A HISTORY OF FISHES

ANGEL-FISH (*Pterophyllum eimekei*).

Photograph by Mr W. S. Pitt.

A HISTORY OF FISHES

by

J. R. NORMAN

F.L.S., F.Z.S.

Assistant Keeper, Department of Zoology, British Museum (Natural History)

ILLUSTRATED BY

LIEUT.-COL. W. P. C. TENISON

D.S.O., F.Z.S.

WITH 9 PLATES AND 147 TEXT-FIGURES

"HISTORY.—A written statement of what is known; an account of that which exists or has existed; a record; a description."—*English Dictionary.*

ERNEST BENN LIMITED

London: Bouverie House, E.C.4

FIRST PUBLISHED IN

1931

PRINTED IN

GREAT BRITAIN

TO

MY FRIEND AND COLLEAGUE

C. D. SHERBORN

CONTENTS

LIST OF PLATES

PREFACE

In the course of my work at the British Museum I am called upon from time to time to supply answers to all kinds of strange questions, some of them but remotely connected with fishes themselves. How fast does a fish swim? How many fishes are there in the sea? Why does a fish die when taken from the water? Where did fishes first come from? To what age does the average fish live? Can a fish think or feel pain? (A favourite query from the angler!) What is Rock Salmon? Are we depleting the stocks of fishes in the sea by over-fishing? It is in the hope that it will provide solutions to these and other problems that the present work has been written, and, believing that it has been planned on more or less original lines, I feel that no apology is needed for its publication. At the same time, it is hoped that it will serve as more than a mere book of reference — a storehouse of facts—and will prove of sufficient interest to provide general reading, not only for the student of fishes and the angler, but for all those who take an intelligent interest in wild life.

The customary method of dealing with any group of animals is to begin with a recognised scheme of classification, and to take up each of the smaller groups in turn, describing the main distinguishing features of some of the better-known members of each group, their mode of life, food, distribution, and so on. Sometimes one or two chapters devoted to the anatomy, development, etc., of the animals precede the more general part, but, as a rule, these subjects are omitted altogether or dismissed in a few lines. In the following pages I have tried to give some idea of the story of fish life in all its varied aspects, to show how the fishes "live and move and have their being." In one chapter the manner in which they swim is considered; in another their food; in another their breeding habits, their development, and so on. Many different kinds of fishes are mentioned in illustration of one point or another, and some inevitably figure in more than one chapter. Special stress has been laid throughout on the evolutionary aspect of fish life, the fishes themselves being regarded, not as museum specimens or corpses on the fishmonger's slab, but as living organisms which have been modified in a multitude of different ways in accordance with the nature of their surroundings, in order to fit them for the particular conditions under which they are compelled to live. The importance of the part played by the "struggle for existence" in moulding the bodies of fishes will be apparent, and I have endeavoured to show how many of the remarkable modifications of the various organs which go to make up the body of a fish, although sometimes meaningless at first sight, may be readily interpreted in terms of environment, animate or inanimate.

The relation of fishes to the life of mankind has not been neglected, and chapters dealing with the fisheries, fishing methods, fishery research and so on have also been included. The enormous development of our own sea fisheries towards the close of the last century led to a great interest being taken in the habits, and particularly in the feeding and spawning habits, of the edible species. Much important research has been carried out on these problems during recent years, but the results are mostly buried away in scientific journals not readily accessible to the public, who remain largely in ignorance of the work which is being continuously done in order to maintain or improve the harvest of the sea.

In preparing this work I have drawn on my knowledge of the vast literature of the various branches of the science of ichthyology, and have consequently consulted a large number of works of a technical nature, some of them in foreign languages, not available to the general reader. It would, of course, be of little value to include a bibliography of such works here, but a short list of the more important and accessible books of reference on fishes and kindred subjects in the English tongue is appended for the convenience of those who may wish to pursue the subject further.

The use of technicalities has been avoided as far as possible, and scientific terms have been included only where their omission would be at the expense of clarity. It has seemed to me convenient, however, to refer to each fish by its scientific name (usually only the generic name, but occasionally the specific name as well) in addition to that by which it is popularly known, except in the case of lesser-known species for which there are no vernacular appellations. In the legends below the figures the name of the species is nearly always given in full.

Regarding the illustrations, the figures in the text are, with very few exceptions, new, and have all been drawn specially for this work by my friend Lieut.-Col. W. P. C. Tenison. I take this opportunity of offering him my sincere thanks, not only for the great care that he has taken in their preparation, but also for the kindly interest he has shown in the book since its inception. We have been content to make the drawings as simple as possible, believing that it is better to show the salient and characteristic features of the fishes rather than to produce an artistic effect. Those illustrations copied from other works are duly acknowledged in their place, and I am especially indebted to Mr. Arthur Hutton, Professor F. B. Sumner, and to Professor Johannes Schmidt, for permission to reproduce the photographs appearing in plates I, II and IV respectively.

It only remains for me to tender my grateful thanks to my colleague Mr. M. Burton for the trouble he has taken in reading through the greater part of the manuscript, and for many helpful suggestions and criticisms; to Dr. E. I. White, for reading and criticising Chapter XVII; to Dr. E. S. Russell, O.B.E., for performing a like service in connection with parts of Chapters XIX and XX; and to Mrs. Tenison for assistance in the task of passing the proofs for press. Finally, I find it impossible to allow this opportunity to pass without recording the great debt which I owe to Dr. C. Tate Regan, F.R.S., the Director of the British Museum (Natural History); his very great knowledge of matters ichthyological has always been at my disposal, and the many valuable hints and suggestions that he has given me from time to time since my appointment to the museum have proved of the greatest assistance to me in my work there, and without them it is certain that the writing of this book would have proved a very difficult task.

J. R. NORMAN.

London, 1931.

Certain sections of Chapters II, III, and XI have already appeared in the *Salmon and Trout Magazine*, and are reproduced here by permission of the Editor.

CHAPTER I

INTRODUCTORY

Definition of a fish. Position in the animal kingdom. Difference between fish and Cetacean. Classes of fishes. Numbers of species and individuals. The science of ichthyology.

"*These (the fishes) were made out of the most entirely ignorant and senseless beings, whom the transformers did not think any longer worthy of pure respiration, because they possessed a soul which was made impure by all sorts of transgression; and instead of allowing them to respire the subtle and pure element of air, they thrust them into the water, and gave them a deep and muddy medium of respiration; and hence arose the race of fishes and oysters, and other aquatic animals, which have received the most remote habitations as a punishment for their extreme ignorance.*"

PLATO.

It is of primary importance in a work of this nature to make it clear from the outset exactly what is meant by a fish, for in popular parlance the word "fish" is often used to include any animal living in the water, a definition which appears in all the older dictionaries. Although convenient, this can hardly be described as scientifically accurate, including, as it does, such diverse organisms as the Whales, Seals, Salmon, Oysters, Cuttle-fishes, Star-fishes, Jelly-fishes, and Sponges, creatures that differ from each other even more widely than do reptiles from birds or birds from mammals. The aquatic animals just mentioned, however, all fall naturally into two main categories in respect of one important bodily feature — those with a vertebral column or backbone and those with none. Man has a backbone, and so have all the mammals, birds, reptiles, amphibians, and fishes; all the others have no backbone. The backboned animals or vertebrates are better known to most people than the majority of the lower animals; indeed, with the exception of a few like the oyster and lobster which are eaten as delicacies, the invertebrate animals are regarded for the most part with lukewarm interest, in some cases with actual disgust. This attitude is partly explained by the superior size of the vertebrates, by the greater ease with which they can be observed and studied, and by the beauty of form and colour displayed by many of the birds and mammals. It has been further fostered by the editors of popular works on natural history, who devote three-quarters of the available pages to the mammals and birds, crowding the unfortunate lower animals—every bit as interesting and quite often of extreme beauty—into a few short chapters at the end.

A fish, therefore, is a vertebrate, and one specially adapted for a purely aquatic life. But this definition is still inadequate,

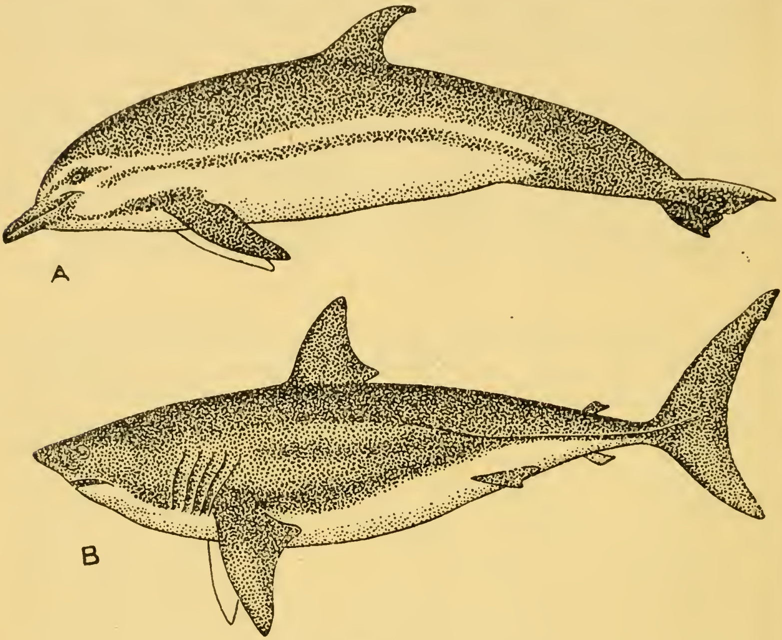


Fig. 1.—CETACEAN AND FISH COMPARED.

A. Common Dolphin (*Delphinus delphis*) ; B. Mackerel Shark (*Isurus oxyrhynchus*). Both much reduced.

for all the vertebrates living in the water are not fishes. What of the Whales, Seals, Otters, Newts, and Frogs? In my official capacity I am sometimes asked to settle arguments, occasionally backed by substantial stakes, as to whether or no a Whale is a fish. Here there is the same fish-like body, the fin-like fore limbs or paddles, and often a fin in the middle of the back (Fig. 1A). Nevertheless, a Whale is not a fish, but a mammal. A close examination of its skin reveals the presence of a few vestigial hairs in the region of the muzzle, the structure of the paddle is quite unlike that of the fish's fin (Fig. 2), being in all its essential parts just like that of the human hand, and the so-called dorsal fin is nothing more than a ridge of fatty tissue. Furthermore, although a Whale is able to remain under water for considerable periods of time, it is forced to come to the surface at intervals to empty its lungs of air and to inhale a fresh supply of oxygen — the familiar process of spouting or blowing. Whales also bring forth their young alive, and after birth suckle them just like any other mammal. In short, a Whale is a mammal which has left its kindred and exchanged a terrestrial life for one passed entirely in the water, a change

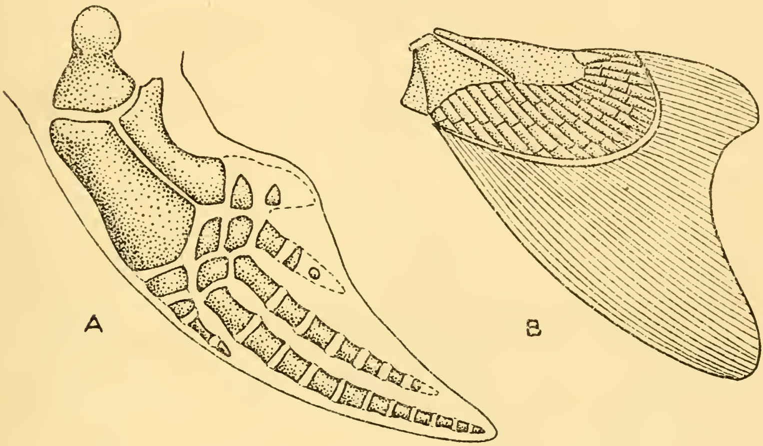


Fig. 2.—PECTORAL LIMB OF CETACEAN AND FISH COMPARED.

A. Skeleton of paddle of the Common Dolphin (*Delphinus delphis*) ; B. Skeleton of pectoral fin of the Comb-toothed Shark (*Heptranchias perlo*). Both much reduced.

which has led to the fore limbs being converted into paddles for swimming, while the hind limbs have completely disappeared. The Seals give us some idea how this change has come about, representing, as it were, a half-way stage between a typical walking mammal and a specialised swimming one. A Seal is amphibious; that is to say, it is equally at home on land or in the water; but the hind limbs have lost a great deal of their power of supporting the body on *terra firma*, and the fore limbs are becoming more and more paddle-like, the shape of the body tapering and fish-like, and the external ears have more or less disappeared. The form of the tail provides a rough-and-ready means of distinguishing at a glance any member of the Whale tribe (*Cetacea*) from a large fish such as a Shark; in the Cetaceans the flukes or lobes of the tail are horizontal, in the fishes they are vertical (Fig. 1). It is of some interest to note that Aristotle (384-322 B.C.) was well aware of the differences between fishes and aquatic mammals, whereas many of the writers in historical times classed them all together as fishes. The distinctions between the two groups do not appear to have been generally understood until the later part of the seventeenth century, and ignorance as to the real nature of the Cetaceans must often have led our pious ancestors to break Lent, since they enjoyed steaks and cutlets of Whale, Porpoise, or Seal on fast days under the fond delusion that they were consuming fish!

The *Ichthyosaurus*, an extinct aquatic reptile, exhibits the same general fish-like form and paddle-like limbs, but these have clearly been acquired independently, as in the Whales, as a result of the adoption of a life in the water (Fig. 3).

There is yet another creature, common in all our ponds and streams during the spring months, often confused with the fishes in the popular mind, namely the tadpole, which is, of course, the young stage of a Frog or Toad. The Newts, Salamanders, Frogs and Toads belong to a class of vertebrates known as Batrachians or Amphibians, the latter name referring to the fact that they are not only amphibious in the popular sense, living partly in the water and partly on dry land, but are also actually adapted during the early part of their life to breathe under water by means of gills like the fishes, and at a later period to breathe air by means of lungs like the reptiles. But some amphibians never breathe under water at any stage of their existence, not even when immature, and others retain their gills throughout life. How, then, is it possible to distinguish any amphibian from any fish? By the organs of locomotion. In all amphibians the paired limbs are legs in the adult state, in fishes they are fins.

To summarise, a fish may be defined as a vertebrate adapted for a purely aquatic life, propelling and balancing itself by means of fins, and obtaining oxygen from the water for breathing purposes by means of gills. Fishes, thus defined, were formerly regarded as representing a single class of the great sub-kingdom of vertebrates, a class equivalent to the birds (*Aves*) or the reptiles (*Reptilia*); but a more thorough knowledge of their anatomy and evolutionary history has led to a different conclusion. The Lampreys and their allies

(Cyclostomes), with their pouch-like gills and mouths devoid of biting jaws, resemble some of the true fishes to a certain superficial extent in outward form, in habits, and in their general manner of breathing, and may well be regarded as "fishes"

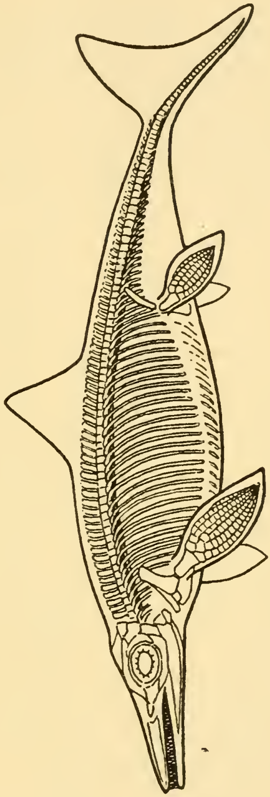


Fig. 3.—EXTINCT REPTILE OF FISH-LIKE FORM.

Restoration of the *Ichthyosaurus*. Much reduced.

in the popular sense. Actually, the two groups of animals are separated by characters just as fundamental as those which divide all the other fishes from the amphibians, and the Cyclostomes must, therefore, rank as a separate class (*cf.* p. 344). The same is true to a lesser extent of the Selachians, a group including the Sharks, Rays, and Chimaeras, which have been separated from the Bony Fishes for a very long period of the earth's history (*cf.* p. 350). In speaking of fishes, therefore, it must be remembered that we are referring to *three* very distinct vertebrate classes, here grouped together merely for the sake of convenience.

Certainly in number of individuals, and probably also in number of species, fishes are at the present time superior to mammals, birds, reptiles, or amphibians. Recollecting that three-quarters of the earth's surface is covered by the seas, and that many of the fresh waters of the land teem with fish life, this superiority of numbers is easier to understand. The surfaces of the great oceans, their middle layers, the abyssal depths and shore regions; the estuaries, mighty rivers, swiftly flowing brooks, turbulent mountain torrents and placid lakes and ponds; each of these possesses its peculiar forms of fish life, variously modified according to circumstances. There are probably more than 20,000 different species of fish in existence to-day, and 100 or more new forms seem to be discovered every year. Aristotle seems to have been familiar with only about 115 species, all of them found in the Ægean Sea. Pliny (*circa* A.D. 200), whose list included as many as 176 species, triumphantly exclaims: "In the sea and in the ocean, vast as it is, there exists, by Hercules! nothing that is unknown to us, and a truly marvellous feat it is that we are best acquainted with those things which Nature has concealed in the deep." *Sancta simplicitas!* Regarding the number of individuals of any particular species, it is wellnigh impossible to give an adequate idea of their abundance. It has been estimated that nearly 400,000,000 Cod and more than 3,000,000,000 Herring are caught each year in the Atlantic and adjacent seas alone, and these numbers must represent but a minute proportion of the individuals in existence at a given time.

The particular branch of zoology which treats of the structure of fishes, both external and internal, their mode of life, their distribution in space and time, etc., is known as "ichthyology," a word derived from the Greek *ichthys*, a fish, and *logos*, a discourse. The scope of ichthyology is enormous, and it is almost impossible to deal with its many branches within the compass of a single volume. The anatomist, investigating and comparing the internal structure of the various kinds of fishes; the embryologist, concerned with the development of the individual from the egg to the adult; the evolutionist, studying the past history of the group; the systematist or taxonomist, classifying the fishes, and arranging them in larger or smaller groups according to their differences and resemblances; the statistician, dealing with minute variations and huge numbers of individuals; the physiologist, studying living activities and the function of organs and tissues; and the "field" naturalist, observing the relation of living fishes to their environment; each of these is continually adding his quota to the sum total of our knowledge of the science of fishes. Moreover, the story of fish life does not begin and end with the fishes living at the present time, but had its commencement ages and ages ago, long before man made his appearance on this planet, and when there were no reptiles or amphibians, no birds, and no mammals. For facts concerning the past history of fishes we are indebted to the geologist, who studies the formation of the rocks wherein the records lie buried, and to the palæontologist, who spends his time searching the dried-up basins of ancient seas and lakes, and describing the fossilised remains which may be found there. As will be shown later on, the story of the rocks—the geological record, as it is called—is necessarily fragmentary and very imperfect, but has already provided a mass of evidence which has confirmed or modified the conclusions drawn from the study of anatomy, embryology, etc. Nor is this all. The body of a fish, as well as its inanimate environment, is continually subject to physical and chemical laws, so that, in order to arrive at a full understanding of fish life, it is necessary to go beyond the realms of pure biology and draw upon the researches of the chemist, physicist, meteorologist, and even the mathematician.

The history of ichthyology, like that of zoology itself, may be said to have begun with Aristotle, who recorded a vast array of facts concerning the fishes of Greece. His information relative to their structure, habits, migrations, spawning seasons, etc., is, so far as it has been tested, extraordinarily accurate, but his ideas of species were exceedingly vague, being simply those of the local fishermen from whom he obtained the names of his specimens. As Dr. Günther has observed: "It is less surprising that Aristotle should have found so many truths as that none of his followers should have added to them." Pliny, Aelianus, Athenæus, and others certainly recorded some original observations, but the majority of scholars from the time of Aristotle until some eighteen centuries later were content to copy from his works, merely adding a number of fabulous stories and foolish myths. In the middle of the sixteenth century the publication of the mighty works of Belon (1518-1564), Rondelet (1507-1557), Salviani (1513-1572) and others, gave a fresh impetus to the study of the science, and established the idea of a species once and for all. From this time onwards the progress of ichthyology was rapid and continuous, and its history includes the names of Linnæus, Risso, Rafinesque, Bloch, Lacepède, and Cuvier, men whose pioneer work, often carried out in the face of great difficulties, with small material and inadequate apparatus and instruments, has laid the firm foundations of the science upon which modern ichthyologists are still building.

CHAPTER II

FORM AND LOCOMOTION

Shape of a typical fish. Fins and their functions. Other animals with a fish-like form. Departures from the ideal form, and compensating factors. Depressed and compressed fishes. Flat-fishes. Fishes with rounded bodies: Globe-fishes, Puffers, Sun-fishes, etc. Elongate fishes. Sea Horses. Methods of locomotion. Muscular movements. Swimming of Mackerel, Eel, and Trunk-fish. Locomotion by means of fin-movements: caudal fin, dorsal and anal fins, pectoral fins. Jet propulsion. Speed. Swimming positions. Leaping. Burrowing.

Of the many and varied forms of animal life found in the seas and in the fresh waters few are more perfectly adapted for dwelling in a liquid medium than the fishes. Many of the invertebrates spend the greater part of their lives attached to the sea bottom, or crawl sluggishly over a small area of its surface; others float more or less passively at the surface or in the middle layers of the water, their movements dependent to a great extent on the action of the tides and currents; the Squids and Cuttle-fishes alone approach the fishes in rapidity of motion and grace of form, but lack their agility in the water, and are generally far inferior to them in mastery of their medium.

The water in which a fish lives and moves is a comparatively dense medium, and in order to attain the most efficient movement with the greatest economy of energy a certain form of body is essential, varying somewhat in detail with the actual speed required. The shape of the body, therefore, is not an arbitrary one, but conforms to a number of definite mechanical conditions induced by its environment. These mechanical principles cannot be dealt with here, since a study of this subject would involve the consideration of such theoretical problems as "curves and displacement," "streamlines," "entering angles," "runs" and the like, the proper understanding of which entails some knowledge of higher mathematics. It must suffice to point out that the fine form of a typical swift-swimming fish such as the Mackerel (*Scomber*) (Fig. 5A) or

Bonito (*Gymnosarda*) (Fig. 4) is one that is admirably adapted from a mechanical point of view for cleaving the water, and is that which is clearly best suited for progression in that medium. The mechanical conditions which led man to construct his submarine to a certain pattern, in order to have a vessel that would move freely in all directions under water, are precisely the same as those which have determined the shape of the fish's body, so that it is not surprising to find that the form of the animate fish corresponds closely with that of the man-made submarine.

The shape of the body of a Mackerel is fusiform; that is, it is shaped somewhat like a cigar, circular or elliptical in cross-

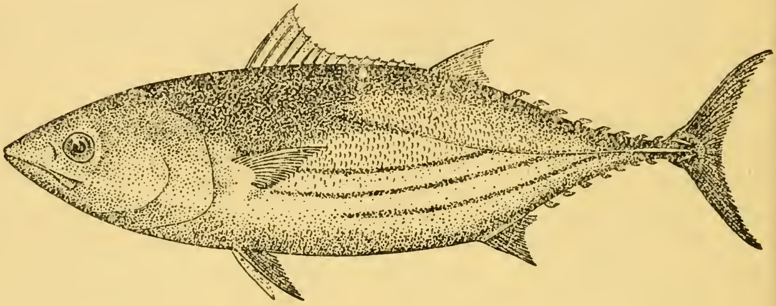


Fig. 4.—A SWIFT PELAGIC FISH.

Oceanic Bonito (*Gymnosarda pelamis*), $\times \frac{1}{8}$.

section and thicker in front than behind. It has been described by one authority as resembling a double wedge, the thick part of which is represented by the head and anterior part of the body, and one of the thin edges by the free hinder margin of the tail. Every line of its smooth, rounded contour is suggestive of swift motion, there being an almost complete absence of irregularities or projections calculated to hinder progression. There is no distinct neck as in the land vertebrates, the head merging insensibly into the trunk and the trunk into the tail, the boundaries between these regions of the body being denoted by the gill-opening and vent respectively. Viewed from the front, the outline of the fish appears as a perfect ellipse of comparatively small size (Fig. 5A). The beautifully moulded, bullet-shaped head, with its pointed snout forming an efficient cutwater; the jaws fitting so close together that it is scarcely possible to insert the blade of a penknife between them; the firm, smooth eyes, carefully adjusted so that their surfaces are level with the adjoining surfaces of the head; and the closely

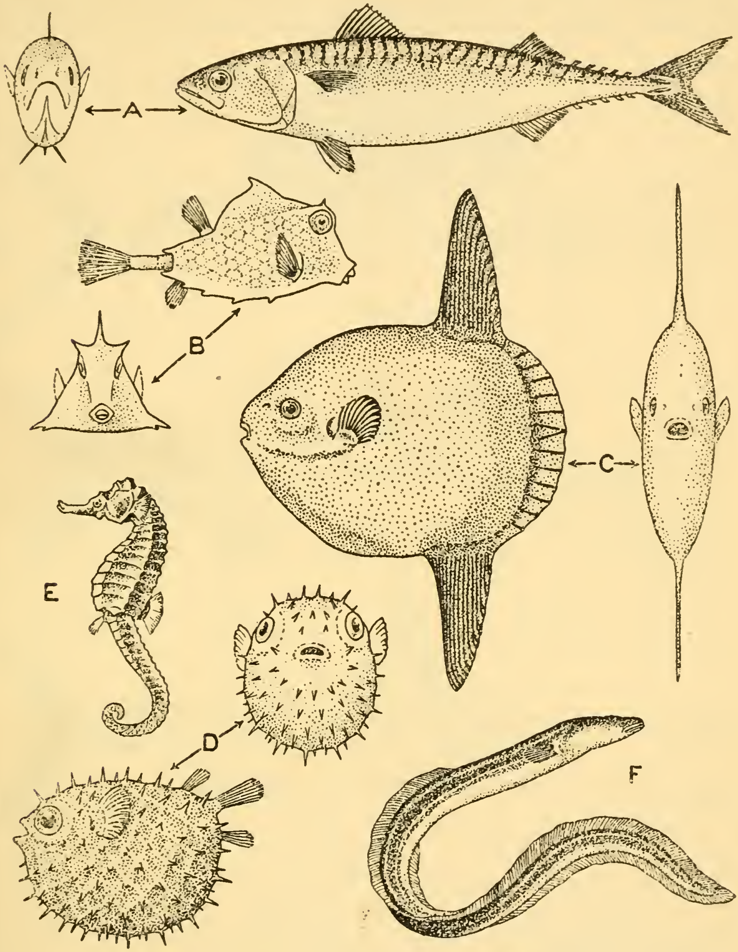


Fig. 5.—DIFFERENCES IN FORM.

