by a study of the plaice.

Therefore the history of the development of a flat-fish recounts not only the adoption of the recumbent lateral posture, the migration of the under eye to an upward site, and the loss of pigment on the under side of the body, but the development of a high power projecting optical apparatus with reflex colour-photographic control of the chromatophores. An interesting fact has also been established in regard to colour changes, that the time required by a particular individual to copy the ground could be decreased by repetition, which clearly indicates the activity of a higher centre in the nervous system controlling the response received from the visual field.

We have elaborated the subject of protective coloration in flat-fishes, because it forms a good illustration of the relation of one of the special senses to the brain pattern. Both the naked-eye and microscopic appearances of the optic lobes of plaice and lemon-sole show a very striking development, and this is clearly related to the great importance of sight both in pursuit of their prey and in providing protection from their enemies through adaptation of their markings to their surroundings.

We approach the subject of the cerebellum with some trepidation tempered, however, with some confidence and conviction, that the methods of comparative anatomy which have been so valuable in the study of the medulla oblongata will throw some light on a hitherto very obscure subject.

It will be convenient to treat the cerebellum by compartments, remembering that there is a great overlapping of the areas devoted to their different functions. I, consists of the central lobe which may be globular or ovoid and at times is prolonged posteriorly into a long tongue-shaped extension which overlaps the medulla; this lobe has a molecular layer enclosing a granular layer with its superficial ring of scattered Purkinjecells. II, on either side of the base of the cerebellum are the acoustic tubercles or acustico-lateralis areas, which some text-books still refer to as the restiform bodies; these are described as a pair of prominent cord-like masses of nerve tissue on the dorsal surface of the medulla oblongata, forming lateral boundaries of the fourth ventricle and are continued upwards as the posterior peduncles of the cerebellum. III, posteriorly at the base of the cerebellum, lying medially between these peduncles is an area of small-celled dark-staining tissue, interspersed with transverse fibres, which at times forms a definite lobe, projecting backwards as in the herring, but in the carps either forms a transverse bulge or a well-defined area, known as the central acoustic area. IV, anteriorly the cerebellum gives off a protrusion from its base, which projects into the cavity enclosed anteriorly by the tecta-optica, known as the valvula; this we have recently discussed, in describing the optic lobes, as sometimes causing a wide separation of the tecta optica.

It will now be our object to consider the functions of each of these four departments as they can with some accuracy be called. Recently a distinguished surgeon and neurologist remarked to the writer how little was known about the functions of the cerebellum and an eminent physiologist told how he had removed the cerebellum of fish without any effect on its equilibrium.

In reference to these remarks we find, that the classic textbook on physiology by Michael Foster devotes 32 pages to the cerebrum and only one to the cerebellum. It is usually taught that the cerebellum is associated with the co-ordination of movements, and this view is based on the effects produced by extirpation of portions of the cerebellum ; it has also been observed that lateral lesions and incisions produce a greater effect than medial or symmetrical ones. But clinical evidence in man is conflicting, as cases have been recorded, in which extensive disease has existed without any obvious disturbance of the co-ordination of movements.

It must be remembered that the acoustico-lateralis system is only developed fully in fish, and consists of three branches connected with roots of the seventh nerve, the eighth or auditory nerve, and the vagus lateral-line branch, and that the fibres of all these nerves are derived from nerve-cells in the acoustico-lateralist area of the medulla. We shall consider first the central acoustic area III.

It was observed in the course of a systematic examination of the brains of Cyprinoids that Engraulicypris and Bleak had minute facial lobes only evident by examining serial sections, and that they possessed a well-marked central acoustic lobe or area. Associated with these facts, it is to be noted that they are surface feeders ; in fact, Engraulcypris behaves like a clupeoid fish and as its name implies is an anchovy-carp. The next quest was the investigation of the facial lobe of the herring, a typical plankton feeder. This has a well-marked central lobe, in the position of a facial lobe, but really due to a median backward projection of the cerebellum and its microscopic structure is like that of an invaginated central acoustic area ; the eighth nerve can be traced to its lateral margins. The evidence seemed to point to an auditory function. It did not appear likely that this specialised area could be connected with the lateral line organs as the herring has no lateral line, but only a few sense organs on the head, one in particular being closely connected with the posterior and anterior spherical air-vesicles which form the accessory auditory organ of this fish.

It was argued that if a central acoustic area was really auditory in function those fish which are known to produce sounds, such as the gurnards, would have this area well developed; sound production without audition would appear to be a useless accomplishment. Certain fish, such as the mullet, are very susceptible to sounds, and fishermen make use of this characteristic reaction in their methods of fishing, and it is interesting to note that fishermen both in the south of England and as far away as Egypt apply the same methods.

To return to the carps it is found that the surface feeding members of this family have the central acoustic area well developed, while the ground feeders have this area very small. The same observation has been made on the fish which abound in the Madras tanks as described by Bhimachar, and he adds further that those fish which have a prominent central acoustic lobe have also an accessory air-breathing organ. It may be mentioned here that the recent work of Bull Manning, Fritsch and others have put the question of hearing in fish beyond dispute, and the minnow is now known to have a range of hearing as wide as that possessed by the human ear.