A. Mackerel (*Scomber scombrus*), $\times\frac{1}{4}$; B. Trunk-fish (*Ostracion gibbosus*), $\times\frac{1}{4}$; C. Sun-fish (*Mola mola*), $\times\frac{1}{20}$; D. Globe-fish (*Chilomycterus antennatus*), $\times\frac{1}{4}$; E. Sea Horse (*Hippocampus punctulatus*), $\times\frac{1}{2}$; F. Common Eel (*Anguilla anguilla*), $\times\frac{1}{8}$.

fitting gill-covers; all these are features whose meaning becomes clear when interpreted in terms of rapid progression. The small scales with which the body is covered offer practically no resistance to forward motion, presenting a comparatively smooth surface, which is still further improved by the presence of a copious supply of slime. This mucous covering is designed to reduce friction with the surrounding water to a minimum,

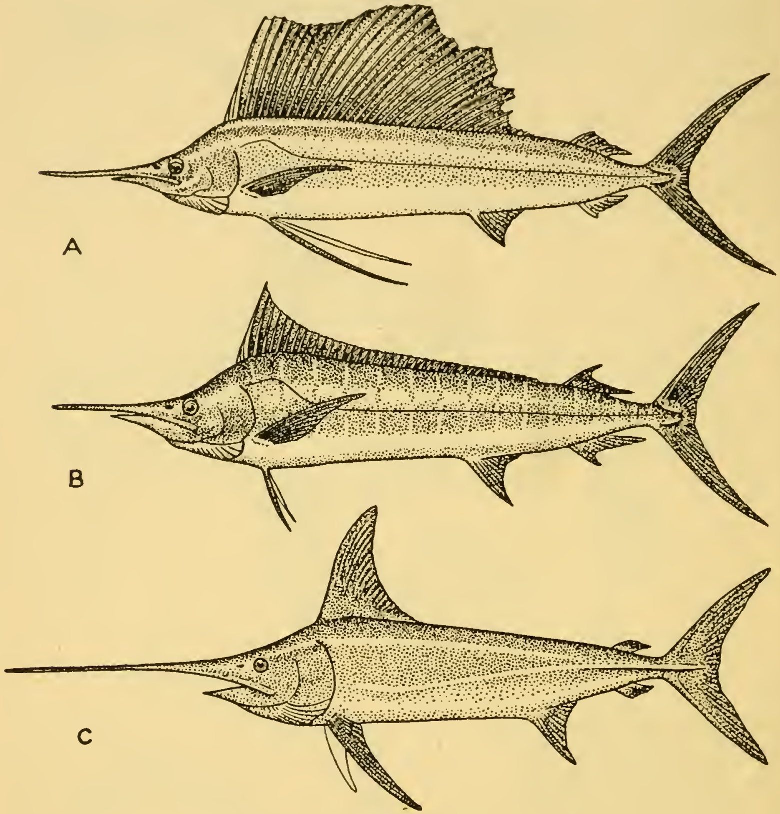


Fig. 6.—" SWORD-FISHES."

A. Sail-fish (*Istiophorus americanus*); B. Spear-fish (*Makaira mitsukurii*); C. Sword-fish (*Xiphias gladius*). All much reduced.

not only on account of its inherent slipperiness, but also because it fills up any small irregularities in the surface of the body. Finally, the smooth hollow curves of the hinder end of the body, extending from the region of greatest thickness backwards to the tail, are admirably adapted to permit of the passage of the water displaced during forward motion.

The fins, which form so characteristic a part of the fish, may well be considered here. Within recent years a French scientist has carried out some very interesting experiments, during which bodies composed of more or less plastic material were drawn through the water at varying speeds. As this took place these artificial bodies tended to become more or less closely moulded to the typical fish-like form described above. At the same time, however, they were inclined to roll over to one side when poised motionless in the water, and to wobble to an alarming extent when moving at any speed, and it was only by the appropriate placing of artificial keels that he was able to stabilise the flight of his models. There can be little doubt

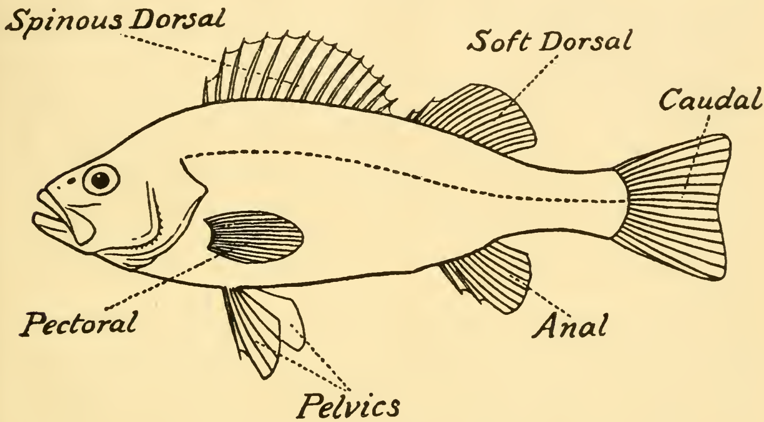


Fig. 7.—TOPOGRAPHY OF FINS.

that it was in order to obtain stability that wedge-shaped body keels have been evolved along the back and belly of a fish, as well as paired balancing and steering organs projecting from the sides. These keels and balancers are the fins, and, although they are discussed in greater detail in another chapter, it will be necessary to study their arrangement and distinctive names in the accompanying figure (Fig. 7) in order to understand the part which they play in locomotion. The fins are of two kinds, median or unpaired, and paired. The median fins or keels consist of a *dorsal* in the middle line of the back, an *anal* on the belly behind the vent, and a *caudal* or tail-fin at the hinder end of the fish, which, in addition to assisting stability, also acts as a rudder and plays an important part in forward movements. In the fast-swimming Mackerel the dorsal and anal fins form sharp, thin keels, and, although these appear prominent when viewed from the side they are much less so in the front aspect of the fish (Fig. 5A). The paired fins are of two kinds only, the *pectorals* and *pelvics*, corresponding to the fore and hind limbs of land vertebrates.

Further evidence that the characteristic form of a typical fish has been determined by its environment is provided by the study of the evolution of other aquatic vertebrates. The Cetaceans, mammals which have forsaken the land and returned to a life spent entirely in the water, have revived the fish-like shape, a result which has been brought about by important anatomical and physiological changes. At the same time, their mammalian ancestry is reflected in the different arrangement of the muscles used in swimming, as well as in the swimming movements themselves. Again, in the extinct reptiles, the Ichthyosaurs, we find the same fusiform shape, powerful tail, wedge-like dorsal fin and paddle-like limbs (Fig. 3), clear evidence of the adoption of an aquatic life. The same external conditions acting over an immense period of time on countless generations has produced much the same result in three totally different groups of vertebrate animals, an excellent example of what is known as convergence in evolution.

So much for the form of a typical pelagic fish. Departures from this ideal shape of body are both numerous and varied, but it must be remembered that many which at first sight would appear to be anything but streamline shapes will prove to be excellent ones when the particular mode of locomotion of their possessors is considered. One fact is quite obvious: any radical departure from the ideal form must inevitably lead to a loss in swimming efficiency, or, at least, to a marked restriction of speed, and this becomes more and more evident the further the fish departs from the typical shape. A fish like the Mackerel depends on its speed, not only to obtain its food, but as a means of escape from enemies, and any marked restriction of its activities would leave it liable to the danger of extinction. It is only where rapid mobility ceases to be of primary importance to the life of the species, and is replaced by some other compensating factor, such as heavy armour, that a fish is able to dispense with the fusiform shape and survive in the struggle for existence.

Three examples selected from the class of Selachians will serve to illustrate this point. The Blue Sharks and their allies

(*Carcharinus*) possess slender, perfectly streamlined bodies, conical heads, pointed snouts, and powerful muscular tails (Figs. 23C; 82A); the Carpet Sharks (*Orectolobus*) have stout thick-set bodies, considerably flattened from above downwards, massive heads, broadly rounded snouts, wide mouths, and much reduced tails with comparatively small dorsal fins (Fig. 82B); the Rays (*Raiidae*) have very broad, flat bodies, the head, trunk and enormously expanded pectoral fins being completely welded together to form a circular or quadrangular disc, from which the feeble tail with its tiny dorsal fins projects as a slender appendage (Figs. 8A; 14B). The Blue Shark is an inhabitant of the open sea, feeding almost exclusively on other fishes which it chases with great vigour; it is essentially a strong, speedy fish, every line of its body intended for rapid progress in pursuit of prey. The Carpet Shark, on the other hand, relies on cunning rather than speed to obtain a meal, lying in wait on the sea floor until the prey comes within reach of its jaws. The loss of swimming power is here compensated for by the remarkable manner in which the Shark resembles its surroundings, its appearance when at rest being that of a weed-covered rock (*cf.* p. 216). The uniform steely blue coloration of the Blue Shark is replaced by a beautiful variegated pattern which harmonises closely with the sea bottom. The Ray is another sluggish, ground-living fish, and also depends to a large extent on its general resemblance to the surroundings to escape observation by enemies. Its flattened form is admirably adapted for this particular mode of life, but, as will be seen later, its unusual method of locomotion enables this fish to move with much greater rapidity than would appear possible from its appearance. Some still more specialised members of this order have acquired other protective devices in addition to their coloration, as, for example, the Torpedo or Cramp-fish (*Torpedo*) with its powerful electric organs (Fig. 61), and the Sting-ray (*Trygon*) with one or more strong, saw-edged and poisonous spines on its tail (Figs. 32B; 36E).

A body flattened from above downward is generally spoken of as "depressed," while that which is flattened from side to side is "compressed." Among Bony Fishes the former type is very rare, but the well-known Angler-fish or Fishing-frog (*Lophius*), in which mimetic resemblance and cunning in obtaining a meal has been brought to a pitch of perfection (Fig. 89) and the little Bat-fish (*Ogcocephalus*), with the upper surface of its body protected by a covering of hard bony warts

(Fig. 40D), provide excellent examples. The compressed body, on the other hand, although unknown in Selachians, is much more common in Bony Fishes. Often it is shortened as well, and, flexibility of the body being no longer an absolute necessity, many of these forms are able to afford heavy protective armour of some kind. The brilliant little Butterfly-fishes (*Chaetodontidae*) of tropical coral reefs are excessively quick in their movements, in spite of their short, deep, flattened bodies, and they rely largely on their agility to escape being eaten, coupled with the fact that their deep bodies and strong, spiny fins make them awkward mouthfuls to swallow (Fig. 83C, D). The beautiful Angel-fish (*Pterophyllum*) of the rivers of South America, a familiar object in aquaria, has a very much compressed and almost circular body, and the large fins have some of the rays drawn out into lengthy filaments (Fig. 8C). It is a very slow swimmer, spending most of its time suspended almost motionless in mid-water, and relies on its remarkable resemblance to the water plants among which it lives to escape detection. The Flat-fishes (*Heterosomata*), a group which includes such well-known edible forms as the Halibut, Turbot, Plaice, and Sole, all have very much flattened bodies, and, like the Rays, spend much of their time on the sea floor, where their mottled coloration harmonises with the ground on which they lie and renders them inconspicuous (Figs. 8B; 40A-C). In the minds of many people the Plaice and the Skate are lumped together as "Flat-fishes," but it is obvious that the resemblance between the two fishes is a purely superficial one. Both have taken to a life on the bottom, where a flattened body is a decided advantage, but the Skate has become flattened from above downwards, whereas the Plaice is compressed from side to side. In other words, the colourless lower surface of the former which rests on the bottom is the true lower or *ventral* side, whereas in the Flat-fish this surface represents the *right or left* side.

The Globe-fishes or Puffers (*Tetrodontidae*) and their relatives the Porcupine-fishes (*Diodontidae*) provide examples of fishes with shortened, rounded bodies, in which the consequent loss of swimming power is compensated for by the development of some sort of bodily armour in the form of spines or small prickles (*cf.* p. 98). In addition to their spiny covering, these fishes possess the power of swallowing water or air and thereby inflating the body like a balloon. When thus inflated they are fond of floating passively with the currents, more often than not upside down. When taken from the water a Puffer will generally inflate at once, but if slow to begin can be persuaded to swell up by gentle tickling. In this condition, and with the spines of the skin all standing erect, the fish is adequately protected against most predatory enemies, who would find it a difficult morsel to bite, much less to swallow. Recent observations made by Dr. Beebe, however, tend to show that such

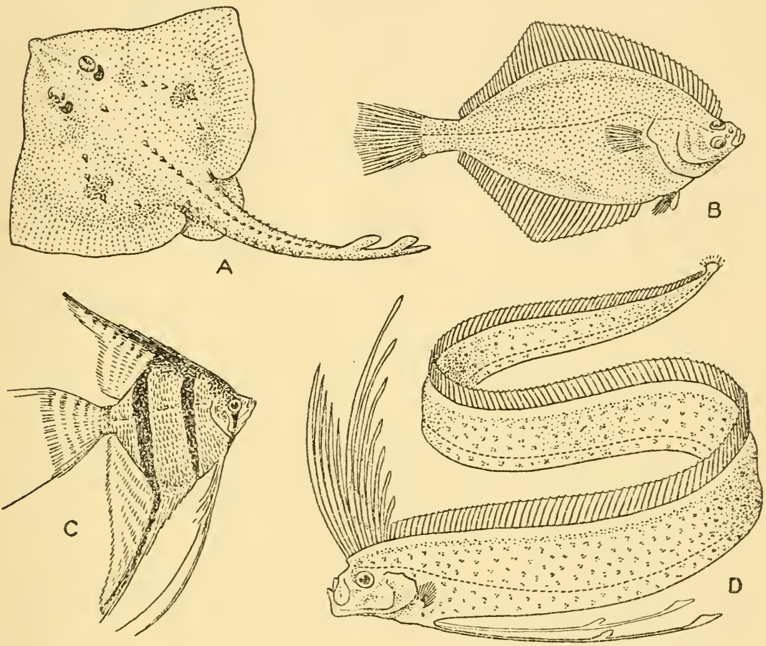


Fig. 8.—FLATTENED FISHES.

A. Female Thornback Ray (*Raia clavata*), $\times \frac{1}{12}$; B. Flounder (*Flesus flesus*), $\times \frac{1}{8}$; C. Angel-fish (*Pterophyllum scalare*), $\times \frac{1}{4}$; D. Oar-fish or Ribbon-fish (*Regalecus glesne*), $\times$ about $\frac{1}{25}$.

protection is not always complete. He watched a number of little Porcupine-fishes, and saw that when they were threatened by a large Gar-fish, four feet in length, they bunched together for protection, giving the appearance of one large, round and prickly fish; occasionally, however, a single individual would become detached from the mass, when it was promptly seized and devoured. The allied Trunk-fishes (*Ostraciontidae*) are also slow-swimming creatures, living at or near the bottom of the sea, and rely on their armour, which here takes the form of a rigid bony case, for protection (Figs. 5B; 42F). Also related to the Porcupine-fishes and Puffers are the gigantic and grotesque Sun-fishes (*Molidae*), of which there are three species, all widely distributed in warm seas. The Round-tailed Sun-fish (*Mola*) has a very remarkable shape, the deep, circular and somewhat compressed body appearing as though the tail end had been amputated just behind the high dorsal and anal fins (Fig. 5C), a feature to which the popular name of "Head-fish" refers. Such a body is probably well adapted for a more or less passive drift in ocean currents, and it has been suggested that its curious shape is in some way associated with the peculiar diving habits of this fish. The presence of small deep-sea fishes in the stomachs of captured Sun-fishes demonstrates that they must descend to considerable depths at times. The Round-tailed Sun-fish attains to a length of eight feet or more and a weight estimated at more than a ton. It is a sluggish, and, from all accounts, singularly stupid fish, often to be observed basking or swimming lazily at the surface of the sea. Underlying the skin, which is very tough and leathery, is a layer of hard, gristly material some two or three inches thick — ample compensation for any loss of locomotive power!

At the other extreme are the fishes with long bodies, which may be rounded as in the Eels (*Apodes*) or very much compressed, as in the Ribbon-fishes (*Trachypteridae*) or Cutlass-fishes (*Trichiuridae*). From their shape one would hardly expect such fishes to be other than slow swimmers, but, as will be shown below, the adoption of a particular method of locomotion gives them a greater speed than the short-bodied forms mentioned above. The peculiar shape of the Eel's body (Fig. 5F) is almost certainly associated with its habit of living in soft river bottoms, wriggling in and out of the mud, creeping through reeds, or insinuating itself into holes and crevices as do its relatives in the coral reefs. Some of the Eels carry the elongation of the body to such an extreme that they have the appearance of a piece of slender whipcord, and the fins are often much reduced. Such a *filiform* type of body is characteristic of the curious Snipe-eels (*Nemichthyidae*), oceanic forms which sometimes descend to considerable depths (Fig. 32G). When observed swimming at or near the surface, these Eels are not infrequently mistaken for snakes. It may be noted here that similarity in eel-like form is not necessarily indicative of close relationship, but may be due to that parallelism in evolution which has been already mentioned (*cf.* p. 14). The so-called Symbranchoid Eels (Fig. 21B), for example, are in no way closely related to the true Eels, and the same type of body in the two groups has been evolved in response to the needs of similar environments, or as the result of the adoption of the same mode of life.

In the Sea Horses (*Hippocampus*) the form of the body is unique, the head being bent at right angles to the trunk in a manner suggestive of that of a horse, and the trunk itself is definitely curved (Fig. 5E). The possession of a distinct neck is not the only remarkable feature, and the tail is also unique in that it is prehensile and can be used by the fish to anchor it to moving or fixed objects. The body is protected by a series of bony, ring-like plates, and the spines or membranous processes with which these are ornamented serve to break up the outline and so render the fish inconspicuous when swaying to and fro among aquatic vegetation. The Sea Horses are defenceless creatures, and depend largely on this mimetic resemblance to escape from predatory fishes.

The locomotion of fishes provides the biologist and physicist with a number of interesting problems, and has also attracted the attention of the marine engineer, some of whose mechanical inventions owe their inception, at least in part, to observations made upon living animals. Owing to the difficulty of studying fishes in their natural habitat, and to the fact that when transferred to the unnatural surroundings of an aquarium they tend to behave in a manner somewhat different from the normal, our knowledge of the different methods of locomotion is still incomplete. Much progress has been made within recent years, however, and the researches of an American investigator, Mr. Breder, have proved very illuminating. Good results may be expected from the use of the cinematograph, and with the improvement of under-water photography it should be possible to take good films of swimming fishes, and to analyse the movements in detail by the use of the slow-motion picture. Although actual swimming and its associated movements forms the main subject for consideration in this chapter, it must be remembered that this is by no means the only locomotor method in use, and walking or creeping over the sea floor, skipping about on sand or mud, burrowing, wriggling on dry land, leaping, flying, and so on, are also indulged in by some fishes for purposes of progression. These are rather in the nature of specialised developments, however — secondary adaptations, evolved in response to a change in habits or environment, and, since they are often accompanied by a modification of certain organs for the particular end, most of them may be conveniently considered in later pages. Flying, for example, which involves the modification of the pectoral fins, may be discussed in the chapter devoted to those organs.

The three classes of vertebrates here grouped together as fishes include a very diversified assemblage of forms, but there is, nevertheless, a basic similarity in their swimming movements, however different these may appear to be at first sight. The earliest fishes probably swam by means of simple rhythmic contractions of the muscles of the trunk and tail, designed to produce certain definite contortions of the body; by the pressure of different parts of the body in succession against the surrounding water the animal was driven forward. Most fishes have retained the primitive arrangement of the great body muscles, the myomeres, as they are called (*cf.* p. 167), which form a series of blocks or segments, arranged in pairs one behind the other and separated by partitions. In this respect fishes differ from all land vertebrates, in which the main muscle masses are more or less concentrated on the fore and hind limbs, these being the normal organs of locomotion, whereas the corresponding pectoral and pelvic fins of fishes more often than not perform quite subsidiary functions, such as balancing and steering. We have already noticed the essential similarity in the shape of the body in the cetaceans and fishes, but, owing to its different ancestry, the arrangement of the body muscles in a whale is quite unlike that found in a fish, and the swimming movements themselves are in a different plane, being up and down instead of from side to side. This explains the dissimilarity in the position of the tail-fin in the two groups (*cf.* p. 4); the fish generally swims more or less parallel with the surface of the water, and the vertical caudal fin is designed to assist in driving it forward and to act as a rudder; the whale is under the necessity of coming to the surface from time to time, and swims by alternately rising and diving in a sort of wave-like curve, the horizontal tail assisting to drive the animal upwards or downwards as the case may be.

Three primary methods are employed by fishes to produce forward movements while suspended in a fluid medium: (1) body movements due to alternate expansion and contraction of the myomeres; (2) movements of the appendages (fins); and (3) movements caused by the action of jets of water expelled from the gill-openings during the process of respiration. The first method is the most common and of the greatest importance, the others being, for the most part, auxiliary to it. It must be borne in mind, however, that in the majority of fishes the three are inter-related, and may all be used at different times, or even at the same time, for the common end of driving the fish forward according to its requirements. Locomotion by means of fin movements, for example, may be employed when

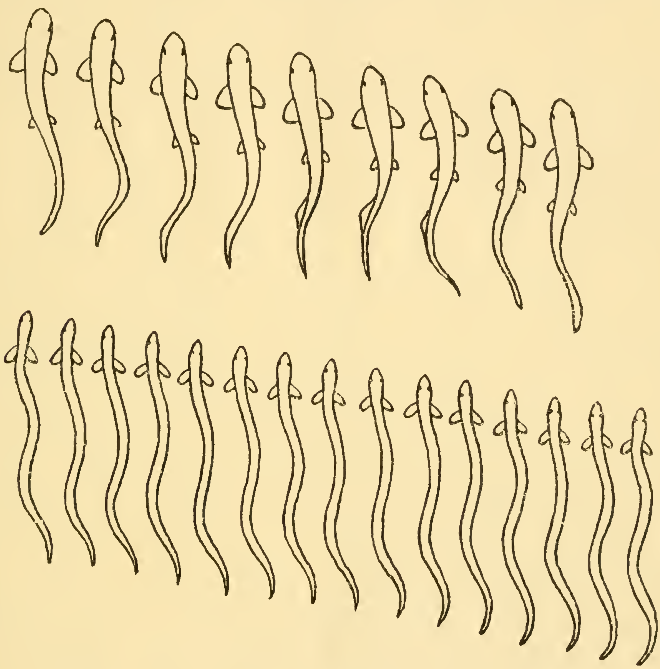


Fig. 9.—BODY MOVEMENTS OF FISHES USED IN SWIMMING.

Shark (above) and Eel. (After Marey.)

slow progress only is wanted, but, should danger threaten or prey appear in sight, body movements quickly come into play, and at the same time the increased rate of breathing due to the emotion of fright or greed assists in the general acceleration of the forward thrust.

The Mackerel (*Scomber*), which depends almost entirely on body movements for forward progression, will serve as an excellent example of the first of these methods. We have compared the body of this swift fish to the man-made and screw-propelled submarine, but here the resemblance ends, since no revolving motion of one part on another is possible in the living animal. It has been stated that the Mackerel is able to twist its tail to such an extent as to be "very much after the manner of a screw in a steamship, and thus to drill the water," but this is, to say the least, very unlikely, and is in no way supported by actual observation. Most standard text-books on fishes contain the statement that they swim by means of lateral flexions of the hinder part of the body, aided by movements of the caudal fin. This is, in the main, correct, but recent investigations tend to show that the part played by the tail in producing a forward thrust is far less important than was previously supposed. In this connection the following experiment carried out by Mr. Breder is of some interest. Two Rudd (*Scardinius*) of equal size were selected, and, the tail of one of them having been carefully amputated, the two fishes were placed in a tank eight feet long, where they rested side by side at one of its ends. The investigator carefully approached this end and gave the glass a smart blow with his hand. Immediately the two Rudd scurried away to the opposite end of the tank, where they came to rest in similar positions. This experiment was carried out several times, and each time it was repeated both fish arrived at the opposite end *at the same time*, having traversed the intervening space side by side. The only noticeable difference between the two specimens was that the fish without a tail-fin "waggled" the hinder part of its body faster and through a wider arc.

When the Mackerel wishes to move forward the first action which takes place is the contraction of the first few myomeres at the front end of the body on one side only, resulting in the throwing of the head sharply to one side. The successive segments then alternately contract and relax from the head towards the tail, and the curve or flexure of the body is, so to speak, passed backwards (Fig. 9). The effort culminates in bringing the tail to the axis of the head with a powerful sweep. Since, at the commencement of the stroke the pivotal point of the swing lies just where the backbone joins the skull, a comparatively short swing of the head is all that is necessary to bring the tail into position for a long and strong sweep; as this is carried out the pivot must necessarily move backwards, until at the end of the stroke it lies nearer to the tail than to the head. The accompanying illustrations of a swimming fish give a good idea of the manner in which the body is undulated, and show how the flexure may be traced backwards from the head towards the tail (Fig. 9).

The actual forward thrust is effected by the pressure of the fish's body against the surrounding water, aided to a certain extent by the tail-fin stroke, due to the action of the muscles. In order to understand the action of the body movements on the surrounding medium it will be convenient to study an elongated type of fish such as the Eel (*Anguilla*), and compare its locomotor methods with those of the Mackerel. The movement is again initiated by the contraction of the first few myomeres on one side. The anterior part of the body is thus thrown into a curve, and this curve is passed backwards in a series of waves by the alternate contractions and expansions of the serial muscle segments. The movement is mechanically the same as that of a long rope held at one end and given a smart jerk with the hand at right angles to its axis. This results in a wave passing down the rope, the curves gradually decreasing in size and eventually dying out because the initial action of the hand was the sole agent of propulsion; in the living fish each successive muscle segment gives an added impetus to the wave, and, as soon as the first wave has started backwards, a second follows, but on the opposite side, and so on. Here the forward thrust is attained almost entirely by the pressure of the fish's body against the water contained in the spaces between the curves. With this elongate form the fish gains much greater pressure areas from its sides than does the Mackerel, but, at the same time, it naturally loses the terminal effect of the tail-fin. Indeed, we find that in all eel-like fishes the caudal fin is either very much reduced or wanting altogether, a good example of the inevitable disappearance of a useless organ. In most Eels the anterior part of the body is cylindrical in cross-section, whereas the hinder part is distinctly compressed; this feature has a mechanical advantage, since a blade-like structure which presents its surface more effectively to the water naturally provides a greater amount of thrust than a rounded one. The elongate Ribbon-fishes (*Regalecus*), and other fishes with long bodies greatly flattened from side to side (Fig. 8D), undulate them into curves which are even more ample than those of the Eel, the extreme ribbon shape making this excessive bending comparatively easy to perform. It is of interest to note here that fishes with the body rounded can move over solid surfaces out of water by applying the same locomotor methods normally used in swimming, whereas those with ribbon-like bodies are unable to progress at all outside the liquid medium. While considering the question of the movements of fishes out of the water, it may be of interest to see why a species with the type of body similar to the Mackerel flops from side to side when taken from its native habitat. In contracting the body muscles on one side in the normal manner, the tail is brought smartly down with a sharp smack, and the accompanying reaction throws the fish upwards. Experiments conducted on living fishes have shown that they are quite unable to direct these movements, progressing indefinitely in any direction, and that only a favourable wind or a slope in the right direction enables them to find their way back to the water.

If the locomotion of the Eel be regarded as one extreme type of body movement, that of the Trunk-fish (*Ostracion*) undoubtedly represents the opposite extreme, the Mackerel and other generalised fishes being intermediate between the two types. In the Trunk-fish (Figs. 5B; 42F), with its head and body enclosed in a hard and inflexible bony case, from which the fleshy tail with a large fan-like caudal fin at the extremity projects freely backwards, undulations of the body are clearly impossible. Normally, the dorsal and anal fins form the chief propelling agents, and the tail acts as a rudder, but where greater speed is required the fish lashes the tail vigorously from side to side, the movements being brought about by the alternate contraction of the muscles on either side of the fleshy part of the tail. A Trunk-fish swimming in this way may be likened to a small boat propelled by means of a single oar from the stern.

The three types of body movements here described, and exemplified by the Eel, Mackerel, and Trunk-fish respectively, are not to be looked upon as other than purely arbitrarily chosen examples. Among fishes we find such a complete gradation from one extreme to the other that it is not easy to say where one begins and the other ends. The extremes are methods employed by comparatively slow-swimming forms, mostly living close to the shore, whereas those of the Mackerel and its kind are of the highest efficiency and pre-eminently suited for high speed. With the sole exception of fishes such as the Sea Horses, in which the locomotor emphasis is placed entirely on the fins, all existing forms fall somewhere within the series described above.

Turning to the second of the primary methods of locomotion, it may be noted that movements essentially the same as those of the body may be localised in one or more of the fins, and the

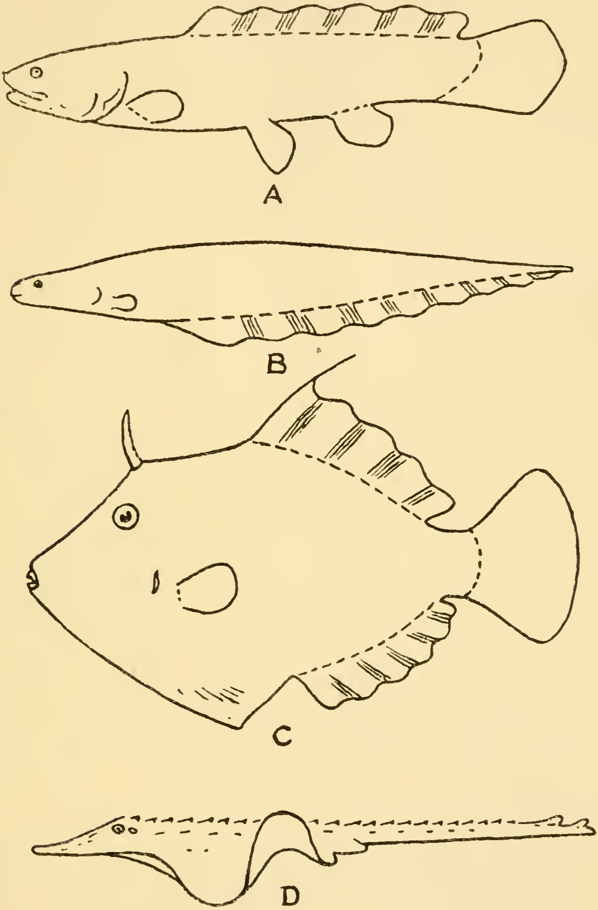


Fig. 10.—FIN MOVEMENTS USED BY FISHES IN SWIMMING.

A. Bow-fin (*Amia calva*), $\times \frac{1}{10}$; B. Electric Eel (*Electrophorus electricus*), $\times \frac{1}{8}$; C. File-fish (*Monacanthus sp.*), $\times \frac{1}{4}$; D. Ray (*Raia sp.*), $\times \frac{1}{8}$. (After Breder.)

same kind of series occurs, ranging from a serpentine, undulating motion like that of the Eel to a fan-like waggle which recalls the tail movements of the Trunk-fish. It has been remarked that the caudal fin is operated primarily by the action of the muscles of the body and tail, but many fishes are capable of moving slowly forward by means of wave-like movements of the fin itself, the waves travelling at right angles to the longitudinal axis of the body. In most fishes the shape of the fins, and more especially that of the caudal, provides a very good index of speed and agility, the same type of fin occurring in quite unrelated groups of fishes whose swimming habits are similar. It is impossible to enter into the mechanical possibilities of the different shapes of caudal fin, but it may be laid down as a general rule that fishes with large tails, the hinder margins of which are square-cut (truncate) or rounded, are comparatively slow swimmers, and, although able to accomplish sudden short bursts of speed, they are incapable of swimming for long periods at a rapid velocity, as are those species provided with deeply forked or lunate tails (Fig. 33). Such fishes have the upper and lower lobes of the fin long and pointed, and the fleshy part of the tail, known as the caudal peduncle, is nearly always very narrow and not infrequently strengthened by one or two fleshy keels on either side as in the "Sword-fishes" (Fig. 6). The Bonito (*Gymnosarda*), reckoned to be among the swiftest of all fishes, provides an excellent example of this type of caudal fin—crescent-shaped, without flesh, almost without scales, composed of bundles of rays, flexible, yet as hard as ivory (Fig. 4). Professor Goode writes: "A single sweep of this powerful oar doubtless suffices to propel the Bonito a hundred yards, for the polished surfaces of its body can offer little resistance to the water. I have seen a Common Dolphin swimming round and round a steamship, advancing at the rate of twelve knots an hour, the effort being hardly perceptible. . . . Who can calculate the speed of a Bonito?"

The other median fins, the dorsal and anal, may also be used by certain fishes as swimming organs, especially in those forms whose bodies have radically departed from the stream-line shape. They may act in conjunction with the caudal fin or as a substitute for it. By appropriate use of the muscles controlling the fin-rays and their supports (*cf.* p. 58) a series of wave-like movements can be produced in the fin, similar to the wriggling contortions of the body of the Eel. In the Bow-fin (*Amia*) of North America, for example, undulating movements of the long dorsal fin are often used to propel the body slowly forward (Fig. 10A), and the Electric Eel (*Electro-*

phorus), in which the dorsal fin is wanting, employs the long anal fin in a similar way (Fig. 10B). The File-fish or Leatherjacket (*Monacanthus*) has both dorsal and anal fins placed a little obliquely, and makes use of both simultaneously for forward progression (Fig. 10C). Other fishes, such as the Globe-fishes or Puffers (*Tetrodontidae*) and Porcupine-fishes (*Diodontidae*), move by flapping the short dorsal and anal fins in a fan-like manner. The Sea Horse (*Hippocampus*), which characteristically swims in an upright position, glides slowly through the water by means of rapid wave-like movements of the dorsal fin, which has the appearance of a tiny propeller revolving in the middle of the fish's back (Fig. 5E). The related Pipe-fishes (*Syngnathidae*) swim in a similar way, but their bodies being elongate and more flexible they are able to make more rapid progress at times by lashing themselves into curves (Fig. 32E). Flat-fishes, when moving about on the sea floor, often make use of the long dorsal and anal fins which fringe the upper and lower edges of the body (Fig. 8B) to obtain a grip of the ground, and by undulating these fins are able to progress at a fair speed.

Turning to the paired fins, the pelvics may be dismissed at once, as these merely assist the dorsal and anal fins in maintaining stability, and rarely, if ever, serve as organs of propulsion. The pectorals, on the other hand, are often used partly, or in some cases almost exclusively, for locomotor purposes, particularly in those fishes of slow or moderate speed. In slow-moving fishes these fins are generally spatulate in shape, and may produce forward movements of the body by a simple synchronised flapping, as in some of the Wrasses (*Labridae*). In others, of which the File-fish (*Monacanthus*) and the Porcupine-fish (*Diodon*) are good examples, wave-like motion similar to that described in connection with the caudal fin, is employed. This type of motion is particularly well marked in the Rays (*Raia*) and their allies, in which the pectoral fins are very much enlarged and constitute practically the sole organs of locomotion. It will be noticed, however, that the waves travel in a vertical plane instead of a horizontal one—up and down instead of from side to side (Fig. 10D). In a few species, notably among the Damsel-fishes (*Pomacentridae*), the pectoral fins seem to be operated after the manner of oars, being brought forward almost edgewise and pulled back broadside on. In fishes of high velocity the shape of the fins is generally long and falcate (*i.e.* sickle-shaped), and these are probably used mainly for changing course or for slowing down, scarcely ever for propulsion (Fig. 4). In fishes, turning when in motion would appear to be effected largely by appropriate movements of the fins, and particularly of the pectorals, but body movements as well as jets of water from the gill-openings also play their part. Stops are nearly always made by using the pectorals in the manner of brakes, but some forms pull up by reversing their primary locomotor apparatus.

Finally, there remains the third primary method of locomotion, namely, by means of jets of water squirted from the gill-openings during respiration. Recent experiments have shown that these exhalations may play an important part in driving the body forward, but the effect varies with different fishes, being of considerable importance to some and of little or none to others. This method is probably always brought into play for high-speed travelling, and assists the muscular activities of the body. The jets reach their maximum strength between the flexures of the body when the fish is straight forward, and when they would clearly produce the best effect. When used in conjunction with movements of the pectoral fins, the motions of the fins are timed so that they do not get in the way of the jets. A particularly powerful jet is usually expelled when a fish commences any swimming movement, thus giving an added impetus to the initial muscular efforts of the body in getting under way. By holding down tightly the gill-opening on one side, and forcing all the water out of the opposite one, the fish may make use of this locomotor method to perform turning movements in any given direction.

Unless a fish is actually resting on the bottom, it is by no means as easy as it would appear to maintain a stationary position in the water. Breathing cannot be suspended for a moment, and although this respiration may be comparatively slow as compared with that taking place when the fish is swimming, the exhalant jets of water are of sufficient strength to cause the body to move forward, and some sort of action is necessary to counteract their force. Observation of a fish resting in mid-water in an aquarium shows that the pectoral fins are in more or less constant motion, and it has been freely stated that they are employed in balancing the body. Experiments, consisting of removing one or both of these fins from a living fish, have shown that they play very little part in maintaining stability, and it seems that they are engaged in constantly backing water, to counteract the forward thrust engendered by the respiratory jets.

The speed attained by fishes has always been the subject of much speculation, but, unfortunately, very little accurate data exists as to the relative speeds of different forms. The average rate of progress of the Salmon (*Salmo*) has been estimated at about seven miles per hour, and that of the Pike (*Esox*) as from eight to ten miles per hour, but these come nowhere near the speed attained by some of the large oceanic fishes. Remarking that the speed of a Bonito might be reckoned by the aid of the electrical contrivances by which the initial velocity of a projectile is calculated, Professor Goode adds: "The Bonitos in our sounds to-day may have been passing Cape Colony or the

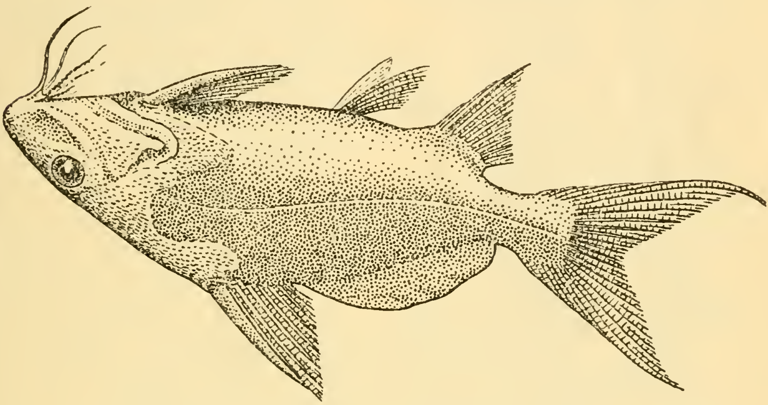


Fig. 11.—A FISH WHICH SWIMS UPSIDE DOWN.

Cat-fish (*Synodontis batensoda*), $\times \frac{1}{2}$.

Land of Fire the day before yesterday!" Of all fishes, the Sword-fish (*Xiphias*) and its allies (Fig. 6) are perhaps the most rapid swimmers. A number of cases are on record in which they have struck ships, and Professor Owen, who was once called upon to testify in court as to the power of the Sword-fish, stated that it "strikes with the accumulated force of fifteen double-headed hammers; its velocity is equal to that of a swivel-shot, and is as dangerous in its effects as an artillery projectile." If the ship struck be a wooden one it is not uncommon for the sword to be driven in with such force that it cannot be withdrawn, and the fish frees itself by breaking it off short! How great must be the speed of these fishes to produce such results!

Practically all fishes adopt a horizontal position when swimming, but one or two species depart from this normal attitude. The vertical position of the Sea Horse (*Hippocampus*) has been already mentioned. The little Shrimp-fishes or Needle-fishes (*Centriscidae*) are curious creatures, with the long compressed body encased in a thin bony cuirass with a knife-like lower edge. One species found in the Indian Ocean lives in small shoals of about half a dozen individuals, and normally swims about in a vertical position with the long tube-like snout pointing upwards (Fig. 12). On occasions, however, it has been observed to move in the normal horizontal attitude, and even vertically, but *upside down*! A Cat-fish from the Nile and other African rivers (*Synodontis batensoda*) has adopted the remarkable habit of floating or swimming leisurely at the surface of the water *with the belly upwards*, an attitude taken up by no other fish unless it be sick or dead. This habit must have been well known to the ancient Egyptians, as it is frequently depicted in their sculptures and wall paintings in this anomalous position.

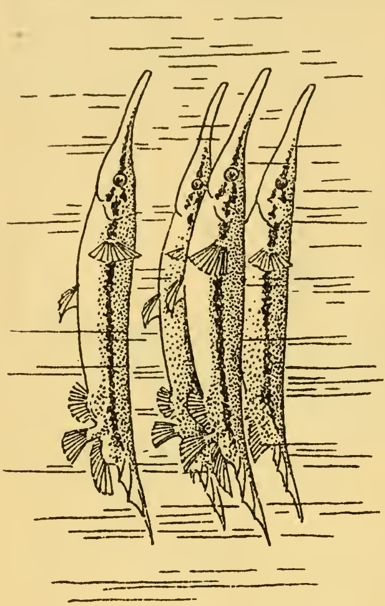


Fig. 12.—A FISH WHICH SWIMS UPRIGHT.

A small shoal of Shrimp-fishes (*Aeoliscus strigatus*), × ½. (After Willey.)

Among the methods of locomotion other than swimming, leaping and burrowing may be considered briefly here, as they result from body rather than fin-movements. A fish may leap out of the water for one of several reasons: to escape from an enemy, to clear a weir or other obstacle, or from pure *joie de vivre*. The strength and agility displayed by the Salmon (*Salmo*) (Fig. 13c) in leaping falls in its journey to the spawning ground is well known, and it has been observed to make repeated efforts to clear an obstacle which was too high for it, and to fall back at last through sheer exhaustion. It is this habit which has given the Salmon its name, the Latin *Salmo* being from the same root as *salire*, to leap. The Tarpon (*Megalops*), a favourite with

American sea-anglers, is another fish famed for its leaping powers, and its indulgence in this habit makes it necessary to employ some skill and perseverance in its capture (Fig. 13B). As Dr. Gill remarks: "Its frequent leaps into the air . . . seem to be mostly in sportive manifestation of its intense vitality, and not for food or entirely from fear." Opinions differ as to the height to which these fishes are able to jump, but it is generally agreed that seven or eight feet probably represents the Tarpon's

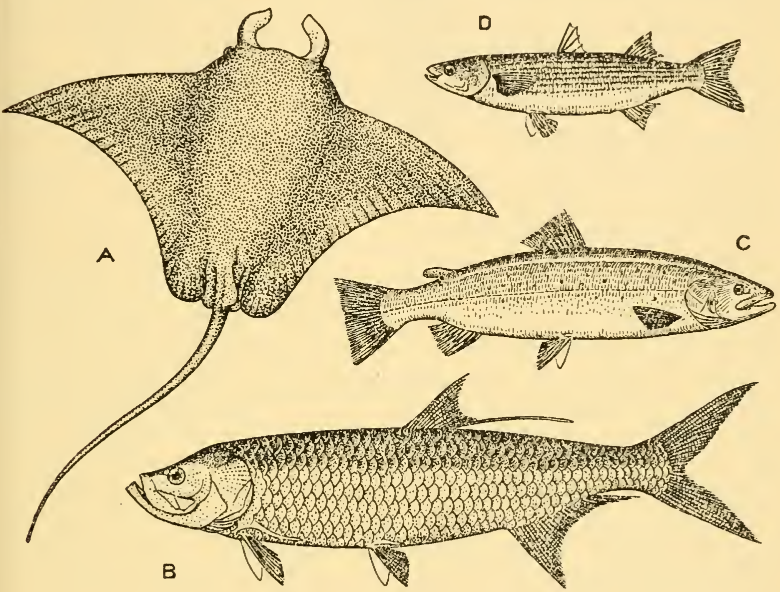


Fig. 13.—FISHES THAT LEAP.

A. Devil-fish (*Manta birostris*), $\times$ about $\frac{1}{50}$; B. Tarpon (*Megalops atlanticus*), $\times$ about $\frac{1}{20}$; C. Salmon (*Salmo salar*), $\times \frac{1}{12}$; D. Grey Mullet (*Mugil sp.*) $\times \frac{1}{10}$.

limit, while the Salmon is only able to better this by one or two feet. How are the jumps accomplished? Generally by the fish swimming rapidly upwards *through* the surface of the water into the air, giving a sharp flick with its tail as it leaves the liquid medium. All the active propulsion is provided by the muscular actions of the body while in the water, but the passing into the relatively less dense air accelerates the speed considerably and makes powerful leaps possible with a fairly slight muscular effort. Both Tarpon and Salmon hold the body in a curve while out of the water, and naturally fall to the concave side. Others, like the Grey Mullet (*Mugil*), keep the body rigidly in a straight line, so that the course in the air is determined solely by such external factors as the velocity of the wind, the angle of its direction to the fish, and so on.

The giant Devil-fish (*Manta*), figuring in so many romances of tropical seas, is another fish which can leave the water on occasion and, by means of an awkward, wheeling, edgewise leap, sail through the air to a height of more than five feet from the surface of the water. A full-grown specimen is somewhere in the neighbourhood of twenty feet long, and weighs more than 1000 lb., so that its sudden jump from the sea is an awe-inspiring sight. The noise made by its body as it returns to the water resembles the discharge of a cannon, being audible at a distance of several miles. The strength of this fish is prodigious, and when harpooned it will drag a boat through the water at great speed, so that it is sometimes necessary to cut the line at once to avoid disaster.

The habit of burrowing is generally associated with the eel-like type of body, but some of the Wrasses (*Labridae*) and the little Mud Minnow (*Umbra*) of North America and Central Europe are adepts at this art. The latter is said to be perfectly at home in the mud, and one author claims that it can "pass through soft mud with as much ease as other fishes do through clear waters." The same writer states that "if suddenly disturbed, they generally dart off by swimming only, and bury themselves *tail foremost* in the mud." The method by means of which burrowing is effected is quite simple, the fish merely employing active swimming movements with the snout pointed into the sand or mud. This is continued until a sufficient portion of the body is covered to enable its surface to obtain an effective grip, when progress is more rapid. Bottom-living forms like the Rays and Flat-fishes, instead of actually burrowing in the sea floor, wriggle their flattened bodies and throw sand over the upper surface until they are completely covered.

CHAPTER III

RESPIRATION

How fishes breathe. Structure of gills in Selachians, in Marsipobranchs, in Bony Fishes. Lophobranchs. Process of respiration in a typical fish, in Lampreys and Hag-fishes, in Rays, in Trunk-fishes. Does a fish drink? Gill-rakers and their uses. Rate of breathing. Fish that can live out of water. Accessory organs of respiration: breathing through the skin, intestinal respiration, labyrinthic organs, air-breathing sacs. Air-bladder and its functions. Origin and evolution of air-bladder.

PARADOXICAL as it may appear, a constant supply of fresh air is as important to a fish as to ourselves, the air being required for its contained oxygen. Respiration may be defined as a physiological process resulting in the aeration of the blood, a process consisting of taking in oxygen and giving off impurities in the form of a gas known as carbon dioxide. This exchange of gases is essentially the same in a fish as in any higher vertebrate, the difference in the respiratory process being in the manner in which the life-giving substance is obtained. Whereas the land animals extract the oxygen from the atmospheric air by means of lungs, fishes make use of the oxygen contained in the air dissolved in the water by the use of special organs known as gills. The supreme importance of this air to the life of a fish may be demonstrated by placing it in a vessel containing water from which all air has been driven out by intense heating, when it will be speedily suffocated. Similarly, if a bowl of Gold-fish be covered over so that it is impossible for any air to reach the water, the fish will succumb as soon as they have used up the supply of oxygen contained therein. The exact amount of oxygen consumed by a fish in a given time varies greatly in different species, and is also dependent on such factors as the amount of muscular activity displayed, with its consequent greater or lesser consumption of energy. On the whole, it seems to be comparatively small, and Dr. Günther has estimated that a man uses up 50,000 times more oxygen than a Tench (*Tinca*), a fish averaging about fifteen inches in length.

A careful study of the nature and origin of gills and lungs leaves no doubt that gill-breathing represents the more primitive method of respiration, and must have gradually given place to lung-breathing as the ancestors of modern terrestrial vertebrates left the water for the dry land. All the higher vertebrates, whether amphibians, reptiles, birds or mammals, provide us with indubitable proof of their fish ancestry by the possession of gill-like structures of one kind or another at some stage of their lives. In a human embryo, say of about three weeks, the sides of the throat are provided with four pairs of clefts, which not only correspond in position to the gill-slits of a fish, but their supporting skeleton and associated blood-vessels provide further resemblances. This fish-like apparatus is, of course, never used for breathing, and as development proceeds it becomes modified out of all recognition.

A proper understanding of the functions of the gills is impossible without some idea of their anatomy, and at the risk of introducing what may appear to be needless technicalities, it will be necessary to give a brief account of the salient features of their structure. The principles of respiration are essentially the same in all fishes, but a marked difference in the type of gills is found in the three main classes, and it will be convenient to describe first of all the conditions found in the Selachians, and then to compare them with those existing in the Cyclostomes and Bony Fishes. All breathing organs, no matter what their form, are closely associated with the upper part of the food channel or alimentary canal (*cf.* p. 168). Such a connection between the nutritive and respiratory apparatus is highly characteristic of backboned animals, and persists even in man himself, but in fishes the two remain more or less intimately connected throughout life, whereas in the higher animals the association is generally a temporary embryonic phase.

In a typical shark the side walls of the pharynx, that is to say, of that portion of the alimentary canal at the back of the mouth immediately in front of the commencement of the narrow gullet, are perforated by a series of narrow openings (Fig. 15A, *ph.*). Each of these pharyngeal openings leads into a kind of flattened pouch, which in turn communicates with the exterior by a comparatively narrow slit, the external gill-cleft, lying on the side of the head between the eye and the pectoral fin (Fig. 14A, *g.c.l.*). As a rule these clefts are not very long, but in the huge Basking Shark (*Cetorhinus*) they extend from the upper to the lower surfaces of the body. They are normally five in number (excluding a small circular opening known as the spiracle, which may lie in front of the first gill-cleft), but in the Frilled Shark (*Chlamydoselachus*) (Fig. 32C), the Comb-toothed or Cow Sharks (*Hexanchidae*), and one of the Saw Sharks (*Pliotrema*), there may be as many as six or seven. In the Frilled Shark each of the partitions between the successive

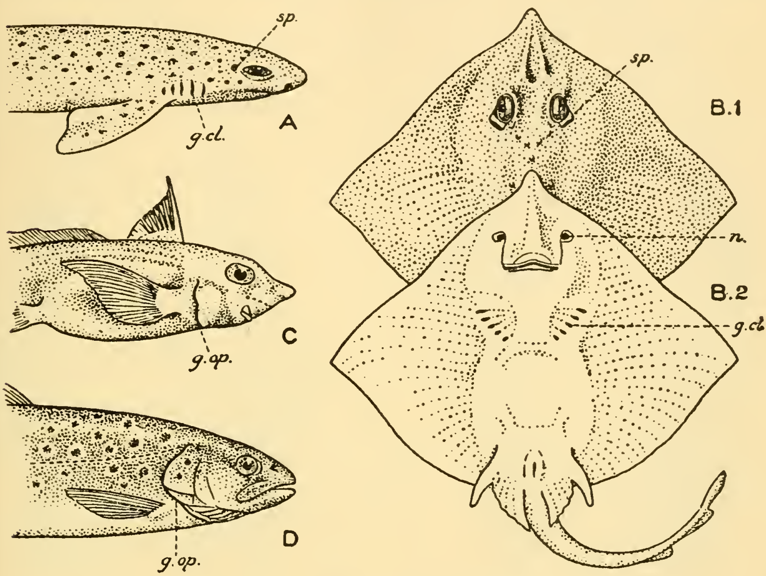


Fig. 14.—EXTERNAL GILL-OPENINGS.