We now come to the acoustic tubercles and shall endeavour to unravel its functions. Presumably if the central area is acoustic in function, the lateral areas must be either connected with the orientation of the body and so with the semi-circular canals, or with the perception of waves received from the lateral-line organs through the movement of the fluid in their canals. Recently a Japanese observer has described experiments in which the effect of ablation of the cerebellum was observed. These experiments supported the view that the main body of the cerebellum is connected with the registration of the position of the body in space.

The acoustic tubercles must, therefore, be chiefly receptors for the sense organs of the lateral line. The question now arises are there any examples of an exceptional development of the acoustic tubercles and is such a condition associated with any special habitat?

The examination of the brain of gadoids revealed the possibility of such associated conditions being present. The pattern of the brain of gadoids is always of the same generalised type, the differences being most noticeable in the lobes of the medulla oblongata and in the size of the optic lobes. We have seen how enormous is the size of the facial lobe in the rockling, and have associated this development with the peculiar adaptation of the dorsal fin. But this is not the only gadoid that has a marked and unusual development of a sensory area.

Molva elongata, one of the deep-sea lings, has exceptionally large acoustic tubercles, as is shown in the plate of the gadoid brains, and this development is associated with a bathysmal habitat, and also with a predacious habit of feeding. If we consider what we have described as the pattern of the brain of the deep-sea gadoid phycis blennioides of a sedentary habit, and not a predacious fish, it will be clear that it is not only a deep sea habitat that is responsible for large acoustic tubercles. Molva elongata hunts not only at great depths, but is essentially a predatory fish so that two conditions must be present to cause the great enlargement of the acoustic tubercles. These considerations are confirmed by what we have noted in the pattern of the hake's brain. The cerebellum is small and on either side are two globular projections in the position of the acoustico-lateralis areas, from which two ridges pass posteriorly and then converge and meet at the caudal end of the medulla.

It must be mentioned that the hake is a near relative of the cods, and strictly is a species of the Merlucciidae. Its habits we have described ; it is a mid-water feeder, but descends to from 300 to 400 fathoms in the winter. It is suggested that the hake, like molva elongata, has this great development of the acoustic tubercles in association with its bathysmal and predatory habits. A still more remarkable confirmation of these suggestions is the pattern of brain in four deep-sea fish of marked predatory habits, all members of the Trichiuridae, Athanopus carbo, Lepidopus caudatus, Promethichthys and Nesiarchus nasutus. In these fish the acoustic tubercles are enormous and the somatic-sensory lobes also large.

It is known that in the deep sea at a depth of two hundred fathoms light does not penetrate. According to Cunningham it is certain that fish, that habitually live beyond this depth, show enlargement of the dermal sensory tubes. We have seen that the deep sea fish such as the scabbard fish and the hake have a special enlargement of the acoustico-lateral area so as to produce a definite lobe, and it is a justifiable assumption to associate this condition with the enlargment of the sensory canals. How are the fish in complete darkness able to find their prey ? They may be able to detect its presence by smell, but it is doubtful at what distance this would be possible, and whether smell could give any exact idea of the position of the prey. It has been pointed out that the lateral-line organs, situated at intervals along the side of an elongated body, would receive different impressions from a moving body, that was the source of waves, according to the angle these undulations hit the side ; and it is obvious that when the pursuer was heading for the prey the waves would have a very different effect than if the undulations were received obliquely. It is also known that the lateral-line organs perceive vibrations of water, and react to them in the same way that the similar organs of the semicircular canals do. The conclusion is therefore drawn that the enlarged acoustic tubercles of deep sea fish are organs for direction finding of a moving prey, and are stimulated by the impressions received from the lateral-line organs.

We must now refer to the valvulæ cerebelli. We are not quite in the dark even about the functions of this difficult area. There is no doubt that those fish like the barbel, the gudgeon and the loaches which grub among stones and gravel for their food have the tecta optica widely separated by the prominence of the valvula and a freak development of a very highly elaborated valvula occurs in a group of fishes with strongly curved snouts, the Mormyridæ: this suggests that this part of the cerebellum may be associated with the grubbing habit, correlating the tactile, olfactory, and gustatory sensations. In this connection it is well to recall that fibres from the lobi inferiores and also gustatory fibres enter an area at the base of the valvula.

Herrick is our authority for some evidence as to the termination of the ascending secondary gustatory tract of both facial and vagal lobes which is stated to be in a nucleus, situated in the lateral wall of the isthmus. The chief gustatory tract arises from it and some of these fibres pass to the lobi inferiores. He also gives a diagram, in which an olfactory conduction path terminates in the lobus inferior. It would indeed be surprising if we could fit in everything in this neurological puzzle; but an attempt has been made by the comparative method to supplement the knowledge that has been gained by other methods; there can be little doubt that more observations will be made and some conclusions confirmed, and others revised or extended.