A. Spotted Dog-fish (*Scyliorhinus sp.*), $\times \frac{1}{4}$; B.1, B.2. Thornback Ray (*Raia clavata*), $\times \frac{1}{6}$; C. Rabbit-fish (*Chimaera monstrosa*), $\times \frac{1}{5}$; D. Trout (*Salmo trutta*), $\times \frac{1}{4}$.
g.c., external gill-clefts of Selachians; *g.o.*, external gill-opening of Chimaeras and Bony Fishes; *n.*, nostril; *sp.*, spiracle.

clefts is produced backwards as a curious fold of skin covering the cleft immediately behind (Fig. 32C).

The partitions, or interbranchial septa, between the separate gill-pouches are fairly thick, and are reinforced by sheets of tough fibre-like substance. Further support is provided by a series of bars of cartilage known as the gill-arches, which lie at the inner edges of the septa and between the pharyngeal openings (Fig. 15A, *g.a.*). Each arch has the form of a half-hoop, and is broken up into several segments movably connected with one another, the lowest of which is nearly always joined by a coupling piece with its fellow of the opposite side (*cf.* Fig. 46A). In this way, the inside of the pharynx is supported by a series of encircling jointed girders, the outer convex faces of which are fringed by a number of slender rods of cartilage, which project outwards into the septa and help to strengthen them. All the parts of the gill-arches are provided

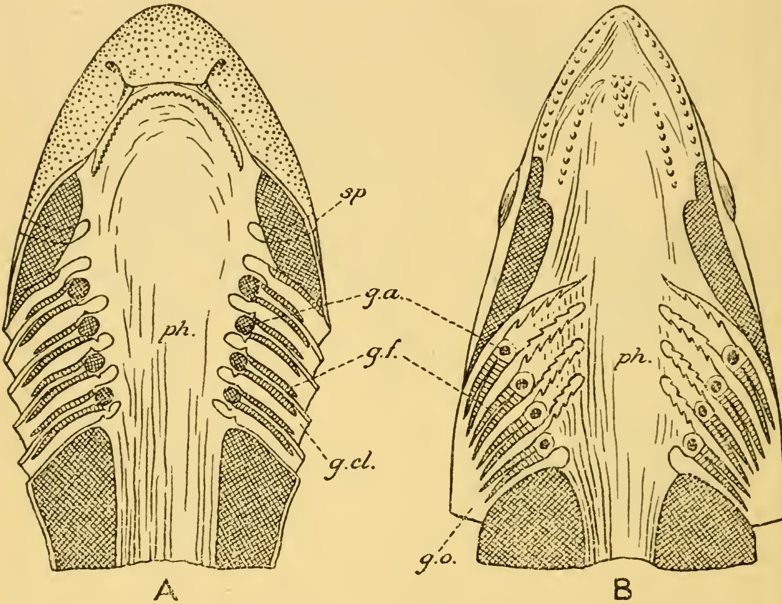


Fig. 15.—GILLS OF SHARK AND BONY FISH COMPARED.

A. Dissection of head of Spotted Dog-fish (*Scyliorhinus sp.*) seen from below, $\times \frac{1}{2}$; B. The same of Salmon (*Salmo salar*), $\times \frac{1}{2}$.
g.a., gill-arch; *g.c.*, external gill-cleft; *g.f.* gill-filaments; *g.o.*, external gill-opening; *ph.*, pharyngeal opening; *sp.*, spiracle.

with their special muscles, which by their appropriate expansion or contraction bring the hoops closer together or move them wider apart, and thus diminish or enlarge the size of the intervening openings.

The opposing walls of each gill-pouch bear a number of closely pleated folds of skin, the branchial lamellae or gill-filaments (*g.f.*), whose free edges project into the cavity of the pouch. These are richly supplied with fine blood-vessels, and present the appearance of a series of thin red straps or plates, a feature from which the earlier name of Elasmobranchs (strap gills) given to the class of Selachians was derived. Reference to the accompanying diagram will show how the gills are arranged in a typical Selachian (Fig. 15A), and it will be observed that the anterior wall of the first pouch has its row of filaments, but the posterior wall of the last pouch is not provided with these structures.

Mention may be made here of the organ known as the spiracle, which is, in reality, nothing more than the vestige of a gill-cleft, and, indeed, in the early embryonic stages of a Shark this differs little from the clefts that lie behind it, although it subsequently degenerates. Even in the adult, however, the spiracle frequently retains a number of branchial lamellae, and probably aids in aerating the blood going to the eye and brain. It varies greatly in size in the different families, being small or absent in some of the larger Sharks, and comparatively large in the Torpedoes, Rays, and Sting Rays, where it has acquired a special function to be described later on (Figs. 14A, B; 15A, *sp.*).

The class of Marsipobranchs (Lampreys and Hag-fishes), a name meaning "purse gills," exhibits a type of respiratory organ which, although in some respects more primitive than that of the Selachians, presents several special and peculiar features. The respiratory lamellae are lodged in a series of muscular pouches, well separated from each other, differing in number in the various species. In the Lamprey (*Petromyzon*) there are seven on either side, each of which opens directly to the exterior by a small rounded opening on the outside of the head, and communicates by a similar orifice internally, not directly with the pharynx as in the Selachians, but with a special canal; this ends blindly behind, but in front opens into the mouth. There are, thus, seven external openings and one internal opening. In the Hag-fish (*Myxine*) each pouch opens directly into the pharynx, but on the outside it is drawn out into a tubular canal running posteriorly; further back all the canals unite and open together by a single external aperture (Fig. 16). The gill-pouches are large in the Lamprey, and are supported by an elaborate cartilaginous structure, the branchial basket, which in the Hag-fish is greatly reduced. In many respects this basket presents a superficial resemblance to the gill-arches of the Selachians, but lies *outside* the gill-pouches instead of between them and the pharynx.

The general appearance of the gills in a typical Bony Fish such as the Salmon (*Salmo salar*) must be familiar to everybody, and may be readily seen by lifting up the bony plate lying on either side of the head behind the eye. How do these gills differ from those already described? In the first place, although

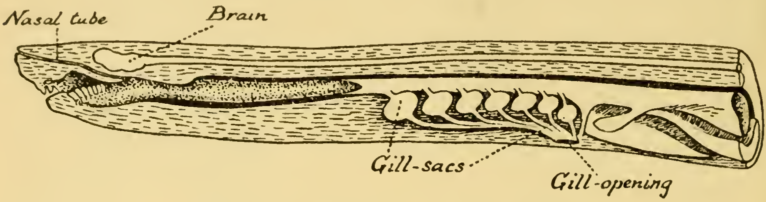


Fig. 16.—GILLS OF MARSIPOBRANCHS.

Dissection of anterior part of Hag-fish (*Myxine glutinosa*), × 1.

the same internal pharyngeal openings (*ph.*) are present, these do not open separately to the exterior, but into a common chamber, the branchial chamber, with a single external aperture behind (Fig. 15B). The outer wall of the chamber is provided by the movable flap already mentioned, which is

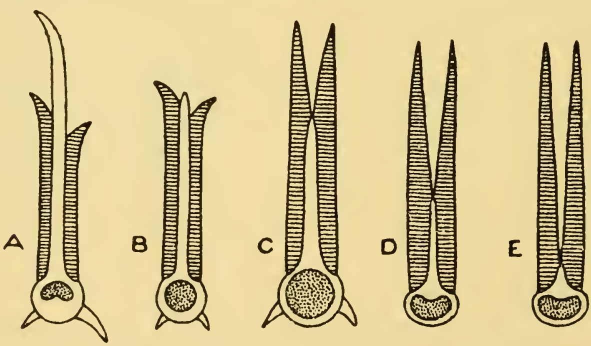


Fig. 17.—CROSS-SECTIONS OF GILL-ARCHES IN DIFFERENT FISHES.

A. Typical Selachian; B. Chimaera; C. Sturgeon (*Acipenser*); D, E. Bony Fishes. Gill-arch (dots); interbranchial septum (white); gill-filaments (cross lines). (After Boas.)

known technically as the operculum or gill-cover (Fig. 14D), and is supported by a series of broad, flat scale-like bones, with or without the addition of a number of slender bony rods below (Fig. 65). The hinder and lower edges of the operculum are nearly always free, so that the external opening is comparatively spacious, but sometimes these margins become more or less joined to the body of the fish and the outer opening is correspondingly reduced to a narrow slit or even to a minute upwardly directed pore. The same hoop-like gill-arches support the walls of the pharynx between the internal openings as in the Selachians, but are here composed of bone instead of cartilage. The more or less extensive interbranchial septa of the Shark have been reduced to minute proportions, and the delicate red filaments form a double row of processes attached by their bases to the convex outer edge of each gill-arch (Figs. 17, 18). The half gill formed by the filaments on the anterior wall of the first cleft in the Selachians has either disappeared

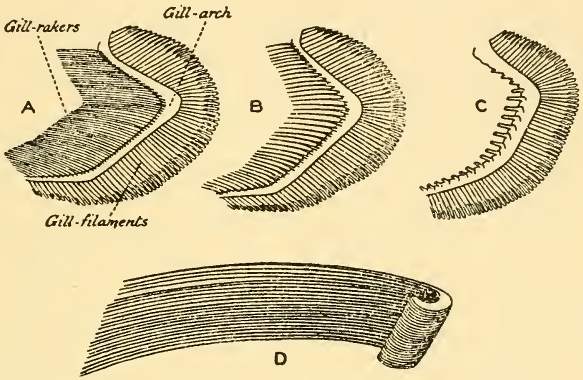


Fig. 18.—GILL-RAKERS.

A. Gill-arch of Allis Shad (*Alosa alosa*) ; B. The same of Twaite Shad (*Alosa finta*) ; C. The same of Perch (*Perca fluviatilis*) ; D. Isolated gill-rakers of Basking Shark (*Cetorhinus maximus*). All about $\frac{2}{3}$.

or is represented by a mere rudiment (pseudobranch), and the fifth (last) branchial arch is gill-less (Fig. 15B). The spiracle is almost invariably wanting, at least in the adult fish.

Certain of the Selachians, namely the Chimaeras and their allies (*Holocephali*), present a type of gill arrangement roughly midway between that of a Shark on the one hand and a Bony Fish on the other. The gills lie in a common branchial chamber, bordered on the outside by a skinny flap, foreshadowing the operculum of the Bony Fishes, and opening to the exterior by a single slit-like aperture (Fig. 14C). The interbranchial septa are somewhat shorter, so that the filaments project a little beyond their outer margins. Passing to some of the more primitive Bony Fishes (*e.g.* Sturgeons), the septa become progressively shorter, until the condition described in the Salmon is finally attained (Fig. 17).

The type of gill structure described here is that found in almost all Bony Fishes, but in the Sea Horses and Pipe-fishes (*Syngnathidae*), sometimes spoken of as Lophobranchs (tuft gills), the filaments are reduced to small rosette-like tufts attached to quite rudimentary arches.

When a fish breathes, the initial movement consists of an expansion of the hoop-like gill-arches, with a consequent enlargement of the cavity of the pharynx; at the same time the mouth is opened a little, and a stream of water is drawn into the pharynx, the external gill-opening or openings being kept tightly closed. This is known as the inspiratory phase. It will be noticed that as a general rule the fish does not use the nostrils for breathing purposes, and, although water is inhaled through these apertures in a few forms like the Chimaeras and Lung-fishes, they usually serve only as organs of smell (*cf.* p. 182). The expiratory phase, which follows immediately, consists in closing the mouth tight, and at the same time contracting the pharynx, thus driving the water outwards over the gills and through the external openings. The actual exchange of gases takes place as the water passes over the gills. The walls of the fine blood-vessels with which the delicate filaments are supplied are exceedingly thin, so that the blood circulating through them is separated from the water by nothing but an infinitesimally fragile and permeable membrane. Fish blood, just like our own, consists of a fluid substance, the plasma, in which float multitudes of red and white corpuscles. The red corpuscles, forming flat, circular discs, contain that remarkable substance known as hæmoglobin, which has the power of taking up oxygen under certain conditions and, later, of giving up this oxygen to the body cells, receiving in exchange their waste products in the form of carbon dioxide.

Most fishes breathe in the manner described, but there are some which, owing to their peculiar mode of life, have been obliged to modify this process in accordance with their change in habits. The Lamprey (*Petromyzon*), for example, has adopted a parasitic habit, and spends a good deal of its time attached to other fishes by means of its sucker-like mouth. It is quite obvious that while in this position it would be impossible to inhale water through the mouth without losing its hold, and, instead, water is often taken into and expelled from the branchial sacs by their external openings, through the alternate expansion and contraction of their muscular walls. The related Hag-fish (*Myxine*) possesses still more singular habits, and bores right into the fishes it attacks. Under these conditions the current of water is inhaled through the single nostril situated on top of the head, and after entering the pharynx passes out through the gill-sacs.

It has already been pointed out that a Skate (*Raia*) is essentially adapted for a life on the sea floor, and it is of interest to note that the method of breathing has also been modified for this end. While swimming or crawling about it is able to breathe in the normal manner, but when resting on the bottom there is a grave danger of taking in sand with the stream of water and thus clogging up the delicate gill-filaments. In all the members of this group of Selachians the mouth and external gill-openings are on the under side of the head, but the spiracle remains on the upper surface, and is represented by a comparatively large opening situated immediately behind the eye and provided with a movable valve (Fig. 14, B.I). To avoid the danger of introducing foreign particles into the gills, the Skate inhales water by way of the spiracles, expelling it through the gill-openings in the usual manner.

The respiratory modifications found in fishes normally inhabiting rapid streams or mountain torrents, where they are in the habit of fixing themselves to stones and other objects to avoid being swept away by the current of water, are dealt with in a subsequent chapter (*cf.* p. 239).

The Trunk-fishes (*Ostraciontidae*), in which the head and body form a firm bony box, are obliged to keep up the flow of water over the gills by a series of rapid panting movements, as many as 180 per minute having been counted in a resting fish. Here the pectoral fins are used to assist respiration, and by their constant motion fan a current of water through the gill-openings. Professor Goode writes: "when taken from the water one of these fishes will live for two or three hours, all the time solemnly fanning its gills, and when restored to its native element seems none the worse for its experience, except that, on account of the air absorbed, it cannot at once sink to the bottom."

The familiar phrase "to drink like a fish" is based on a complete misconception; it is assumed that the constant and regular opening and shutting of the mouth is a proof that the fish is drinking, whereas, as has been explained, this is really nothing more than an outward sign of the act of breathing. It is very doubtful whether the fish drinks at all, and, in any case, during respiration the gullet is so tightly constricted behind the last pair of pharyngeal clefts that little if any water is able to find its way into the stomach. This closing of the gullet is brought about by the action of special muscles encircling the throat, which function in exactly the same way as does a double string running round the neck of a bag. The pressure of any food against the closed gullet, however, causes these muscles to relax somewhat, and the solid nourishment is pressed down into the stomach without the entrance of any water.

In those fishes whose normal food consists of more or less minute creatures swimming about in the water there is obviously a danger of some of these escaping by way of the pharyngeal openings and perhaps clogging or injuring in some way the delicate filaments. To lessen this danger special structures known as gill-rakers have been evolved, taking the form of a double row of stiff appendages on the inner margin of each hoop-like gill-arch (Fig. 18). These, by projecting across the pharyngeal openings, serve to strain the water which is to bathe the gills, and to prevent any solid particles from passing over with it. Generally the front row of rakers on each arch interlocks with the hinder row on the adjoining arch, and the two together form an effective sieve. In the Pike (*Esox*), feeding almost entirely on other fishes, the gill-rakers are represented merely by bony knobs, which may serve to block the passage of larger food particles. In the fishes of the Herring kind (*Clupeidae*), on the other hand, whose food consists of minute shrimp-like creatures, the rakers are very numerous and take the form of long, slender, and close-set bristles. In some of the members of this tribe the filtering mechanism is even more perfect, each primary gill-raker giving off secondary and tertiary branches, the whole apparatus having the appearance of the finest gauze. The form and number of the gill-rakers may differ considerably even in two closely related species, but this difference may generally be correlated with a difference in the normal diet. The two species of Shad (*Alosa*) found in our own seas and rivers provide an excellent example of this, the Allis Shad (*A. alosa*), having about eighty rakers on the lower limb of each arch in the adult fish, whereas the Twaite Shad (*A. finta*) has only thirty (Figs. 18A, B). The Allis Shad feeds largely on small crustaceans, although it takes a certain number of larval fishes. The Twaite Shad does not eat the crustaceans to nearly the same extent, but is much more destructive to the young fry of other fishes.

As a general rule, gill-rakers are wanting in the Sharks, most of which feed on other fishes, but the huge Basking Shark (*Cetorhinus*) and Whale Shark (*Rhineodon*) are both provided with many close-set, flattened and tapering gill-rakers, each perhaps four or five inches long (Fig. 18). In appearance they recall the baleen plates of the Whalebone Whales, which have exactly the same function, namely to act as a filter to strain off the most minute forms of animal life. When feeding, the Basking Shark merely opens its mouth and takes in a mass of water containing myriads of the minute crustaceans forming its usual food. The water rushes out over the gills, and the animals are left sticking to the inner walls of the throat and to the filtering mechanism, where they can be conveniently swallowed.

The rate of breathing seems to vary greatly in different fishes, ranging from about twelve to fifteen respirations per minute in the Wrasse (*Labrus*) and the Rockling (*Motella*) to as many as 150 in the Minnow (*Phoxinus*) and Stickleback (*Gasterosteus*). Professor Bashford Dean noticed that in the Australian Lung-fish (*Epiceratodus*) the normal rate was about twelve per minute on a cool day, but rose to as many as thirty-one as the water warmed up. If the water is at all deficient in oxygen the rate of breathing is naturally accelerated and the fish appears to "pant" or respire hurriedly, while other factors which lead to an increased rate are excessive activity or the stress of some emotion such as greed or fear.

All the breathing organs so far described have been what are known as internal gills, but in certain fishes external organs are developed similar to those found in larval newts and frogs. In the young Selachians they take the form of long, delicate filaments, protruding for some distance through the external gill-clefts. These seem to aid in some way the breathing of the embryo while enclosed in its egg-case, for they completely disappear when it is hatched (*cf.* p. 332). Similar structures are developed in the young of certain Bony Fishes, but are soon discarded in favour of the more adequately protected internal gills. In the young Bichir (*Polypterus*) there is a leaf-like external gill projecting backwards from each side of the head above the ordinary gill-opening. Here they are retained for a somewhat longer period, but gradually become reduced in size as growth proceeds (Fig. 19).

The vast majority of fishes are quite incapable of living for any length of time out of the water, and, as a general rule, those with wide external gill-openings expire more rapidly than those in which the apertures are reduced. This is due to the fact that as the filaments dry up they tend to stick together and are thus mechanically prevented from functioning. The importance of moisture in enabling a fish to cling to life is emphasised by the length of time some fishes will remain alive if packed in damp grass or other vegetation. The author has more than once received a parcel containing Roach or Bream

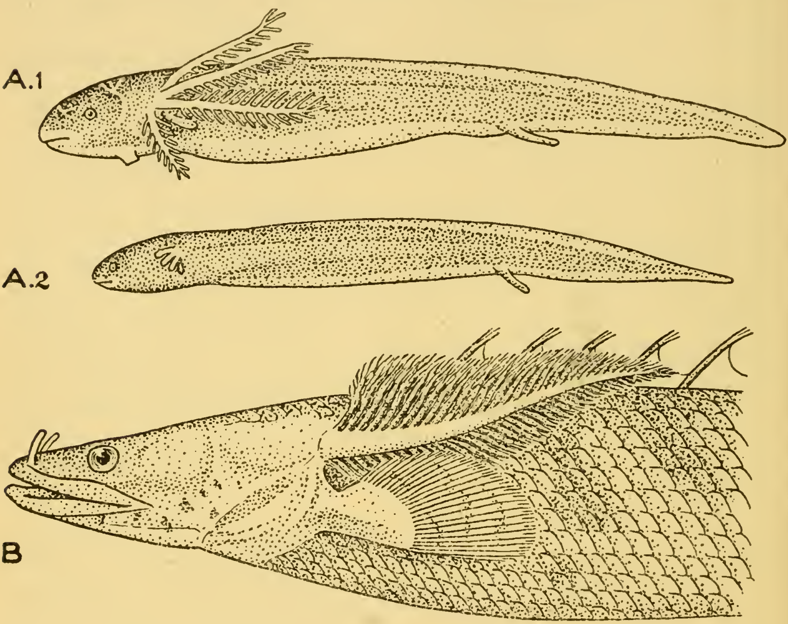


Fig. 19.—EXTERNAL GILLS.

A.1. Young South American Lung-fish (*Lepidosiren paradoxa*), 30 days after hatching, × 3 ; A.2. The same 40 days after hatching, × 2 ; B. Young Bichir (*Polypterus endlicheri*), × 1½.

thus packed, which have come to life successfully several hours after capture when tipped into a bowl of water. Fresh-water Eels (*Anguilla*) are able to survive for a considerable time away from their native element, and to wriggle across damp grassy meadows at night in order to get from one piece of water to another. It had always been supposed that these land excursions were made possible by the small size of the external gill-openings, but a French investigator has shown that Eels from which the gill-covers have been cut off were able to live out of water just as successfully as normal specimens. He suggested that breathing was carried on *through the skin*, a statement which is not nearly so improbable as it sounds. Since respiration is nothing more than an exchange of gases by the blood, there is no reason why these gases should not penetrate through thin membranes like the skin, and reach the blood contained in the fine vessels situated therein. The remarkable little Mud-skipper (*Periophthalmus*) of tropical countries spends a great part of its time walking or skipping about on the mud-flats of mangrove swamps at low tide in search of food, and is also fond of climbing on to the mangrove roots themselves or of basking in the sun perched on a stone in a pool (Fig. 34f). While out of the water the large gill-chambers are kept filled with air, and the tail is, more often than not, left hanging down in the water, serving as an additional organ of respiration. These little fishes have become so accustomed to a life out of the water that they are said to be unable to live in what should be their native element for any length of time.

Another remarkable method of breathing is adopted by some of the Loaches (*Cobitidae*) and the Mailed Cat-fishes (*Loricariidae*), which use the intestine for this purpose at times. The Giant Loach (*Cobitis*) of Europe, known in Germany as the "Wetter-fisch" (weather fish) on account of its susceptibility to atmospheric changes, has been specially studied, and the process of breathing found to take place in the following manner. The fish rises to the surface, and by thrusting its mouth above the water, swallows a certain amount of air, which is passed down into the intestine. There is a bulge in the intestine just behind the stomach which serves as a reservoir; the fine blood-vessels lining the walls of this chamber extract the oxygen from the air, and the latter is finally voided by the vent.

It is well known that when the air dissolved in the water fails a fish is obliged to ascend to the surface to avoid suffocation. The habit of seeking oxygen by swallowing bubbles of air is found in many different kinds of Bony Fishes, but in certain forms living in shallow ponds and streams which dry up periodically, or in pools rendered foul by decaying vegetation, this gulping of air becomes a necessity if the fishes are to survive at all. As a result, it is found that the intensification of the air-breathing habit over a very long period of time has led to the development of special accessory breathing organs in addition to the gills, thus enabling the fishes to survive for a comparatively long time out of water. These organs take the form of reservoirs for the storage of air, which are outgrowths either from the pharynx itself or from the branchial chamber, and contain certain special structures richly supplied with blood-vessels for the aeration of the blood.

The so-called Labyrinthic Fishes (*Anabantoidea*) of the fresh waters of tropical Asia and Africa derive their name from the possession of a labyrinth-like accessory breathing organ on either side of the head. This group of fishes includes a number of species familiar in aquaria, such as the Climbing Perch (*Anabas*), Gourami (*Osphronemus*), Paradise-fish (*Macropodus*), Fighting-fish (*Betta*), and so on, but it will only be necessary to mention the accessory breathing organs of the first of these.

The Climbing Perch (*Anabas*) was first made known in a memoir printed in 1797 by one Daldorf, a lieutenant in the service of the Danish East India Company at Tranquebar. The fish derives its name from a legend current in the East that it climbs palm trees and sucks their juice, and Daldorf stated that he had taken one in a slit in the bark of a palm which grew near a pond. The recent researches of an Indian naturalist, Dr. Das, have shown that, although the stories of the Climbing Perch being found in trees are quite well founded, the explanation of the facts is an erroneous one. The fish is in the habit of migrating from pond to pond at night, and after a shower of rain it comes out of the water and invades gardens in search of earthworms. During its overland travels it is not infrequently seized by crows or kites, and deposited high up in the forks of branches of the trees to be devoured at leisure. Hence the origin of the story of its tree-climbing activities! The method of progression adopted on land is of interest, the gill-covers as well as the fins assisting in locomotion. The gill-covers are alternately spread out and fixed firmly to the ground by the sharp spines with which they are armed, while a vigorous push is given by the pectoral fins and the tail. When in the water, the Climbing Perch frequently comes to the surface to breathe air, and so vital has this method of respiration become to the fish that it will suffocate even in water saturated with oxygen if deprived of access to atmospheric air. The ease with which these fishes are able to survive out of water is taken advantage of by the natives of India and the Malay Peninsula, who carry them about alive for days on end in moistened clay pots, thus ensuring a regular supply of fresh fish. The jars must, of course, be kept tightly covered, or the intended meal will climb out and walk away!

The air inhaled is taken into two chambers situated one on each side above the gills, forming outgrowths from the ordinary branchial chambers. Each contains a more or less rosette-like structure, made up of a number of concentrically arranged, shell-like plates with wavy edges, all richly supplied with fine blood-vessels. Each air reservoir is in communication, not only with the branchial chamber, but also with the pharynx, the entrance from the throat being controlled by a special valve.

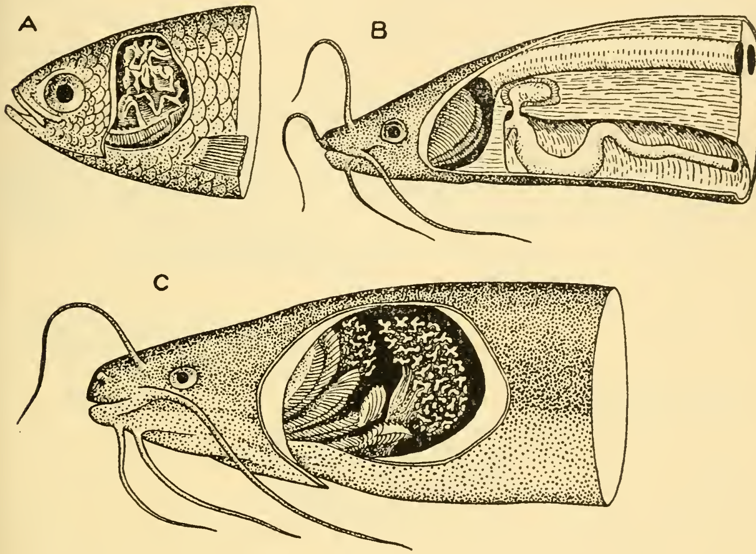


Fig. 20.—ACCESSORY BREATHING ORGANS.

A. Dissection of head of Climbing Perch (*Anabas scandens*); B. The same of an Indian Cat-fish (*Saccobranchus fossilis*); C. The same of an African Cat-fish (*Clarias lazera*). All about natural size.

Air enters by this aperture and passes out through the external gill-opening (Fig. 20A).

The related Snake-heads (*Ophiocephalus*), long, cylindrical fishes with slightly flattened and somewhat serpent-like heads (Fig. 21A), inhabit rivers and ponds as well as stagnant pools in the marshes. The larger species grow to a length of three or four feet. Their habit of "walking" over land by the aid of rowing movements of the pectoral fins is well known, and Snake-heads are frequently exhibited as curiosities by Indian jugglers. They are extremely tenacious of life, and are carried alive by the Chinese to San Francisco and to Hawaii, where they are now naturalised and known as "China-fishes." They are able to survive prolonged drought, burying themselves in the mud and remaining in a torpid state during hot, dry weather. The various species differ in the extent to which they have developed the air-breathing habit, as well as in their power of living out of water. The accessory respiratory organs are of a much simpler character than those of the Climbing Perch, consisting of a pair of simple cavities lined with a thickened and puckered membrane supplied with blood-vessels, and do not contain any special structures. These lung-like reservoirs

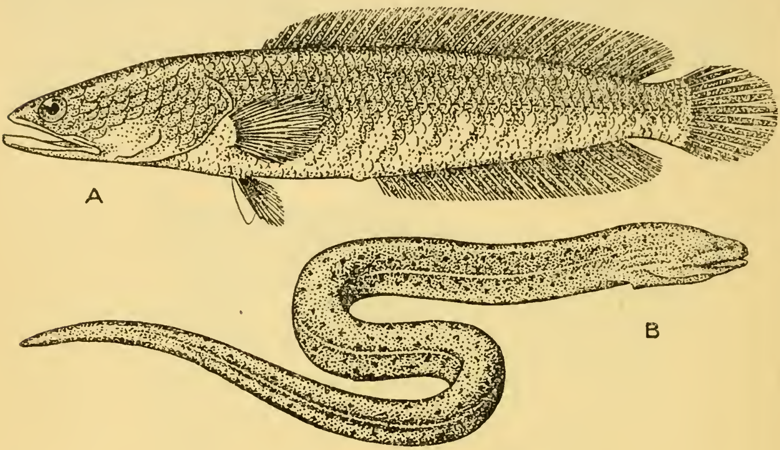


Fig. 21.—FISHES THAT CAN LIVE OUT OF WATER.

A. Snake-head (*Ophiocephalus striatus*), × 1/3 ; B. Cuchia (*Amphipnous cuchia*), × 1/6.

are not developments of the branchial chamber, but are *pouches of the pharynx.*

Other fishes provided with accessory breathing organs are certain Cat-fishes of the rivers and swamps of Africa and Asia, and the famous Cuchia (*Amphipnous*) of India and Burma, a member of the group of Symbranchoids (Fig. 21B). In one of these Cat-fishes (*Clarias*) the organs take the form of elaborate tree-like structures, growing from the upper ends of the gill-arches and contained in a pair of air-chambers situated above the gills (Fig. 20C). Another form (*Saccobranchus*) has the organs of a simpler nature, but the air-chambers bear a marked resemblance to lungs, extending backwards as far as the tail as long tubular sacs growing out from the branchial cavity, and situated close to the backbone (Fig. 20B). The Cuchia, which grows to a length of about two feet, bears a superficial resemblance to some of the Eels, to which, however, it is not at all related. Like the other fishes just mentioned, it is an inhabitant of the fresh and brackish waters of India and Burma, and spends much of its time in the grass on the banks of ponds like a snake. The air-breathing organs consist of a pair of sacs growing out from the pharynx above the gills. This curious fish seems to have lost practically all its power of aquatic respiration, for when in the water it is forced to come to the surface at frequent intervals to gulp air, and the true gills are very much reduced, being represented by a few rudimentary filaments attached to the second of the three remaining gill-arches.

The accessory respiratory organs just described are not the only structures used for air-breathing among fishes, and before concluding this chapter some more lung-like organs must be considered. The air-bladder, or, as it is sometimes called, the swim-bladder, must be a familiar object to those who have had occasion to examine the inside of a fish. Situated within the body cavity, and immediately below the backbone, it generally has the appearance of a long, cylindrical bag with glistening silvery walls. It is very variable both in size and form in different fishes, and may be present in one species and entirely absent in a closely related form. That it normally contains air or gas of some kind may be readily demonstrated by puncturing it with a needle, when the walls promptly collapse. There is no other single organ in any group of vertebrates which performs such a variety of functions as does the air-bladder of Bony Fishes. In the majority it serves as a hydrostatic organ or float, enabling its possessor to accommodate itself to the varying pressure encountered at different depths (*cf.* p. 174), in others it is an organ for the production of sound (*cf.* p. 156), and in others, again, it is more or less connected with the sense of hearing (*cf.* p. 193). For the present it must suffice to consider its relation to air-breathing and its connection with the lungs of higher vertebrates.

Like the lungs of a man, the air-bladder is intimately associated with the alimentary canal, and a study of the development of this organ shows that it begins as a minute pouch budded off from the gullet. This gets larger and larger, until it is finally separated off from the gullet, remaining connected only by a narrow tube known as the pneumatic duct. In some fishes this duct remains open throughout life, but in others it closes up or disappears altogether. It nearly always opens into the pharynx by a small aperture in the roof, but in the Lung-fishes (*Dipneusti*) and Bichirs (*Polypterus*), in which the air-bladder is a true breathing organ, the opening takes the form of a small slit, the glottis, with well-defined lips, situated in the

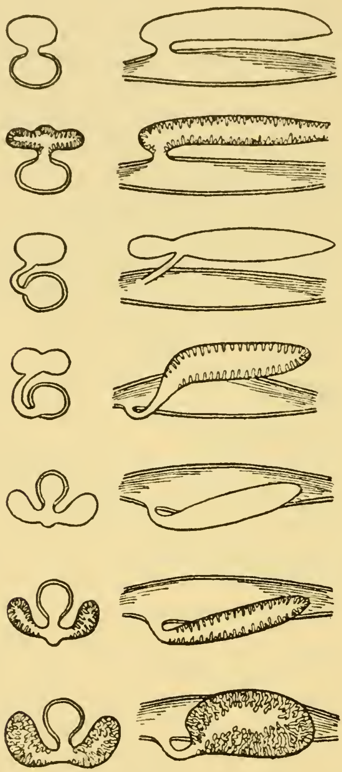


Fig. 22.—AIR-BLADDER AND LUNG.

A series of diagrams showing the relation of the air-bladder or lung to the gullet in different fishes, as seen in cross-section (left-hand column) and from the side. (After Dean.)

floor of the gullet (Fig. 22). The lungs of higher vertebrates arise in exactly the same way, as an outgrowth from the gullet, and the glottis occupies the same position as in the Lung-fishes. Furthermore, whereas in the generality of fishes the air-bladder is a simple sac filled with a mixture of gases, in the Bow-fin (*Amia*) and Gar Pike (*Lepidosteus*), two other air-breathing forms, and to a more marked extent in the Lung-fishes, the inner walls are richly supplied with blood-vessels, and the area of their surface is greatly increased by being produced into recesses or alveoli, each of which is further subdivided much in the same way as in a true lung (Fig. 22). Another important point is the fact that, whereas in nearly all fishes the bladder is a *single* structure, in the Bow-fin, Gar Pike, Bichir and Lung-fishes it tends to become divided, giving rise to a structure resembling the paired lungs of higher vertebrates. In the Bichirs, for example, it is divided into two unequal parts, a long right-hand portion and a much shorter left-hand one; the two unite in front and open by a single aperture in the floor of the gullet. The air-bladder of the African (*Protopterus*) and South American (*Lepidosiren*) Lung-fishes is divided into two except for a small portion in front, and thus has the form of a pair of lungs. Finally, it may be noticed that the arrangement of the vessels taking the blood to and from the bladder in the Bichirs and Lung-fishes is essentially similar to that of the vessels connected with the lungs in Amphibians and reptiles.

There is good reason for supposing that the air-bladder originally had a purely respiratory function, and that its use as a hydrostatic organ is secondary. The essential similarity of the mode of development of the air-bladder and the lungs is a striking argument in favour of this view; and further, the bladder is connected with the gullet by a pneumatic duct during the early embryonic or larval stages of most, if not all, Bony Fishes, and this connection is retained throughout life in nearly all the more primitive forms. The air-breathing fishes of to-day, such as the Lung-fishes, Bichirs, Bow-fins and Gar Pikes, are without exception survivors of very ancient groups which flourished at a very early stage of geological time, whereas, all those in which the air-bladder serves as a hydrostatic organ are of comparatively modern origin. We may note here that no trace of an air-bladder is found in any Selachian, nor is one developed in the Lampreys and their allies. The statement so often made that the lungs of higher animals have developed from the air-bladder of fishes is quite untrue, and this idea rests on a misconception similar to that which leads many people to speak of man having descended from monkeys. It would be more correct to speak of the air-bladder as a modified and degenerate lung, but actually both bladder and lung seem to have been derived from some sort of primitive respiratory sac, which itself originally arose as a pouch growing out from the gullet. What, then, were the causes that led to the origin of this air-breathing sac? To answer this question it is necessary to go back to the early Silurian and Devonian epochs when the evolution of this organ probably took place.

It may be assumed that the earliest fishes swarming in the sea close to the shore found a sufficiency of oxygen dissolved in the water to make air-breathing unnecessary, but in course of time stress of competition must have led many of them to ascend the rivers just as certain Sharks and Rays do to-day, and to become permanent inhabitants of fresh water. In the course of further penetration a number of species would find their way into the smaller streams, ponds, marshes, and so on. Here the water might be expected to be thick with sediment, or, owing to the heat or to the decay of vegetation, poorly aerated, thus making gill-breathing a matter of difficulty. These conditions would necessitate the fishes coming to the surface at intervals to gulp air, just as the Bichirs and Lung-fishes do to-day when the water in which they are living becomes foul. At first, the air-breathing would perhaps be performed by the walls of the gullet, but as the habit persisted the process would be improved by the development of a more or less definite pouch or reservoir. This would gradually assume the appearance of a lung, and eventually divide down the middle to form the double structure characteristic of the higher vertebrates. In the early fishes which took up their abode in the rivers and marshes the air-bladder probably served merely as an accessory respiratory organ, the bulk of the work of breathing falling on the gills. Conditions being favourable to their progress, these fishes must have multiplied rapidly. Later on, however, owing to a number of factors, among which the arrival of fish-eating reptiles may be mentioned, a large number of them appear to have been driven back to the sea, where, with an adequate supply of oxygen for gill-breathing, the air-bladder gradually lost its respiratory function to a greater or lesser extent, and either became modified for totally different ends or disappeared altogether.

That this invasion of fresh water by the early fishes was a very important step in the evolution of higher vertebrates there can be no doubt, for once the habit of breathing air had become established, the abundance of food and the complete absence of enemies would be an inducement for some species to venture further on to dry land. Here the fins would be gradually converted into limbs for terrestrial locomotion, and the first lung and gill-breathing amphibians would come into being, to be followed in their turn by the reptiles breathing by means of lungs alone.

CHAPTER IV

FINS

Different kinds of fins. Their origin and evolution. Structure of fins: dorsal and anal, pectorals and pelvics, caudal. Types of tail. Development of tail. Modifications of dorsal and anal in different fishes, of caudal, pectoral and pelvic fins.

THE nature and functions of the fins have been indicated in an earlier chapter (*cf.* p. 13). Briefly, they are of two kinds: (1) median or unpaired, sometimes described as vertical fins; and (2) paired fins. The median fins include a *dorsal* in the middle line of the back, an *anal* along the belly behind the vent, and a *caudal* at the hinder end of the fish. The paired fins are of two kinds only, *pectorals* and *pelvics*, corresponding respectively to the fore and hind limbs of land vertebrates (Fig. 7). The pectorals, sometimes referred to as the breast-fins, are always placed close behind the head, but the position of the pelvics varies in different groups of fishes.

Before considering the structure of the fins, it will be as well to discuss the manner in which they have arisen in course of evolution. It is generally agreed that the earliest fishes possessed no true fins, but swam entirely by undulations of the body, and the fins were probably first developed as stabilising keels to counteract the tendency of the body to roll over sideways when in motion. In this connection some ingenious experiments carried out by Professor Cunningham may be of interest. Having coated an ordinary penholder thinly and evenly with wax, he held this firmly at one end, and, keeping it in a horizontal position, moved it rapidly to and fro in a vessel containing warm water. He found that very soon a vertical ridge made its appearance above and below the pen in exactly the same position as that occupied by the dorsal and anal fins of a fish, and that this gradually increased in height until, after five minutes' movement, an upper and lower ridge about half an inch high had developed. Experiments made by a French investigator on plastic bodies (*cf.* p. 13) produced similar results.

During the embryonic or larval stages of almost any fish the development of the ordinary fins is preceded by a stage at which there is a continuous fold of skin extending along the back, round the tail, and forward along the belly as far as the vent. We have already seen that the development of a particular organ in the individual fish frequently repeats to a greater or lesser extent the evolutionary history of that organ, and the development of the fins provides yet another example of the light thrown on the past by the study of embryology. There can be little doubt that the median fins arose as such a continuous fold of skin, which in course of time became strengthened by the development of slender supporting rods or fin-rays. Still later, certain parts of this fold, not definitely required, tended to degenerate and finally to disappear altogether, leaving the separate dorsal, anal, and caudal fins. Since the median fins are the only ones present in the primitive Lampreys and their allies, and since they appear first in embryonic development, we may be justified in assuming that their evolution preceded that of the paired fins, an assumption which is largely confirmed by a study of fossil forms (Fig. 23).

The origin of the paired fins is not quite so clear, and the subject has been, and still is, a matter for some controversy. It must be understood, therefore, that the following explanation, while appearing to be that which best fits the facts provided by a study of anatomy, embryology, and palaeontology, does not meet with universal support.

It seems probable that at some stage after the median fin-fold had made its appearance a further advance was made by the continuation of this fold forward towards the head. Since the vent lay in its path, the original fold split into two portions, each of which ran forwards and somewhat upwards along the lower part of the side and ended just behind the gill-opening. This hypothetical condition is illustrated in the accompanying figure (Fig. 23A). No fossil fish has yet been discovered exhibiting such complete lateral folds, nor is such a stage found during the development of any living form. At the same time, two or three very primitive Sharks are known in which the condition of the fins may be described as providing an intermediate stage. In a form known as *Cladoselache*, for example, the paired fins are lappet-shaped, like the dorsal and anal, with broad bases, and their position strongly suggests that they have originated from once continuous lateral folds. In *Climatias*, another archaic species, both pectoral and pelvic fins are preceded by a strong spine, and there is also a row of similar spines along the sides of the body *between these fins*. As in the case of the median fins, the appearance of the continuous folds must have been followed by the development of a series of rods of cartilage designed to strengthen these structures. Shortly afterwards, the middle portions of these folds degenerated and disappeared, and the parts at either end became enlarged and

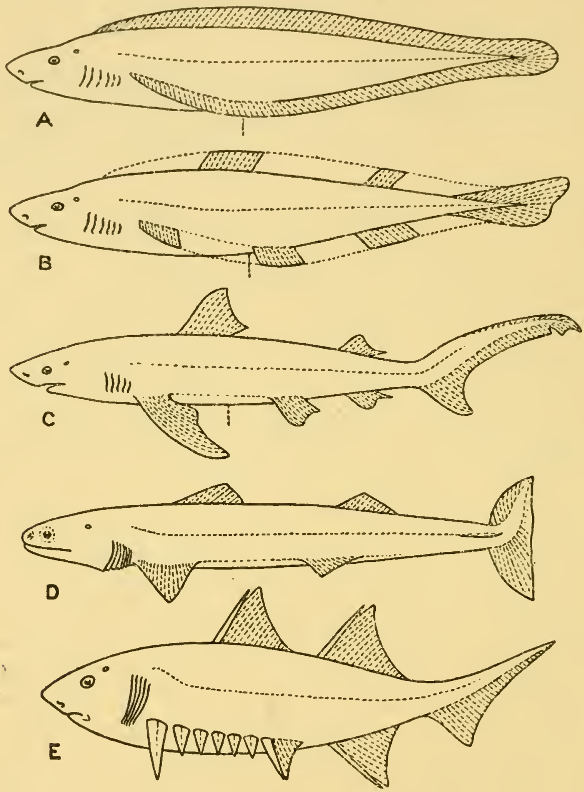


Fig. 23.—EVOLUTION OF FINS.

A, B. Hypothetical primitive Shark-like fishes; C. Blue Shark (*Carcharinus lamia*); D. *Cladoselache fyleri*; E. *Climatius macnicoli*.

gradually took on the definitive form of the pectoral and pelvic fins. The cause of these gaps is not known, but may have been in some way connected with the undulating movements of the fish.

As pointed out above, the primitive fin-folds very soon became strengthened by the appearance of a series of parallel rods of cartilage set at right angles to the body, and at the line where the folds joined the body each rod later split into two portions. The lower pieces, known as the *basals*, were situated within the body, and the upper pieces or *radials* were in the fins themselves. Something very like this primitive condition is found to-day in the Lampreys and their allies, where the median fins are supported solely by such a series of cartilaginous rods. In the Selachians the radials may be further subdivided into two or more portions, and form the main supports for the fins, sometimes extending almost to their margins (Fig. 24A). The fins, however, are considerably larger than those of the Lampreys, and further strengthening is provided by the presence of numerous

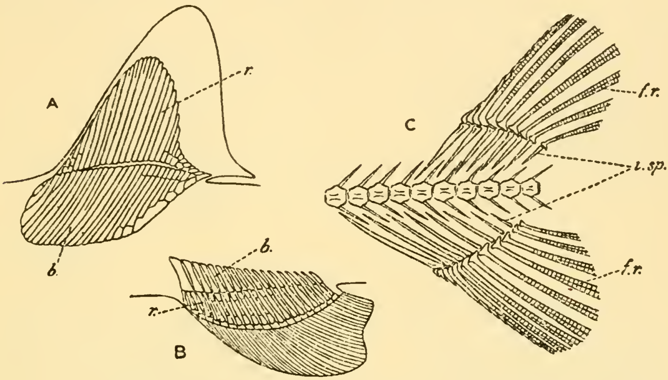


Fig. 24.—STRUCTURE OF DORSAL AND ANAL FINS.

A. First dorsal fin of Mackerel Shark (*Isurus punctatus*), dissected to show cartilaginous supports ; B. Anal fin of Chinese Sturgeon (*Psephurus gladius*), similarly dissected ; C. Skeleton of dorsal and anal fins, and portion of vertebral column of Gar Pike (*Lepidosteus platystomus*).
b., basal cartilages ; *f.r.*, fin-rays ; *i.sp.*, interspinous bones ; *r.*, radial cartilages.

hair-like, horny rays situated outside the radials, each ray tapering off to a fine point near the edge of the fin. In these fishes the horny fin-rays, as well as the cartilaginous radials, are completely enveloped by the skin and muscles associated with the fins, and are, therefore, quite invisible externally.

Among the Bony Fishes the Sturgeons (*Acipenseridae*), living representatives of a very archaic group of fishes, present fins of a distinctly primitive type. The dorsal and anal fins are each provided with a fleshy lobe at the base, composed of fin-muscles surrounding a series of rod-like structures — basals within the body and radials in the muscular lobe of the fin (Fig. 24B). The whole structure is not unlike that of the Selachians, but instead of horny fibres the outer part is supported by bony fin-rays. The conversion of the fibres into bony supports obviously lends additional strength to the fin, and in order to retain the necessary flexibility, these are segmented into a number of sections. In all the higher Bony Fishes the lobe at the base of the fin disappears, the radials are reduced to mere nodules of bone or cartilage sunk within the adjacent muscles of the body, and the sole support of the fin is provided by the bony fin-rays. The basals, which may be joined to the reduced radials, persist as a series of fine rod-like structures alternating with the spines of the backbone, and are, therefore, known as interspinous bones (Fig. 24C). The bony fin-rays being developed in the skin on either side of the fin are necessarily of a double character, and, as will be shown later on, are of two kinds, spines and soft-rays. It may be noted here that in the Lung-fishes (*Dipneusti*) and Sturgeons (*Acipenseridae*), just as in the Selachians, the fin-rays are much more numerous than the supporting radials; in all the higher Bony Fishes the former are reduced in number and equal to the radials.

The paired fins, owing to the need for free movement in various directions, have naturally been more modified than the median fins, and in living fishes little trace remains of the primitive parallel arrangement of the supporting radials and basals. It would be out of place to follow all the changes in detail in a work of this nature, and reference must be made to the zoological text-books for further information on this matter (*cf.* p. 435). It must suffice to point out that the basals and radials have been variously crowded together and fused, to provide not only a strong supporting axis for the remainder of the fin, but also fin-girdles designed to connect the fins with the body (Fig. 65). As might be expected from their more important position, evolution has proceeded considerably further in the pectoral fins than in the pelvics, and its course has been mainly in the direction of a progressive shortening of the base, in order to permit of free movement in different planes. In the Selachians this shortening has been effected by an outward rotation of the main basal supporting cartilage (Fig. 2B), and in the Bony Fishes by a simple crowding together and reduction of the supporting elements. Some of the more interesting types of pectoral fin structure are shown in the accompanying diagrams (Fig. 25). It will be observed that in the Australian Lung-fish (*Epiceratodus*) there is a definite central axis to the fin formed of basals, with a series of projecting radials on either side.

So far no mention has been made of the supporting skeleton of the caudal or tail-fin. This is of a somewhat different nature to that of the dorsal and anal, and involves a special modification of the hinder end of the vertebral column. The tails of adult fishes may assume one of three different forms, known respectively as "diphycercal," "heterocercal," and "homocercal," terms which may be freely translated as "twofold tail," "unequal tail," and "equal tail" respectively.

The diphycercal is undoubtedly the most primitive type, and here the hinder end of the vertebral column is quite straight

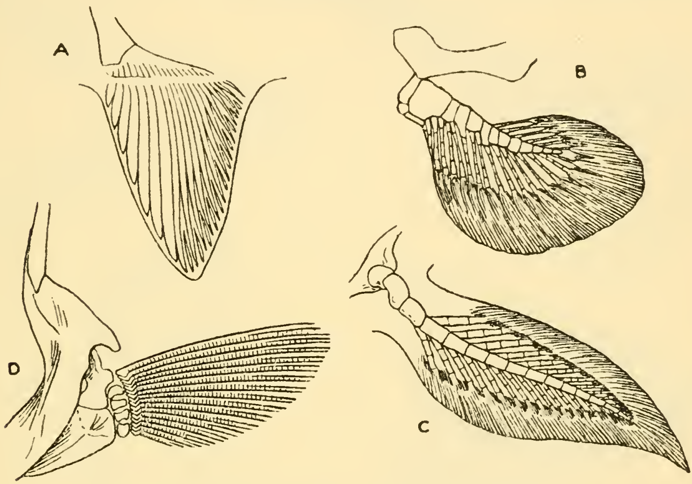


Fig. 25.—STRUCTURE OF PECTORAL FINS.

A. *Cladoselache fyleri.* (After Dean) ; B. *Pleuracanthus decheni.* (After Fritsch) ; C. Australian Lung-fish (*Epiceratodus forsteri*) ; D. Cod (*Gadus callarias*).

and divides the fin into two equal lobes. Around the central axis are arranged a series of rods which support the membrane of the fin. Although characteristic of many of the early fishes, it is doubtful whether any forms living to-day, however straight and symmetrical their tails may appear to be, have a truly primitive diphycercal tail. We find such a tail, however, in almost all larval or embryonic fishes at a stage just before or just after they leave the egg, but merely as a transitory stage.

The heterocercal tail, characteristic of adult Selachians and some of the more primitive Bony Fishes, may best be studied in such a form as the Dog-fish (*Scyliorhinus*) or Sturgeon (*Acipenser*). Instead of being continued straight backwards, the hinder end of the vertebral column is bent upwards, and the two lobes of the fin, which still retain their continuity around the tip of the tail, become differentiated into a small upper lobe and a much larger lower lobe, the latter taking its origin entirely from the lower side of the upturned backbone (Fig. 26A). In some of the more generalised Bony Fishes such as the Gar Pikes (*Lepidosteus*), Bow-fin (*Amia*), and Bichirs (*Polypterus*), the upturned part is so much shortened that the lower lobe of the tail-fin

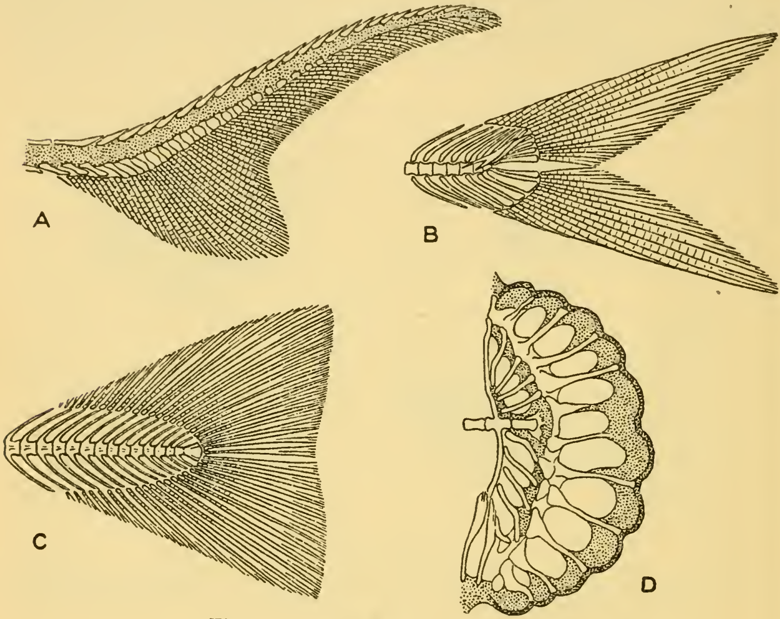


Fig. 26.—STRUCTURE OF CAUDAL FINS.