To sum up the new views that have been suggested by the methods of comparative anatomy: the cerebellum is the centre whereby the position of the animal in space is recognised and the semi-circular canals are in close connection with its main body; the central, acoustic area is the auditory centre and most of the fibres of the eighth nerve enter it; the lateral-acoustic areas are associated with direction, and direction in a vertical plane is well shown by a study of their enlargement in abysmal fishes; the valvula is associated with habits of grubbing, and the taste and olfactory functions, and may also be a correlation centre of these functions.

The posterior crura of the cerebellum or the continuation of the acoustic-lateralis area into the medulla oblongata leads into those parts of the medulla bounding the anterior portion of the fourth ventricle: this area is the skin area and is often enlarged and globular, forming the somatic-sensory lobes or fifth lobes; these lobes are usually much developed in predatory fishes. This is well shown in a study of the gadoid brain in which we find such fish as the cod, ling and pollack, with large fifth lobes and, among flatfish, as turbot and particularly the halibut, the same enlargement is present.

Our task is nearly finished and we return with relief to the seventh or facial nerve and taste-buds. As has been pointed out, these organs apparently subserve different kind of sensory stimuli, which we have called gustatory and "sentinel." The taste-buds. with gustatory function are usually in the front of the mouth and on the lips, and the sentinel in the branchial region and at the entrance of the pneumatic duct into the gullet.

These groups are supplied by the facial, the glossopharyngeal and the vagal. When taste-buds are also situated on barbels it is found that the nerve fibres from the barbels enter the facial lobe with the fibres from the lips and body, but separate within the lobe, the barbel fibres passing to the posterior part of the lobe. The facial lobe only undergoes great enlargement when there are barbels present.

In the carps the mud-eating members of the family have a specialised area, carrying taste-buds called the palatal organ, which sifts the mud from the nutriment ; this area is supplied by the IX and vagal nerves and is the cause of the great enlargement of the vagal lobes. It is interesting to note how taste-buds may form special taste areas as is seen in the rocklings, which have adapted the dorsal fin to a taste organ. The dorsal fin is adapted in other fish for other purposes besides propulsion and gustation, it becomes a weapon of defence in the weever and a lure in the angler fish ; in the rocklings, however, it causes a great enlargement of the facial lobe.

The question has not yet been answered, is the adaptation of an organ to a specialised function as the palatal organ, the cause of the increased size of the vagal lobe, or vice versa, does the necessity of providing a sorting organ, cause an enlarged vagal to stimulate the formation of a palatal organ : also how far random variation is responsible for the existence of the palatal organ, and the enlarged vagal.

It is a matter of common knowledge that, in the higher vertebrates, the importance of the special senses vary to a considerable extent.

In man we all realise how little the sense of smell is developed compared with the condition found in the lower animals. This fact is even borne out in the study of language. Logan Pearsall Smith in the appendix to his book, "Words and Idioms," gives a list of "corporeal" idioms, and points out that the human head with its eyes and ears, nose and mouth, is the source of more than two hundred idioms. If a list of the idioms, relating to the eye, ear and nose (as an olfactory organ and not a feature) is made it will be found that there are forty-three idioms related to the eye, twenty-two relating to the ear, and nine relating to the nose, so that roughly the relative importance of these three senses is in man five—three—one. We cannot apply this test to a dog, but probably the relative importance of these senses in a dog would be smell, as indicated by its marvellous scent, then hearing and lastly sight; but we imagine the proportional significance of each sense would not vary to the same extent, that would appear to be the case with man. As regards hearing in the dog, it is known that it can be called by a Galton whistle when the note sounded is beyond the range of human hearing, and it is usually held that a dog is colour blind.

Contrary to general opinion the range of hearing in a fish, such as the minnow, is as wide as in man, and there is good reason to believe that fish are not colour-blind.

Fortunately the brain of a fish is so constituted that their is no difficulty in estimating the relative importance of the different senses in the make-up of the brain, as we have already had occasion to note, in describing the various lobes and their different sizes in the four groups of the carp family. There will, therefore, be no difficulty in coming to some definite conclusions as regards the brain of the sole, and these are, as we have already indicated, olfactory, auditory and tactile, as shown by the size of the olfactory central acoustic and somatic-sensory lobes: the facial lobe is insignificant, as there are no taste-buds on the papillary area. Why the gustatory system should be negligible in the sole and so important in other bottom feeding fish is difficult to explain, and we have no answer available.

The fact that the sole is able to live in brakish water makes it seem probable that it may be in an early evolutionary stage towards becoming anadromous, like the flounder. The sole likes warmth and has been known to live in fresh water, and this accounts for its occasional wanderings into estuaries.

This raises the question of choice. Recently Professor F. Balfour-Browne gave an interesting Presidential Address on the species problem in relation to water-beetles, and the conclusions he drew may help us to understand the history of the sole. If choice can be attributed to water-beetles, it can also be attributed to flat-fishes, which are far higher up the ladder of evolution. He pointed out that although the struggle for existence undoubtedly occurs, choice also plays a part in the formation of different communities associated with different types of habitat and that even localisation under particular climatic conditions may be due to choice. Choice of a particular food by certain individuals of a species may give rise to biological races.

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