A. Sturgeon (*Acipenser sp.*); B. Ten-pounder (*Elops saurus*); C. Haddock (*Gadus aeglifinus*); D. Sun-fish (*Mola mola*).

comes to lie at the end of the fish, and externally has the appearance of a symmetrical structure.

In most of the higher Bony Fishes (*i.e.* in the Salmon, Perch, Plaice, etc.) the tail is of the homocercal type. Outwardly such a tail seems perfectly symmetrical, the prolongation of the axis of the body appearing to divide the fin into equal-sized and continuous upper and lower lobes. Dissection, however, reveals that this superficial appearance is misleading and that this type of tail is nothing more than a modified heterocercal condition. The hinder end of the vertebral column turns upwards in exactly the same manner, but, whilst the upper lobe has been reduced to a mere rudiment, the lower lobe is enormously developed and forms the greater part of the fin. The upturned part of the backbone is generally converted into a single bone, known as the urostyle, and the rays of the caudal fin are attached to the lower spines of the hinder vertebrae, which are greatly enlarged and at the same time inclined backwards so as to be more or less parallel to the axis of the body (Fig. 26B).

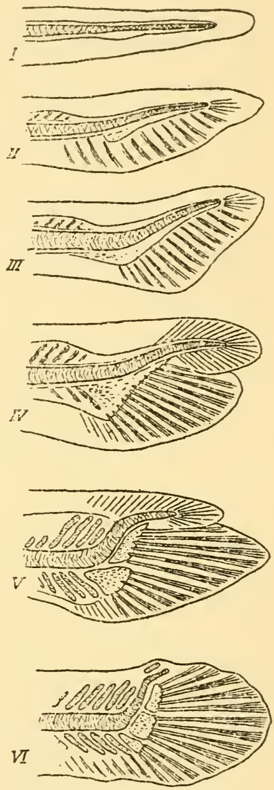


Fig. 27.—DEVELOPMENT OF CAUDAL FIN.

Six stages in the development of the tail region in the American Flounder (*Pseudopleuronectes americanus*). (After Agassiz.)

In some of the more specialised forms certain modifications of the homocercal tail occur. The term "leptocercal" (leaf tail) is applied to those tails of an attenuate or whip-like form, in which the vertebral column tapers to a fine point, as in the Grenadiers or Rat-tails (*Macruridae*) (Fig. 62A), and in some of the Blennies (*Blenniidae*). In other fishes the upturned part of the backbone is scarcely recognisable, and the fin-rays seem to be equally derived from the upper and lower lobe, resulting in a superficially diphycercal tail. In others, again, an apparent diphycercy is produced by the atrophy of the hinder part of the vertebral column in the adult, the upper and lower lobes of the caudal fin coalescing round the end of the abbreviated tail (Fig. 26D). In the Cods and their allies (*Gadidae*) occurs yet another modification, known as the isocercal (equal tail) type. This is actually, and not only apparently symmetrical, consisting of equal numbers of fin-rays separated by the axis of the vertebral column, which is continued straight backwards, the separate vertebrae growing progressively smaller behind (Fig. 26C). This symmetry has clearly been secondarily acquired, and has resulted from the loss of the original heterocercal tail and the meeting of the dorsal and anal fins round the hinder end of the fish. In other words, the tail-fin of the Cod is not a true caudal fin at all, being composed in the main of dorsal and anal rays.

A study of the embryonic development of the tail provides another interesting example of that recapitulation which has been already mentioned (*cf.* p. 55). In the tail of a larval American Flounder (*Pseudopleuronectes*), for example, in the very young fish this is without fin-rays and is truly diphycercal (Fig. 27 I). The hinder end of the vertebral column soon commences to turn upwards, numerous hair-like rods make their appearance along the lower edge of this axis, and the tail becomes definitely heterocercal (II, III). Later, the terminal portion becomes more bent, the upper lobe degenerates, and the lower lobe increases enormously in size, is directed backwards, and finally forms a superficially symmetrical tail (IV, V, VI). Thus, during the lifetime of a single individual the tail is transformed from a perfectly symmetrical organ through a distinctly asymmetrical stage into a superficially symmetrical one, all three types being represented in the order in which they were originally evolved. A study of the evolutionary history as revealed by the record of the rocks provides a similar story. The earliest known forms had a diphycercal tail, but very soon the heterocercal type appeared, with a very slight upward bend of the backbone and a small dorsal and large ventral lobe. Such a type of tail is found in all the ancient Selachians and Sturgeon-like fishes, and persists to-day in their living descendants. The homocercal tail, however, also made its appearance at an early stage, and is found in a fish (*Dapedius*) known to have flourished during the epoch known as the Lower Lias. Other curious forms of the Triassic and Liassic periods actually had two tails at one time. Of these, *Diplurus* and *Undina* (Fig. 129) are of special interest, exhibiting the true tail very much reduced in size and appearing as a tiny appendage bearing a minute caudal fin. In front of this is another fin, in all probability the functional tail-fin, made up entirely of rays derived from the hinder parts of the dorsal and anal. If these enlarged dorsal and anal rays increased still further in size and eventually superseded the true caudal fin the secondarily symmetrical tail of the Cods would come into being.

Having outlined the main facts concerning the origin and structure of the fins, it will be convenient to examine some of the more interesting modifications which these organs have undergone in certain fishes in order to fit them for the performance of new functions for which they were not originally intended. It will be convenient to deal first with the median fins, commencing with the dorsal.

In the Sharks (*Pleurotremata*) the dorsal fins retain their primitive function of acting as stabilising keels, but in the Rays (*Hypotremata*), fishes adapted for a life on the sea floor, the need for such keels has disappeared and the dorsal fins are progressively reduced (Fig. 8A), until in the more specialised forms such as the Sting Rays (*Trygonidae*) and Eagle Rays (*Myliobatidae*) they are altogether wanting (Figs. 8A; 14B; 32B). In some of the Sharks, notably in the Bull-headed Sharks (*Heterodontidae*) of the Pacific and the so-called Squalid Sharks (*Squalidae*), each of the two dorsal fins is preceded by a stout, sharp spine (Figs. 53B; 60A). The origin of these spines is somewhat obscure, but they are believed to owe their existence to the fusion of some of the shagreen denticles covering the front parts of the fins (*cf.* p. 85). Such spines provide formidable defensive weapons, especially when associated with poison glands, as in our own Spiny Dog-fish (*Squalus*) (*cf.* p. 140).

Many of the Sharks now extinct possessed similar spines, and, not infrequently, where the remainder of the fish's body has been destroyed, these spines, which are grouped together under the name of "Ichthyodorulites," are the only record left. Many have been discovered in Devonian and Carboniferous strata, some saw-edged, some smooth, some straight, some curved, and some with elaborate sculpturing. The owners of some of these spines may never be discovered, but must have been of gigantic build, for a fin-spine found in the carboniferous limestone of Bristol measured no less than *three feet* in length.

Among the Bony Fishes the dorsal fin exhibits great diversity both in size and form, and sometimes becomes specially modified for the performance of peculiar functions. It is rarely wanting altogether, but in the group of South American freshwater fishes known as Gymnotids, to which the Electric Eel (*Electrophorus*) belongs, it is either absent or reduced to a mere fleshy filament (Fig. 60C). In the more primitive forms the fin (or fins) is supported entirely by flexible and articulated rays, those at the front end generally being simple, while the majority are branched at their tips. Such fishes were grouped together by the older naturalists as Malacopterygians (soft fins) to distinguish them from the Acanthopterygians (spiny fins), in which the rays supporting the front parts of the dorsal and anal

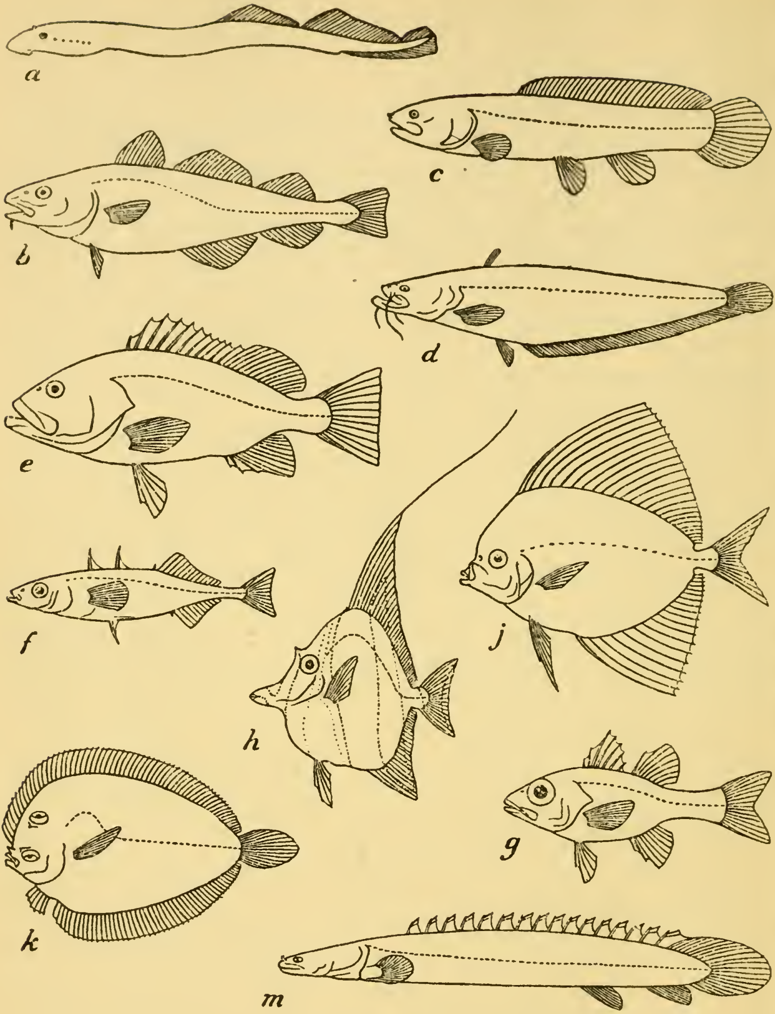


Fig. 28.—DORSAL AND ANAL FINS.

a. Sea Lamprey (*Petromyzon marinus*), $\times \frac{1}{10}$; b. Cod (*Gadus callarias*), $\times \frac{1}{10}$; c. Bow-fin (*Amia calva*), $\times \frac{1}{8}$; d. Wels or Sheat-fish (*Silurus glanis*), $\times \frac{1}{12}$; e. Sea Perch or Grouper (*Epinephelus drummond-hayi*), $\times \frac{1}{10}$; f. Stickleback (*Gasterosteus aculeatus*), $\times \frac{1}{2}$; g. Cardinal-fish (*Apogcn frenatus*), $\times \frac{1}{4}$; h. Moorish Idol (*Zanclus cornutus*), $\times \frac{1}{4}$; j. Sail-bearer (*Velifer hypselopterus*), $\times \frac{1}{5}$; k. Flat-fish (*Engyprosopon grandisquama*), $\times \frac{1}{3}$; m. Bichir (*Polypterus bichir*), $\times \frac{1}{8}$.

fins, as well as the outer rays of the pelvics, are converted into stiff-pointed spines. Occasionally these spines are slender and flexible, but they may always be readily distinguished from true soft rays by the absence of joints or branches.

Among the more generalised Bony Fishes the dorsal fin may retain its primitive form as a long fringe along the middle line of the back, especially in those species which use it as an organ of locomotion (Fig. 28c). In all the Eels (*Apodes*) the dorsal and anal fins are united with the caudal when this is present, and in the Morays or Muraenas (*Muraenidae*) the skin covering the fins is so thick that no trace of the rays is visible externally (Fig. 83A). A peculiar conger-like Eel from the West Indies (*Acanthenchelys*) is worthy of mention, in which the greater part of the dorsal fin is supported by soft rays in the usual manner, but in a small section near the tail these have been converted into stiff spines. Examples of spines following soft rays are very rare indeed, but the Viviparous Blenny or Eel Pout (*Zoarces*) of our own shores provides another case. The elongate dorsal fin occurs again in the Ribbon-fishes (*Trachypteridae*), which swim by means of wave-like movements of the body, aided by similar undulations of the fin. In the Oar-fish (*Regalecus*), a large oceanic species attaining a length of more than twenty feet, this fin extends all the way along the upper edge of the compressed body, and the first few rays are prolonged into rather long filaments, each of which ends in a membranous flap (Fig. 8D). The fins are bright scarlet in colour, and the general appearance of the head is not unlike that of a horse (*cf.* p. 429). In the closely related Deal-fish (*Trachypterus*) the form of the dorsal fin in the young fish is remarkable, the first six or so of the rays being produced into fine filaments more than four times as long as the fish itself. These streamers are ornamented with little membranous tags placed at intervals along their length (Fig. 121B). Another member of the same tribe, known as *Velifer*, derives its name from the relatively huge size of both dorsal and anal fins (Fig. 28j).

In the majority of Malacopterygians the primitive elongate fin is either considerably reduced in size or is split up into two or three separate fins. Thus, in the Herring (*Clupea*) and Carp (*Cyprinus*) there is a single rather small fin in the middle of the back composed entirely of soft rays, of which the first three or four are simple and graduated in size, the remainder being branched at their tips (Figs. 32D; 43). Two extreme sizes of single dorsal fin are encountered in the Feather-back (*Notop-*

terus) or the Wels (*Silurus*), with a tiny flag-like fin in the middle of the back (Fig. 28d), and one of the fancy varieties of the Gold-fish (*Carassius*), in which it takes the form of a huge sail-like structure. In some fishes allied to the Carp, one of the simple rays of the fin is stiff and spinous, and not infrequently saw-edged behind, but no true spinous fin is developed. In the Cat-fishes (*Siluroidea*) a strong spine nearly always precedes the remainder of the fin, and this has resulted from the modification of one or more soft rays. It is often serrated on one or both of its edges, or is provided with formidable barbs, forming a powerful defensive weapon capable of inflicting a nasty wound (Figs. 34K; 41D). Sometimes this spine is attached to the body by means of an elaborate ball-and-socket joint at its base, enabling the fish to keep it erect when alarmed. When thus fixed, the spine cannot be depressed without breaking it, but a rotary movement upwards and towards the body serves to lower it again.

A curious modification of the dorsal fin is found in the Tarpon (*Megalops*), as well as in some of the members of the Herring family (*Clupeidae*), the last ray being drawn out into a long filament which is concave on its hinder edge and tapers to a fine point (Fig. 13B). The purpose of this seems to be connected with the leaping habits of this fish. According to Mr. Mowbray, the Tarpon, preparatory to making a leap, "lashes this whip around to one side of the body and clamps it tight to its side." This adheres by suction to the body, and, by keeping the fin rigidly to one side, aids the fish in determining the course of the jump, the turn naturally being made towards the side to which the ray is pressed.

Among those soft-rayed fishes with more than one dorsal fin, mention may be made of the Gadoids, which belong to the order of fishes known as Anacanthini (without spines), a group including such well-known food-fishes as the Cod, Pollack, Whiting, Haddock, Hake, and Ling. In the first four of these fishes there are three dorsal fins (Fig. 28b); in the others only two. As their name implies, the fins of these fishes are supported entirely by soft rays. The little Rocklings (*Motella*), members of the same order, have a series of free rays just in front of the ordinary dorsal fin, and these may be continuously and rapidly vibrated for long periods. The function of such rays appears to be that of a sensory organ for locating and detecting food.

The Salmon (*Salmo*) also possesses two dorsal fins, but while the first resembles that of the Herring and is supported by soft rays, the second takes the form of a small flap, without any supporting structures, composed entirely of fatty tissue and covered with skin (Fig. 13C). This is known as the adipose fin, and is found in all the members of the Salmon family, as well as in many Characins, and in the majority of Cat-fishes. In some of the latter the adipose fin is comparatively large (Fig. 11), and in certain species may develop a few soft rays. It is of interest to note that in the Mailed Cat-fishes (*Loricariidae*) this fin is a triangular flap of skin, the front edge of which is supported by a stout, movable spine (Figs. 32F; 42C), but in some related naked forms (*Cyclopium*) from mountain streams the spine has disappeared and the adipose fin has reacquired the typical Cat-fish form. This provides one of the very rare cases of reversible evolution, where an organ has become changed and afterwards reverted to its original structure.

The position of the dorsal fin or fins also exhibits a fair amount of variation in different fishes. In the Gar Pikes (*Lepidosteus*) of North America (Fig. 48), and in the quite unrelated Pike (*Esox*), both dorsal and anal fins are placed well back towards the hinder end of the fish; in the Herring (*Clupea*) and Carp (*Cyprinus*) the dorsal occupies a position more or less in the middle of the back (Fig. 43); and in some of the Cat-fishes the rayed fin is considerably nearer to the head than to the tail (Fig. 28d). During growth the vertical fins tend to undergo some change in form, those of young fishes being generally higher than those of adults. The position may also alter during the life of the individual fish, as in the Herring (*Clupea*). In the larval stages the dorsal at first lies close to the tail, but moves gradually forwards as growth proceeds. In the grotesque Shrimp-fish (*Centriscus*) the arrangement of the vertical fins is unique. The thin, bony cuirass encasing the body ends behind in a long, stout spine, and the two dorsal fins, crowded together at the hinder end of the fish, are placed below the spine, the second actually pointing *downwards*. The tail has been deflected at an obtuse angle from the trunk, and terminates in a small caudal fin, also pointing downwards (Figs. 12; 42H).

Among the spiny-rayed fishes, the rays at the anterior end of the dorsal fin may be transformed into spines as in the Sea Perch (*Epinephelus*) (Fig. 28e) or Fresh-water Sun-fish (*Lepomis*) (Fig. 34e), or the spinous portion may be separated off as a distinct fin, as in the Mackerel (*Scomber*) (Fig. 5A) or Cardinal-fish (*Apogon*) (Fig. 28g). The evolution of spinous rays added a new function to the fins, that of attack and defence, and pugnacious fishes like the little Sticklebacks (*Gasterosteus*) know how to use their formidable dorsal and pelvic spines to the best advantage (Fig. 28f). The spines vary greatly in different fishes, both in height and thickness, and may even be soft and flexible as in some of the Gobies and Blennies (Fig. 34f). The Flat-fishes (*Heterosomata*) provide an example of the secondary transformation of spines into soft rays. It is known that these fishes have evolved from spiny-rayed forms not unlike the Sea Perches, but have become very much modified for a life on the sea bottom. In a primitive form from tropical seas (*Psettodes*) the dorsal fin commences well behind the head, and the front part is still supported by stiff spines, but in all other Flat-fishes the fin has grown forward on to the head, and the spines have been reconverted into flexible articulated rays, thus allowing of the wave-like movements essential for progression (*cf.* p. 27). In some of the more specialised Soles (*Synaptura*), and in the Tongue-soles (*Cynoglossus*), both dorsal and anal fins are united with the much reduced caudal, so that the three, together with the pelvic, form a complete fringe round the body.

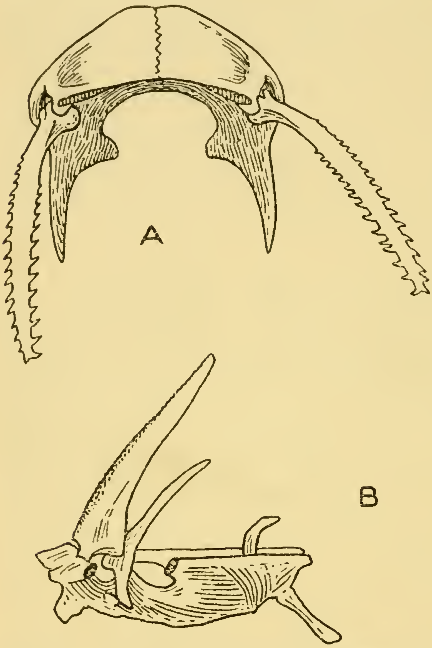


Fig. 29.—LOCKING MECHANISM OF FIN-SPINES.
A. Shoulder girdle and spines of pectoral fins of a South American Cat-fish (*Doras sp.*), ventral view, × ⅔; B. Dorsal fin-spines and associated bones of the Trigger-fish (*Balistes sp.*), lateral view, × ⅔.

In many of the Sea Perches and their allies the spines are unequal in size and strength, a somewhat delicate spine alternating with a stout one. In the Pine-cone Fish (*Monocentris*) of Japan the spines are particularly formidable and are curiously arranged, being alternately directed to the right or left, none of them being truly vertical as in other fishes (Fig. 42E). The closely related Soldier-fishes (*Holocentrum*) of the coral reefs of tropical seas derive their name from the stout and sharply pointed spines with which the fins are provided. In a few fishes, notably in the Weever (*Trachinus*) (Fig. 58A) and in the Poison-fish (*Synanceia*) (Fig. 58B), the spines of the dorsal fin are associated with poison glands, thus adding greatly to their efficiency as defensive weapons (*cf.* p. 142).

In the majority of fishes the dorsal and anal fins are capable of being erected or depressed at will, the separate spines or soft-rays being provided with special muscles for this purpose. When the fish is moving at any speed, the fins are always lowered, and in a fast-swimming form such as the Mackerel (*Scomber*) both the dorsal and anal can be folded away into more or less deep grooves in the body, the object being to prevent them from breaking the streamline form and so impeding progress. In the allied Sail-fish (*Istiophorus*) the spinous dorsal fin is of enormous size, and is believed to be projected from the surface of the sea and used like a sail to assist progression, but the whole structure can be tucked away into a deep groove when not required (Fig. 6A). After a rapid burst of speed, most fishes erect the dorsal and anal fins to their fullest extent, and these act as brakes and assist in slowing down.

Among other fishes with more or less modified dorsal fins, the Trigger-fishes and Bichirs are worthy of mention. The Trigger-fishes (*Balistidae*) owe their name to the structure of the spinous dorsal, this being supported by three spines, the first very strong and hollowed out behind to receive a bony knob at the base of the second; by this mechanism the first spine remains immovably erect until the second, which acts as a trigger, is depressed (Fig. 29B). The Bichirs (*Polypterus*) are not really Acanthopterygian fishes, but the anterior part of the dorsal fin takes the form of a number of separate, flag-like finlets, each consisting of a stout spine supporting a sail-like membranous flap (Fig. 28m), hence the name *Polypterus* (many fins)!

In the Mackerel (*Scomber*), Tunny (*Thunnus*), Bonito (*Gymnosarda*), and allied forms the soft dorsal fin is followed by a row of separate finlets, each of which is made up of a single much branched ray (Figs. 4, 5A). Their function is a little obscure, but they may act as subsidiary rudders.

The Remoras or Sucking-fishes (*Echeneididae*) are remarkable for the possession of an oval adhesive disc of complicated structure placed on the broad and flat upper surface of the head. It is provided with a varying number of transverse plates with free hinder edges, the whole being surrounded by a membranous fringe (Fig. 30). By means of this disc the fish can attach itself to any flat surface, a slight erection of the plates creating a series of vacuum chambers. The adhesion is so strong that a Remora can only be dislodged with difficulty, unless it is pushed forward by a sliding movement. Some naturalists state that when attached these fishes seem to become quite insensitive, and show no sign of life however roughly

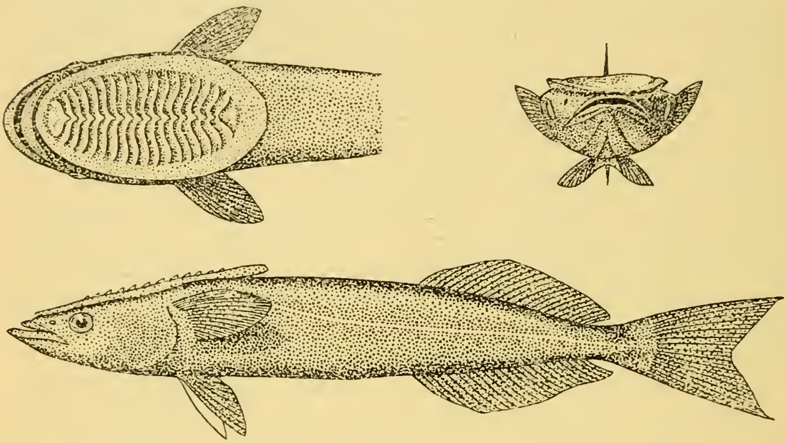


Fig. 30.

Remora or Sucking-fish (*Remora remora*), $\times \frac{1}{6}$.

treated. Feeding as they do on other fish, the Remoras are in the habit of attaching themselves to Sharks, Whales, Porpoises, Turtles, and even occasionally to ships (*cf.* p. 427), and in this way they are not only protected from their enemies, but are carried without effort to fresh feeding grounds. Once among a shoal of fish they soon detach themselves, dart off and swim actively about in pursuit of prey, seeking a fresh anchorage when their appetite has been satisfied. The point of special interest about the sucker is that it is nothing more than a very much modified spinous dorsal fin, whose rays have become divided into two halves, bent outwards in opposite directions, and have been transformed into the transverse plates. The peculiar mode of life of the Remoras, and the structural adaptation associated with it, probably arose from the habit found in many fishes of accompanying larger creatures either for protection or gain, and of concealing themselves under the shelter of any large object in the sea. "It is evident," writes Dr. Regan, "that the Sucker-fishes must have been derived from fishes which had, as the Pilot-fish has to-day, the habit of associating with Sharks. The spinous dorsal fin of the Pilot-fish (*Naucrates*) and of other oceanic fishes of the same type, with the spines folded back within a groove, might possibly have some power of adhesion if the edges of the groove were applied to another object and the spines were then slightly raised."

Another remarkable modification is found in the Angler-fishes or Pediculates (*Pediculati*), in which the first ray of the spinous dorsal fin is placed on the snout and transformed into a line and bait. In the Common Angler or Fishing-frog (*Lophius*) of our own shores, for example, this ray is quite flexible and bears a membranous flag-like appendage at its tip, its function being to attract the attention of small fishes when waved about in the water in front of the Angler's formidable jaws (Fig. 89). In the related Frog-fish (*Antennarius*) and Bat-fish (*Ogcocephalus*) (Fig. 40D) the line and bait is much reduced in size, and is sometimes represented merely by a short tentacle lodged in a cavity above the mouth. Among the Ceratioids, oceanic Angler-fishes spending their lives in a region of more or less perpetual darkness, the bait generally takes the form of a bulb of varying size which can be made luminous at will, and acts as a lamp to attract other fishes to destruction (Fig. 31). In one species (*Lasiognathus saccostoma*) the basal part of the dorsal fin-ray has been converted into a stout rod, followed by a slender line, which is provided, not only with the usual luminous bulb, but also with a series of curved horny hooks—a complete angler indeed (Fig. 31C)!

The anal fin, placed on the lower edge of the body between the tail and the vent, may be briefly dismissed. Like the dorsal it exhibits some variation both in size and form in different fishes. In the Gymnotids, Eels, and other forms in which it functions as a locomotor organ, the anal fin is very long (Figs. 5F; 10B); in other fishes, where it acts mainly as a balancing keel, it is considerably shorter (Fig. 28); in the Ribbon-fishes (*Trachypterus*, *Regalecus*) it is absent altogether (Fig. 8D). It may be supported entirely by soft rays, or the first few rays may be converted into stiff spines, often of some size (Fig. 28e, g).

In some fishes, of which the John Dory (*Zeus*) and the Horse Mackerel (*Trachurus*) may be mentioned, the spinous portion is separated off from the remainder as a distinct fin (Fig. 41B). In the Cod (*Gadus*) and related species the anal fin is divided into two portions, each being composed entirely of soft rays (Fig. 28b). In many of the South American Cyprinodonts (*Poeciliinae*), tiny fishes inhabiting fresh and brackish

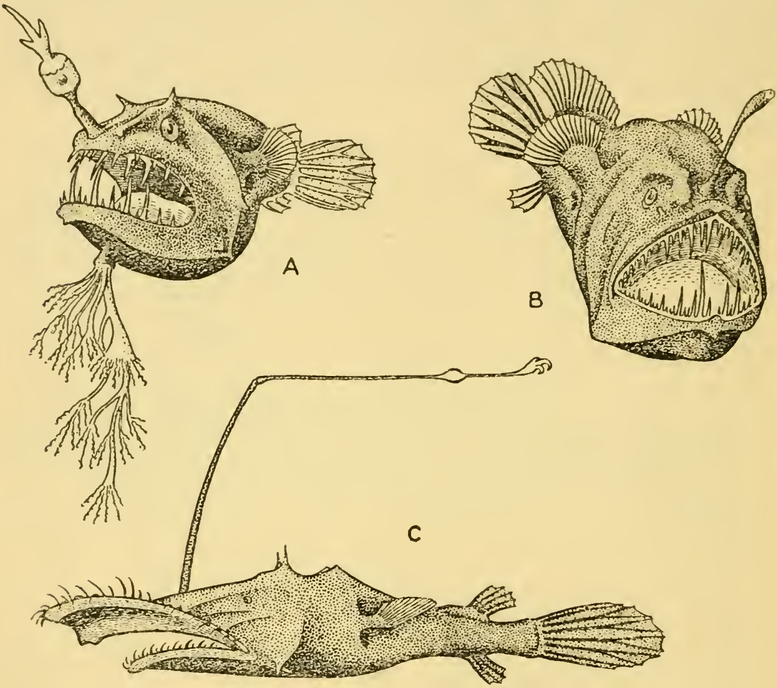


Fig. 31.—CERATIOID ANGLER-FISHES.

A. *Linophryne arborifer*, × ½; B. *Melanocetus johnsoni*, × ½; C. *Lasiognathus saccostoma*, × 1.

waters, the males are much smaller than the females, and the anal fin is specially modified to form an organ of elaborate structure used for purposes of copulation (*cf.* p. 296).

The last of the median fins, the caudal, has already been mentioned in discussing the tail itself, and little need be added here. Like the dorsal and anal, it is composed of simple or branched rays supporting a thin membrane; true spines are never developed in this fin, but rudimentary or procurrent rays

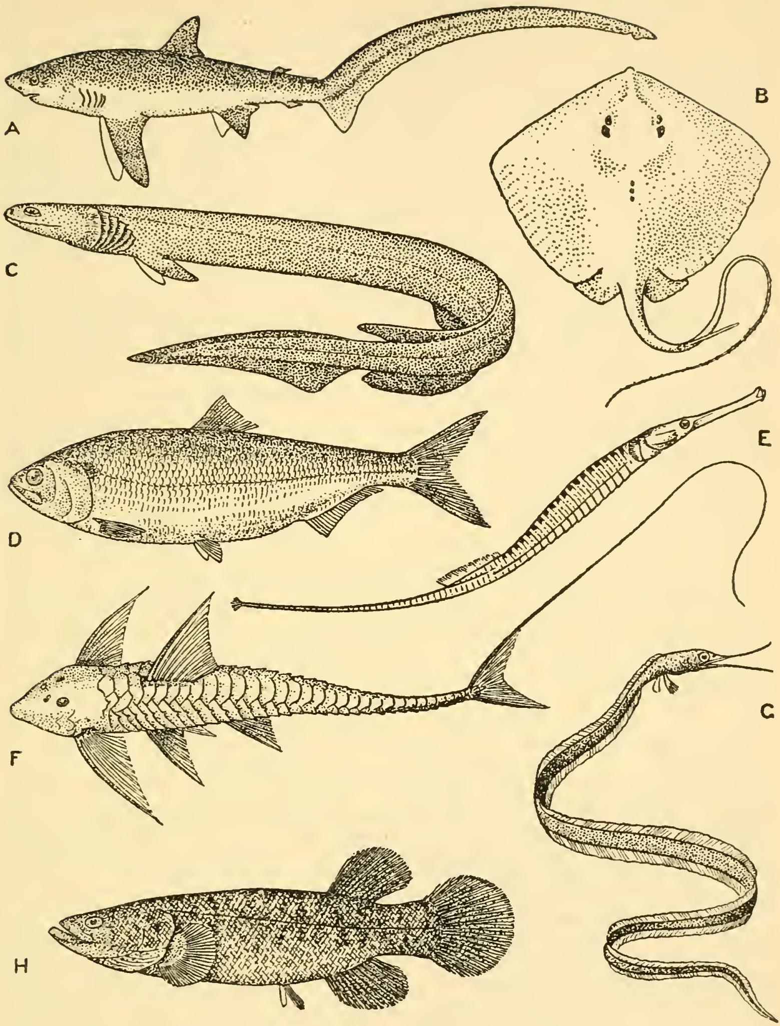


Fig. 32.—CAUDAL FINS.

A. Fox Shark or Thresher (*Alopias vulpes*), $\times \frac{1}{25}$; B. Sting Ray (*Trygon latus*), $\times \frac{1}{25}$; C. Frilled Shark (*Chlamydoselachus anguineus*), $\times \frac{1}{10}$; D. Allis Shad (*Alosa alosa*), $\times \frac{1}{4}$; E. Pipe-fish (*Microphis boaja*), $\times \frac{1}{3}$; F. Mailed Cat-fish (*Loricaria apeltogaster*), $\times \frac{1}{4}$; G. Snipe Eel (*Nemichthys scolopaceus*), $\times \frac{1}{5}$; H. *Black-fish* (*Dallia pectoralis*), $\times \frac{2}{3}$.

resembling spines may be found at the base of the lobes (Fig. 81A). The Sea Horse (*Hippocampus*), which is unique in using the tail as a prehensile organ, shares with some of the Eels (*Apodes*) and a few other fishes the distinction of being without a caudal fin (Fig. 5E). The caudal fin of the Sharks varies somewhat in form, but is rarely outwardly symmetrical, and the supporting rays are never visible externally. The function of the curious notch found in the upper lobe of the tail-fins of these fishes has never been satisfactorily explained, and it is possible that it may have possessed some special use in the past which no longer exists to-day (Figs. 1B; 32A). The Thresher or Fox Shark (*Alopias*) is remarkable for the great length of the upper lobe, which forms half the entire length of the fish (Fig. 32A). This Shark is said to swim round a shoal of fishes, splashing the water with its tail, and thus driving them into a compact mass, when they form an easy prey. Among the bottom-living Rays (*Raiidae*) the caudal fin tends to be much reduced in size, whilst in the more specialised Sting Rays (*Trygonidae*) and their allies it is wanting altogether, the long whip-like tail simply tapering to a fine point (Fig. 32B).

Among Bony Fishes with outwardly symmetrical tails, the shape and size of the caudal fin exhibits a good deal of variation (Fig. 33). Six main types of fin may be recognised, described respectively as lunate or crescentic (Tunny), forked (Herring, Mackerel), emarginate (Trout, Carp, Perch), truncate (Flounder), rounded (Turbot and Lemon Sole) and pointed (Goby). The shape of the tail generally provides a good index of speed and agility. As a general rule, fishes with lunate or deeply forked tails are capable of swimming for long periods at high speed, whereas those with squarish or rounded tails, although capable of sudden, short bursts of speed, are on the whole comparatively slow swimmers.

The Deal-fish (*Trachypterus*) and Sun-fish (*Mola*) may be selected as examples of fishes with unusual caudal fins. In the former this fin is unique in being directed upwards at right angles to the axis of the body. In the young fish the rays of the lower lobe are prolonged into lengthy filaments like those of the dorsal and anal fins, but these become progressively shorter as growth proceeds and finally the lower lobe of the fin disappears (Fig. 121B). It will be recalled that in the Sun-fishes the body ends abruptly behind the short, high dorsal and anal fins, and this is margined by a low, rounded caudal with a slightly wavy edge (Figs. 5C; 26D). Such a tail, to which the term "gephyrocercal" (bridge tail) has been applied, is found only in the Sun-fishes and the Pearl-fishes (*Fierasfer*), and represents a very specialised condition.

So much for the median or unpaired fins. The paired fins, corresponding respectively to the arms and legs of the land vertebrates, are absent in the Lampreys and Hag-fishes (Cyclostomes), but, with few exceptions, one or both pairs are developed in other fishes.

The pectoral fins vary very little in position, being situated just behind the gill-opening or openings, and placed near the lower edge of the body in some fishes and higher up on the sides in others. The pectorals of the Sharks are considerably larger than those of the generality of Bony Fishes, being used

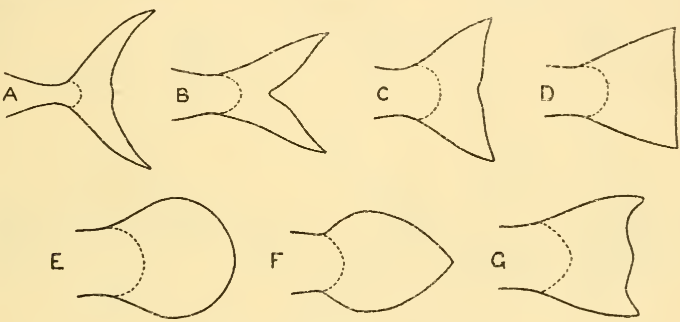


Fig. 33.—SHAPES OF CAUDAL FIN.

A. Lunate or crescentic ; B. forked ; C. emarginate ; D. truncate ; E. rounded ; F. pointed ; G. double emarginate.

almost entirely for steering purposes (Fig. 34b). A Shark seems to be quite incapable of making a sudden stop, and never uses the pectorals as brakes, being compelled to swerve to one side of an obstacle which lies in its path. The enormous, flattened, lobe-like pectoral fins of the Rays and their relations (*Hypotremata*), joined to the sides of the head and body and forming the principal organs of locomotion, have been already described (Fig. 34a). They may also be used for steering, especially in those forms in which the tail has degenerated to a mere filament. As in the case of the median fins, the paired fins of the Selachians are completely covered by skin and muscles, no trace of the rays being visible externally.

In the Bony Fishes these fins are nearly always relatively small, paddle-shaped organs, and only that part of the fin

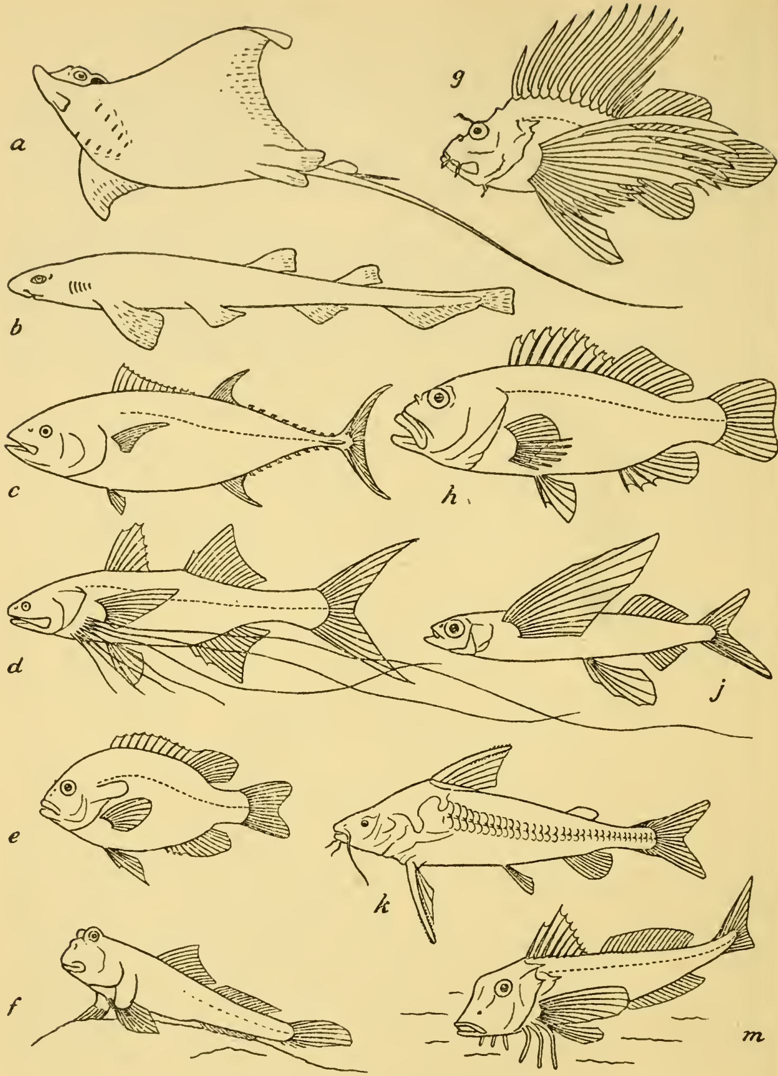


Fig. 34.—PECTORAL FINS.

a. Eagle Ray (*Myliobatis freminvillii*), $\times\frac{1}{20}$; b. Spotted Dog-fish (*Scyliorhinus caniculus*), $\times\frac{1}{8}$; c. Tunny (*Thunnus thynnus*), $\times\frac{1}{30}$; d. Thread-fin (*Polynemus paradiseus*), $\times\frac{1}{2}$; e. Fresh-water Sun-fish (*Lepomis megalotis*), $\times\frac{1}{4}$; f. Mud-skipper (*Periophthalmus koelreuteri*), $\times\frac{1}{4}$; g. Scorpion-fish (*Pterois volitans*), $\times\frac{1}{10}$; h. Cirrhitid (*Paracirrhites forsteri*), $\times\frac{1}{5}$; j. Flying-fish (*Exocoetus volitans*), $\times\frac{1}{8}$; k. South American Cat-fish (*Doras sp.*), $\times\frac{1}{3}$; m. Gurnard (*Trigla pini*), $\times\frac{1}{10}$.

which is supported by the fin-rays is visible without dissection. These rays may be simple or branched, and in some of the Cat-fishes there is a stout spine along the outer edge of the fin, which may be saw-edged along one or both of its margins and attached to the body by an elaborate joint (Figs. 29A; 34k). In the Mad Toms or Stone Cats (*Noturus*, *Schilbeodes*) of the United States, each of the spines is provided with a special poison gland at the base. A South American Cat-fish (*Doras*) uses the spines of the pectorals for progression overland, projecting itself along on the tips by the elastic spring of the tail (Fig. 34k).

The shape of the pectorals also varies to some extent. Fishes of moderate or slow speed, which may use these fins for propulsion or for backing water, have broad, rounded or spatulate pectorals (Fig. 34e). In speedy fishes, on the other hand, where they are employed in executing wheeling or turning movements, the fins are always longer and frequently sickle-shaped (falcate) (Fig. 34c). The peculiar leaf-like paired fins of the Australian Lung-fish (*Epiceratodus*) have been described on an earlier page (Fig. 99C). In the other Lung-fishes from Africa (*Protopterus*) and South America (*Lepidosiren*) the central lobe becomes long and narrow, the marginal fringe is reduced or entirely suppressed, and the fins take the form of long, tapering filaments (Fig. 99A, B). Rarely are the pectoral fins wanting, although they may be much reduced in size and efficiency. In some of the Pipe-fishes, however, and in certain of the Eels, they are absent.

The pectoral fins, therefore, are concerned mainly with propulsion or steering. The older authors laid considerable stress on their use as organs of balance, but more recent experiments tend to show that neither of the paired fins plays any important part in the maintenance of equilibrium. A number of fishes have been experimented upon by removing some or all of these fins, and in no case was the horizontal position seriously affected, provided the individuals remained at rest and attempted no turning movements. True, sick or dead fishes generally float belly upwards, but this is probably due to physiological causes. As in the case of the dorsal and anal, the pectorals have become variously modified in certain fishes for the performance of new functions, and the more interesting of these adaptations may now be examined.

The Flying-fishes (*Exocoetidae*) have greatly enlarged pectorals, often extending backwards as far as the tail (Fig. 34j), and use these to make the flights through the air for which they are famed. In order properly to understand these flights, it is necessary to look at some more generalised members of the same order, the Skippers (*Scombresox*), Gar-fishes (*Belone*), and Half-beaks (*Hemirhamphus*). These fishes, especially the Half-beaks, are experts at leaping or "skittering" over the surface of the sea, but the pectoral fins, being comparatively small, are only able to raise the head and forepart of the body out of the water, the tail remaining submerged and vibrating rapidly. There can be little doubt that the prolonged aerial excursions of the Flying-fishes are improvements upon the spasmodic jumps of the Gar-fishes and their allies. They are undertaken primarily in order to escape from enemies, or when the fishes are alarmed by approaching ships, but sometimes without any apparent cause. The actual flight seems to be carried out as follows: the fish accelerates its speed, rushing along near the surface of the water with its tail moving very rapidly from side to side; it then makes a sudden leap out of the sea and is borne along through the air with the pectoral fins outstretched and practically motionless. The chief motive power of this soaring flight is supplied by the tail, there being little, if any, actual flapping of the "wings" as in birds or bats; the pectoral fins act merely as parachutes which enable the fish to *glide* through the air. The flight appears to be checked by movements of the pelvic fins, which are often enlarged, and the fish returns to the water tail first, although, according to Dr. Hankin, in one species "they plunge head foremost into the water without any visible attempt to check their speed." He estimates the longer flights as from 200 to 400 metres in length, and the average speed under favourable conditions as from 10 to 20 metres a second. The fish seems to be quite incapable of steering itself in the air, but during the flight the hinder part of the body may become re-immersed in the water, and by a vigorous flip of the tail the fish changes its direction to the right or left and, at the same time, gains increased speed. As a rule the flights are close to the surface of the sea, but the fishes are not infrequently carried upwards to a height of 15 or 20 feet by a current of air, and in this way often land on the decks of ships in stormy weather. In the Flying Gurnards (*Dactylopteridae*) the pectoral fins are even more enlarged, but here they seem to be actually vibrated during flight, moving up and down like the wings of a butterfly. These flights, however, are more clumsy and less successful than those of the true

Flying-fishes. Among other fishes capable of short and generally erratic flights, the little Chisel-jaw (*Pantodon*) of African rivers and swamps, and a peculiar deep-bodied Characin fish from South America (*Gasteropelecus*) may be mentioned. The pectoral fins of the Chisel-jaw are not particularly long, but are joined to the body by flaps of skin.

The little Mud-skipper (*Periophthalmus*), found on the coasts of tropical Africa, Asia, and Australia, is renowned for its habit of leaving the water and walking or skipping about on the sand or mud in search of food. It chases its insect prey among weeds and rocks, and on land is quite as agile as many lizards. The pectoral fins are specially modified in relation to this habit, each being attached at the end of a kind of muscular arm, which can be moved backwards and forwards and is used exactly like a limb. Among other structural peculiarities designed to assist its progression on land, the low anal fin and the stout lower rays of the caudal may be noticed (Fig. 34f). Dr. Regan writes: "When walking on the mud each step is accomplished by a forward movement of both pectoral fins, which are then put on the ground and draw the rest of the body after them; these steps are repeated rapidly, and as each results in an advance of about half an inch, very fair progress is made; the pelvic fins support the body during the turning forward of the pectorals. But, as their name implies, the Mud-skippers often leap along the mud, or from one stone to another; short jumps may be accomplished by the action of the pectoral fins alone, but longer ones, which may be as much as a yard long, are made by a stroke of the tail. This is their way of getting along when they are in a hurry, and they may often be seen playing on the mud, jumping about in chase of each other." In the Sea Toads (*Chaunacidae*) and Frog-fishes (*Antennariidae*) these fins again take the form of arms, ending in many fingered "hands," by means of which they are able to crawl slowly about on the sea floor or to hang on to rocks or weeds (Fig. 85). In the related Bat-fishes (*Ogcocephalus*) the "arms" are even more muscular (Fig. 40D).

In certain fishes some or all of the rays of the pectoral fins may be drawn out into delicate filaments which serve as organs of touch. In the Thread-fins (*Polynemus*), for example, some four to eight of the lower rays are detached from the rest of the fin, and take the form of hair-like structures which may be longer than the fish itself (Fig. 34d). In a deep-sea fish known as *Bathypterois* the eyes are very much reduced in size, but the loss of vision is amply compensated for by the sensitive feelers formed by the rays of the pectoral and pelvic fins In the Perch-like Cirrhitids or Firm-fins (*Cirrhitidae*), of which the Australian Trumpeter (*Latris*) is perhaps best known, the lower rays of the pectorals are simple, thickened, free at their tips, and sometimes more or less prolonged; here, again, they act as sensory organs, and probably aid the fishes in their search for food (Fig. 34h).

The Gurnards (*Trigla*) and Sea Robins (*Prionotus*) have two or three of the lower rays of the pectoral fins detached from the remainder and modified to form stout finger-like appendages (Fig. 34m). These are used for turning over sand or stones, exploring shells, and otherwise searching for food, but also serve a locomotor purpose, the appendages acting as limbs, forward movement being produced by placing the tips of the rays in contact with the sand and pushing backwards. In the Flying Gurnard (*Dactylopterus*) the upper wing-like portion of the pectoral is used for parachuting, and the lower part, as well as the long thin pelvic fin, for creeping about on the sea floor. According to Dr. Beebe, the pelvic leg-like fins work alternately, one after the other.

Coming, finally, to the pelvic or ventral fins, corresponding to the legs of land vertebrates, it may be noted that, unlike the pectorals, their position varies considerably in the different groups of fishes, and is of some importance in classification. In all the Selachians, and in the lower kinds of Bony Fishes, such as the Herring (*Clupea*), Salmon (*Salmo*), and Carp (*Cyprinus*), the pelvics are placed in the middle of the belly between the pectorals and the anal, and are said to be *abdominal* in position (Figs. 13B, C). In other Bony Fishes, of which the Perch (*Perca*), Bass (*Morone*), and Mackerel (*Scomber*) will serve as examples, they are *thoracic* in position; that is to say, they lie farther forward in the region of the chest and more or less below the pectorals (Figs. 5A; 34c, e). In others, again, such as the Cods (*Gadidae*) and certain of the Blennies (*Blennioidea*), they are described as *jugular* in position, and actually lie in front of the pectorals in the region of the throat (Fig. 28b). In a number of Bony Fishes, and particularly in those forms which spend most of their time in burrowing, these fins are either very much reduced in size or are wanting altogether. All the living members of the order of Eels (*Apodes*) are without pelvics, but these have undoubtedly been derived from fishes which possessed a full set of fins, confirmation of this view being provided by a fossil Eel (*Urenchelys*) from the Chalk of Mount Lebanon which shows distinct traces of having possessed both paired fins as well as a separate caudal fin. Pelvics are absent in all the Pipe-fishes (*Syngnathidae*), Symbranchoid Eels (*Symbranchii*), Gymnotids (*Gymnotiformes*), Globe-fishes (*Tetrodontidae*) and Porcupine-fishes (*Diodontidae*), and are also suppressed in many of the Blennies and Cusk-eels (*Blennioidea*, *Ophidioidea*). Even when developed, they may be reduced to mere filaments, as in some of the members of the Cod tribe (*Gadidae*), and in the Oar-fish (*Regalecus*), where they are represented by a pair of long rays, each expanded into a blade-like structure at the tip (Fig. 8D). In the Sticklebacks (*Gasterosteus*) each pelvic is composed of a sharply pointed spine and one soft ray (Fig. 28f), and in the Pine-cone Fish (*Monocentris*) (Fig. 42E) and in some of the Trigger-fishes, etc. (*Plectognathi*), is reduced to a spine alone (Fig. 42D). In certain species of File-fishes (*Monacanthidae*) the pelvic bone with its spine is freely movable, and is connected with the body by a wide flap of skin (Fig. 10C); this is said to be used by the fish for fixing itself into crevices in the rocks or coral reefs.

It is very rarely that the pelvic fins have any connection with locomotion, and they mainly function as "bilge keels" or as accessory manœuvring organs. During rapid swimming they are generally drawn in close to the body. As in the case of the pectorals, some or all of the rays may be drawn out into lengthy filaments, as in the Dwarf Cod-fish (*Bregmaceros*) and Gourami (*Osphronemus*).

The most important modification of the pelvics is to form a sucking disc to enable the fish to cling to rocks, stones, and other fixed objects. The little Bornean Sucker (*Gastromyzon*), found only in the mountain torrents of Borneo (*cf.* p. 239), has the whole of the lower surface of the body modified to form a large sucker, in which the long and horizontally placed pectoral and pelvic fins play an important part (Fig. 35C). The Gobies (*Gobioidea*), a large and varied sub-order of fishes, mostly of small size, found mainly among the rocks between tide-marks, have the pelvic fins united to form a rather deep cup-like sucker (Fig. 35D). In the Lump-sucker (*Cyclopterus*) and Sea-snail (*Liparis*) a somewhat similar sucking disc is developed, but the pelvics have been so much modified as to have completely lost their fin-like appearance (Fig. 35A). This disc is very powerful, and some difficulty is experienced in removing a fish from an object to which it has attached itself. The Cling-

F

fishes (*Gobiesocidae*) are curious little creatures found between tide-marks among loose stones and shells, to which they adhere firmly by means of their adhesive discs. The disc is relatively large and of a complicated structure; it is composed largely of pads of thickened skin, but the widely separated pelvic fins and even the much modified bones of the pectoral girdle may contribute to its formation (Fig. 35B).

Among the Flat-fishes (*Heterosomata*), the asymmetry so

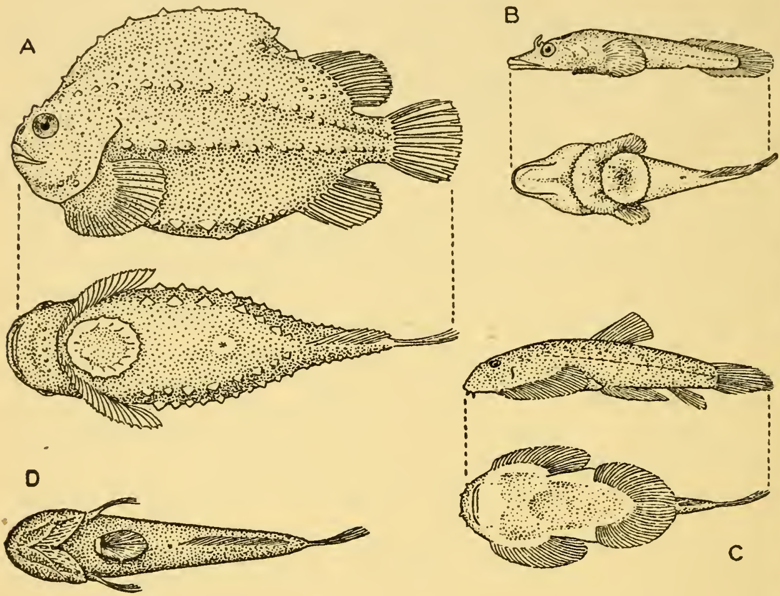


Fig. 35.—FISHES WITH VENTRAL SUCKERS.

A. Lump-sucker (*Cyclopterus lumpus*), × ¼ ; B. Cling-fish (*Lepadogaster gouani*), × ⅓ ; C. Bornean Sucker (*Gastromyzon bornunsis*), × ⅓ ; D. Lower surface of Black Goby (*Gobius niger*), × ½.

characteristic of the group extends to the pelvic fins in a large number of species. In the Scald-fish (*Arnoglossus*), for example, the pelvic of the left side, that is to say, of the upper or coloured side, is large and placed along the lower edge of the body like a fringe, whereas that of the lower side is quite small and placed at some distance from the edge. In some specialised Australian Flat-fishes (*Rhombosolea*) the pelvic fin of the blind side, in this case the left side, has disappeared altogether, and the other elongate fin has become joined to the anal, thus completing a more or less continuous fin round the edge of the fish's body.

In all living Sharks and Rays the hinder parts of the pelvic fins in the male are specially modified to form elaborate organs known as "claspers" or mixopterygia, which not only serve to grasp the female during copulation, but also assist in the process of fertilisation (*cf.* p. 294). A few members of the group of Bony Fishes known as Cyprinodonts (*Microcyprini*) have the fins in the male modified for a similar purpose (*cf.* p. 296).

CHAPTER V

SKIN, SCALES, AND SPINES

Structure of skin. Dermal denticles of Selachians. Tail-spine of Sting Rays. Saw-fishes. Scales of Bony Fishes: ganoid scales, cycloid and ctenoid scales. Tubercles. Bony scutes. Armoured fishes. Bony plates, rings, spines. Scales of Lung-fishes. Arrangement of scales, scale counts. Axillary scales. Lateral line. Scale-reading and age-determination. Replacement scales.

THE skin of a fish, like that of any other vertebrate, is composed of two layers, a thin outer epidermis and an inner dermis. The epidermis is made up of several layers of simple cells, of which the outer are being constantly worn away by wear and tear, and replaced by new ones budded off at its base. The dermis has a more complicated structure, being made up of a thick layer of what is known as connective tissue, with which are mingled muscle fibres, clusters of fine blood-vessels, and nerves. The inherent slipperiness of a fish's body is due to the presence of a slimy mucous which is constantly being poured out in large quantities by special glands situated in the epidermis, its function being to minimise friction with the surrounding water and to enable the fish to glide easily along. The slime excreted varies greatly both in quantity, and probably also in composition, in different species. In some of the Lampreys the glands are especially numerous, while a single Hag-fish (*Myxine*) placed in a bucket of water will soon convert the fluid into a thick mass of whitish jelly.

In addition to the skin, there is generally an outer covering of scales of one kind or another, generally spoken of as the exoskeleton, to distinguish it from the endoskeleton (skull, backbone, etc.). Where it is overlaid by scales the skin itself is nearly always thin and delicate, but in those fishes without scales, plates or spines it is strengthened in some way. Thus, in the naked Cat-fishes (*Siluroidea*) it is thick and leathery, and in the Sun-fish (*Mola*) the tough roughened skin is further reinforced by an underlying layer of cartilaginous material two or three inches in thickness. The curious Horse-fish (*Agriopus*) of South Africa is unique in being able to cast off its skin in patches like a snake, a new and brightly coloured skin developing below the old one.

The scales of a fish are products of the activity of the skin, and owe their existence to the presence of lime salts in the tissues of the body, which become deposited in the dermis. The form of the scales, spines, or other related structures varies considerably in the different groups of fishes, and provides an important character for their classification.

In the Cyclostomes scales are altogether wanting, but a study of their fossil ancestors suggests that this is a feature of de-

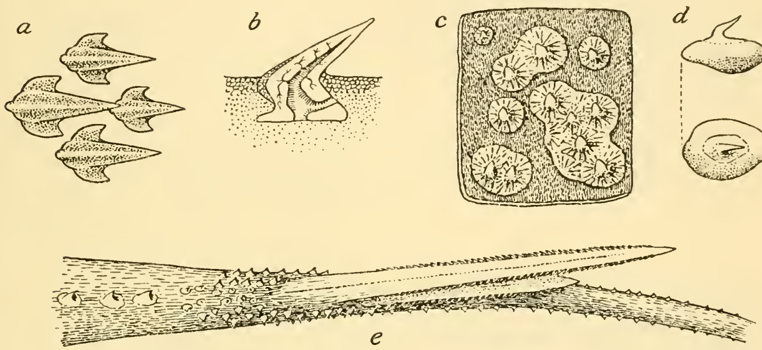


FIG. 36.—DERMAL DENTICLES.

a. Isolated denticles of the Spotted Dog-fish (*Scyliorhinus caniculus*), greatly enlarged; b. Diagrammatic cross-section of a denticle of a Selachian, showing the enamel covering and the central pulp cavity, greatly enlarged; c. Portion of skin with dermal denticles of the Bramble Shark (*Echinorhinus spinosus*), $\times \frac{1}{2}$; d. "Buckler" of Thornback Ray (*Raia clavata*), lateral and dorsal view, $\times \frac{3}{4}$; e. Tail-spine of Sting Ray (*Trygon sp.*), $\times \frac{1}{3}$.

generation rather than a primitive character. The dermal denticles of Sharks and Rays, sometimes known as odontoids or placoid scales, almost certainly represent the most primitive type of scale, and may conveniently be described first. The surface of a shark's body is generally prickly to the touch, due to the presence of innumerable tooth-like structures arranged in regular oblique rows, covering the whole of the head, body, and part of the fins. Each of these denticles consists of two portions, a bone-like base which is embedded in the skin and therefore invisible during life, and a superficial enamel-covered spine projecting freely outwards and backwards (Fig. 36a, b). Such denticles provide the familiar "shagreen," and the proved durability of shark-leather is largely due to the reinforcement provided by these structures (*cf.* p. 401).

In embryonic development the denticles make their appearance as minute conical or papilliform outgrowths of the skin; the outer epidermal layer of each of these cones becomes transformed into a coat of hard enamel by the deposition of lime salts; the dermal portion gives rise to dentine or ivory—the characteristic substance of teeth—with a central pulp cavity containing the blood-vessels and nerve (Fig. 37A). The base of the cone spreads out to form the bony plate, in the centre of which is a hole for the passage of the blood-vessels and nerve. The important point to notice about these denticles is that, both in their structure and in the manner of their development, they are strictly comparable to the teeth, which have quite clearly been derived from them (*cf.* p. 120).

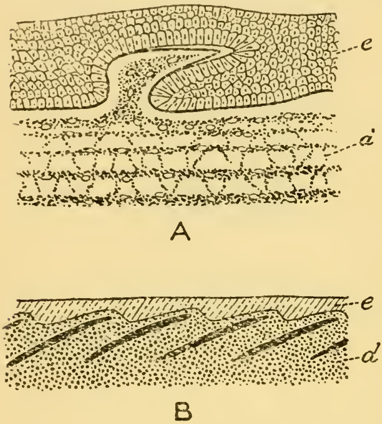


Fig. 37.—DEVELOPMENT OF DENTICLES AND SCALES.

A. Vertical section through the skin of an embryo shark. (After Gegenbaur); B. Diagrammatic longitudinal section through the skin of a Bony Fish, to show position of scales. (After Boas.) *d.*, dermis; *e.*, epidermis.

The arrangement of the denticles already described is that found in the familiar Dog-fishes (*Scyliorhinus*, *Squalus*, *Mustelus*), as well as in most other Sharks, but the denticles themselves present considerable differences in form and size, being sometimes flat, sometimes spine-like, and sometimes taking the form of rounded knobs. In the Bramble Shark (*Echinorhinus*), however, they are distributed irregularly over the body, and appear as large rounded tubercles of varying size, each surmounted by a tuft of fine spines (Fig. 36c). In the Rays (*Raia*) they are generally scattered sparsely and unevenly over the upper surface of the disc formed by the head, body, and pectoral fins; they are usually most prominent along the middle line of the back and on the upper part of the tail, and may be sharply pointed, flattened, or reduced to mere knobs (Figs. 14B; 107). In the Thornback Ray (*Raia clavata*) the greatly enlarged denticles are known as "bucklers" (Fig. 36d), and in other species of the same genus each principal spine has smaller accessory spines developed round its base. In the Torpedoes (*Torpedinidae*), on the other hand, and in some of the Sting Rays (*Trygonidae*) and Eagle Rays (*Myliobatidae*), the denticles have been discarded and the skin is quite smooth.

Mention may be made here of the tail-spine or "sting" of the Sting Rays and related forms, which in these fishes takes the place of the dorsal fins. Its origin is somewhat obscure, but it may have arisen through the enlargement or fusion of certain denticles in the tail region. It is generally serrated along both margins, and may be as much as from eight to fifteen inches in length. It provides a formidable weapon, and when the tail is lashed from side to side or curled round the intended prey,

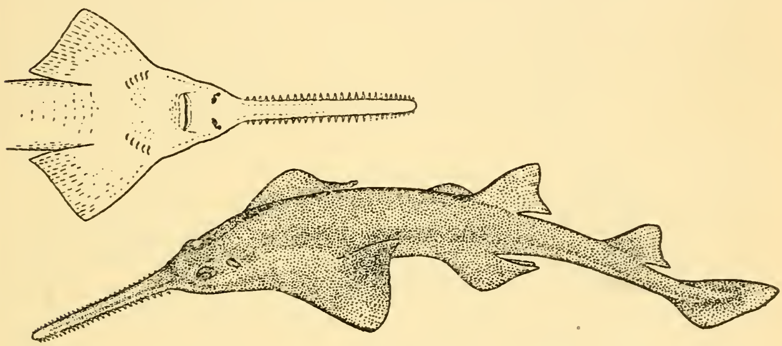


Fig. 38.

Saw-fish (*Pristis pectinatus*), $\times \frac{1}{20}$.

inflicts painful jagged wounds. The "stings" are shed from time to time, and replaced by new ones growing from underneath; sometimes two or three may be present in one fish at the same time (Fig. 36e).

In the Saw-fishes (*Pristis*), ray-like fishes found in all warm seas, the snout is produced to form a long flat blade, armed on either margin with a series of strong tooth-like structures (Fig. 38). These are modified dermal denticles, and are not only very much enlarged, but are firmly implanted in sockets in the cartilage of the rostrum. Saw-fishes grow to a large size, specimens twenty feet in length being quite common, and "saws" six feet in length and a foot across the base are by no means rare objects in the windows of curio or natural history dealers. Normally, this effective weapon is brought into use among a shoal of fish, and, wielded with a side-to-side movement, inflicts great execution. When attacking larger prey, the Saw-fish is said to use the saw to tear off lumps of flesh from the body of the victim, the detached fragments being seized by the mouth and swallowed at leisure.

It is of interest to note that in the Chimaeras and their allies (*Holocephali*), although the skin is naked in the adult, small patches of denticles, essentially similar in structure to those of the Sharks and Rays, still remain on the claspers (Fig. 80), and in the young there may be a double row of denticles along the back.

The scales of all the Bony Fishes differ from the denticles of the Selachians, not only in their structure, but also in being derived entirely from the dermal layer of the skin (Fig. 37B). Since the epidermis plays no part in their development, enamel no longer enters into their make-up. The ancestors of practically all living Bony Fishes, the Palaeoniscids, ranging from the Lower Devonian period to the end of the Jurassic, had the body completely invested in an armour of shining bony plates, arranged in regular parallel, oblique and longitudinal series (Fig. 127). These "ganoid" scales represent the most primitive type known in Bony Fishes, and persist to-day in the Bichirs (*Polypterus*) and in the Sturgeons (*Acipenser*) and their allies. Those of the Bichir take the form of juxtaposed plates, roughly rhomboid in shape, articulated with one another by a kind of peg-and-socket joint between the upper and lower edges of adjacent plates. Each scale is made up of three distinct layers; on the surface is a shining, enamel-like substance called ganoine (from which the term ganoid is derived); within is a thick layer of bone; and between the two another substance known as cosmine, containing minute blood-vessels. Where flexibility of the body is a consideration the advantage of jointed plates over solid armour is obvious, and the actual shape of the first scales was probably determined mainly by purely mechanical factors. The scales are in close connection with the underlying muscles, and when the flexures of the trunk and tail in swimming cause these muscles to contract the skin tends to be wrinkled into definite circumscribed areas.

In the existing Sturgeons (*Acipenser*), clearly descended from the Palaeoniscids mentioned above, the sole remains of the elaborate armour plating is a patch of small ganoid scales on the upturned part of the tail (Fig. 26A). There are, however, five widely separated rows of bony scutes or bucklers running along the body from the head to the tail, which have the same structure as the rhomboid scales. In young fishes the scutes are all touching one another, and each is armed with a strong knife-like spine, but as growth proceeds they become separated and the spine disappears (Fig. 41A). Between the scutes are oblique series of small denticles. The related Paddle-fishes, of which the curious Spoon-bill (*Polyodon*) of North America is best known (Fig. 47G), are even more degenerate in their bodily armour, the skin being naked and the rudimentary scales of the tail still further reduced.

The Gar Pikes (*Lepidosteus*) of the rivers and lakes of North America (Fig. 48), not to be confused with the marine Gar-

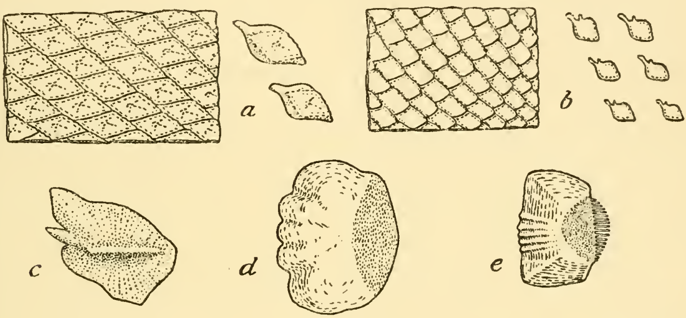


Fig. 39.—SCALES.

a. Portion of skin and isolated scales of the Gar Pike (*Lepidosteus sp.*), × about 1; b. The same of the Bichir (*Polypterus bichir*), × ½; c. Isolated scute of large Sturgeon (*Acipenser sp.*), × ⅙; D. Cycloid scale of Tarpon (*Megalops atlanticus*), × ¼; e. Ctenoid scale of Soldier-fish (*Holocentrum ascensionis*), × 8.

fishes (*Belonidae*), have an armour of shining diamond-shaped plates similar in appearance to those of the Bichirs, but they differ in lacking the middle layer of cosmine (Fig. 39A). They are very much the same in other respects, and articulate with one another by peg-and-socket joints.

Body armour composed of articulated rhomboid plates, although more efficient than solid mail, has certain disadvantages, and must restrict to some extent the flexures of the body in swimming. As fishes came to rely more and more upon their speed and agility rather than upon the strength of their armour for protection, the ganoid plates were gradually superseded by thinner and more flexible structures. Mechanical factors may also have played some part in the change, for an increase in the speed might be expected to lead to a change in the shape of the areas into which the skin is wrinkled. A study of extinct fishes provides a tolerably clear story, first of the gradual development and perfection of heavy armour, followed later by its gradual but no less definite decline when greater freedom of movement became all-important. Interesting transitional forms have been discovered, of which *Aetheolepis* from the Jurassic of Australia has retained the articulated ganoid plates on its relatively immobile trunk, whereas they have been transformed into thin, overlapping scales on the flexible tail. In other fossil forms all the scales are of the ganoid type, but whereas those on the body are articulated with one another, those in the tail region are quite free.

The typical scaly covering in a modern Bony Fish may best be studied in such fishes as the Carp (*Cyprinus*) or the Perch (*Perca*). In the Carp (Fig. 43) the whole body with the exception of the head and fins is protected by a number of regularly arranged, thin, flexible, bony plates known as cycloid scales, overlapping one another like the tiles on the roof of a house. Each scale, which is shaped roughly like the human finger-nail, has the front end inserted deep into a pouch in the dermal layer of the skin, the hinder portion being quite free. The overlapping (imbrication) of the scales is, from a mechanical point of view, important, and may be explained in the following manner. The muscles attached to the dermis tend to exert a somewhat unequal pull, and, therefore, to depress the scale areas, particularly at their front margins; in this way the growing scale is forced to lie obliquely, and at a later stage its hinder end appears through the skin (Fig. 37B). Only this free portion is covered by an epidermal membrane. In the Perch the scales are very much smaller, but have exactly the same arrangement. A closer study of a scale under the hand lens shows that its hinder end is provided with a row of small tooth-like spines instead of being smooth as in the Carp (Fig. 39E). Such a scale is known as ctenoid (comb-like).

The arrangement of scales just described may be taken as typical of most Bony Fishes, but a large number of deviations from this occur, either in the direction of degeneration or of further specialisation. Cycloid (smooth) and ctenoid (spinate) scales are not so widely different as would appear from the above descriptions, as the one type is linked up with the other by an almost complete series of intermediate stages. For example, the posterior edge of a cycloid scale may be wavy (crenulated), or the spines of a ctenoid scale may be soft and scarcely noticeable, in which case the scale is spoken of as ciliated. In some fishes the spines may extend on to the hinder free portion of the scale, giving it a roughened appearance. As a general rule, fishes with soft-rayed fins (*e.g.* Herring, Salmon, Roach) have cycloid scales, whereas the scales are ctenoid in the majority of Acanthopterygians (*e.g.* Perch, Bass), but exceptions to this rule are numerous. Both types of scale may be developed on different parts of the body in the same fish. Thus in many of the Sea Perches (*Epinephelus*) the scales above the lateral line are mostly ctenoid and those below it cycloid, and in the Dab (*Limanda*) the spiny ones occur on the upper or coloured side, those on the blind or white side being quite smooth.

The scales exhibit great diversity in shape in the different species, ranging from the roughly circular to the long oval. They also vary greatly in size. In the Tarpon (*Megalops*), for example, each scale is more than two inches in diameter, and these large structures are in some demand for ornamental work (Fig. 39d). Those of the Mahseer (*Barbus*), the famous game-fish of the rivers of India, are even larger, each being of the same size as the human palm. At the other extreme we have the minute cycloid scales of the Tunny (*Thynnus*) and Mackerel (*Scomber*), and the microscopic scales of the Common Eel (*Anguilla*).

In fishes of the Herring family (Herring, Sprat, Pilchard, Shad, etc.), the outer epidermal covering is very thin indeed, and the scales, which are placed in shallow pockets, appear to be lying on the surface of the body. Such scales are known as deciduous, because of the ease with which they are rubbed off when the fish is handled. In other fishes, of which the Plaice (*Pleuronectes*) will serve as an example, they are more or less deeply embedded in the skin. They are often also reduced in size, and instead of overlapping, remain quite separate from each other. The Common Eel (*Anguilla*) has a very slimy skin, which is, to all appearances, quite naked, but if a piece be examined under a microscope the presence of numerous minute scales embedded therein is revealed. This is clearly the result of degeneration as in the Plaice, and we are justified in assuming that these scales are the remnants of once much larger structures, which have gradually deteriorated as they ceased to be of importance to the fishes. It may be noted here that the ancient Hebrews, misled by the naked appearance of the Eel's skin, included this species among the fishes forbidden to them by Moses. His classification of the fishes into "all that have fins and scales ye shall eat; and whatsoever hath not fins and scales ye shall not eat; it is unclean unto you" had a certain practical object, for it excluded all the Cat-fishes, which, although pleasant to the palate, were known to be unwholesome and to cause diarrhœa and skin eruptions. These strict laws, forbidding as they did many plentiful and tasty species, naturally became gradually modified; fish with "at least two scales and one fin" were soon permitted, and, finally, any part of any fish on which traces of scales were visible!

The Dab (*Limanda*), with its ctenoid scales on the upper surface and cycloid scales below, has already been described. In other Flat-fishes the scales on the middle of the upper side are smooth, those on the head and near the edges of the body being spinate. In the Flounder (*Flesus*) most of the scales on the head, in the region of the lateral line, and also a series along the bases of the dorsal and anal fins, have been transformed into little thorny tubercles, generally stronger on the coloured side of the fish (Fig. 8B); the remainder of the body is covered with embedded cycloid scales, but in an allied species, the Diamond Flounder (*Platichthys*) of the Pacific coast of North America, these have been almost entirely suppressed, and the whole of the head and body is armed with irregularly scattered spiny tubercles (Fig. 40A). In another related form from Japan (*Kareius*) the tubercles are aggregated into clusters, and take the form of bony patches of varying size (Fig. 40C). In another group of Flat-fishes (*Bothidae*) the closely related Turbot (*Rhombus maximus*) and Brill (*R. laevis*) have quite different forms of scaly covering. In the Brill the body is armed with small cycloid scales, which are more or less overlapping, whereas the Turbot has a naked skin, but the coloured side bears a number of small, scattered, bony tubercles. The Black Sea Turbot (*R. maeoticus*), a distinct species, has very much larger tubercles, and these are developed on the lower as well as on the upper surface (Fig. 40B). Among other fishes with a somewhat similar armature, mention may be made of the Lump-sucker (*Cyclopterus*), whose thick skin is studded with bony warts, some of which are enlarged to form a series of cone-like projections along the back and three rows on either side of the body (Fig. 35A).

Two domesticated varieties of the Common Carp (*Cyprinus carpio*) produced by continental fish-culturists may be briefly described, since both these artificial forms exhibit modifications of the normal scaling. In the Mirror Carp (*Spiegelkarpfen*) there are one or two series of relatively enormous scales along the middle of each side, and generally some smaller ones near the bases of the fins; all these are more or less widely separated from one another, and the rest of the body is naked (Fig. 143D). The Leather Carp (*Lederkarpfen*) has a thick, roughened skin, which is entirely devoid of scales.

In some of the Cat-fishes (*Siluroidea*), Frog-fishes (*Antennariidae*),

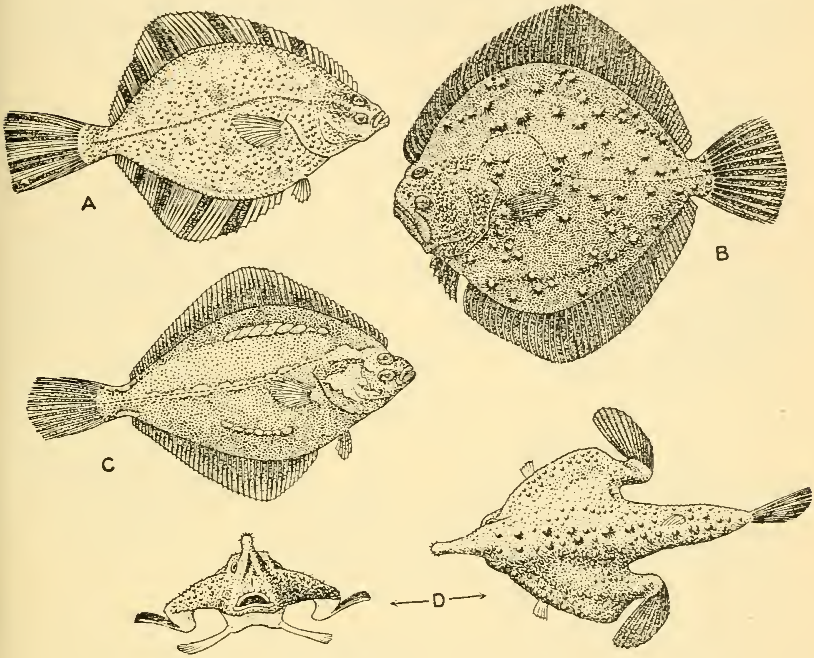


Fig. 40.—FISHES WITH TUBERCLES.

A. Diamond Flounder (*Platichthys stellatus*), $\times \frac{1}{4}$; B. Black Sea Turbot (*Rhombus maeoticus*), $\times \frac{1}{8}$; C. Japanese Flounder (*Kareius bicoloratus*), $\times \frac{1}{4}$; D. Bat-fish (*Ogcocephalus vespertilio*), $\times \frac{1}{4}$.

and in the Cling-fishes (*Gobiesocidae*), the scales are reduced to soft papillae of the dermis. In many of the more specialised Flat-fishes (Soles, Tongue Soles, etc.) some of those on the under side of the head become transformed into tiny membranous filaments, which are very sensitive and act as organs of touch.

Among other instances of specialisation may be mentioned the presence of bony scutes along the middle of each side in the region of the lateral line. These may result from the modification of ordinary scales or may develop as entirely new structures. In the Scad or Horse Mackerel (*Trachurus*), a member of a large tribe of fishes known as Pampanos or Carangids (*Caringidae*), the lateral line is armed with a row of numerous keeled, bony shields, which in the tail region are armed with sharp, knife-like spines (Fig. 41B). Somewhat similar spinous structures in this region occur in many of the Gurnards (*Trigla*). The members of a family of Cat-fishes found in the rivers of South America (*Doradidae*) possess a row of strong, bony scutes

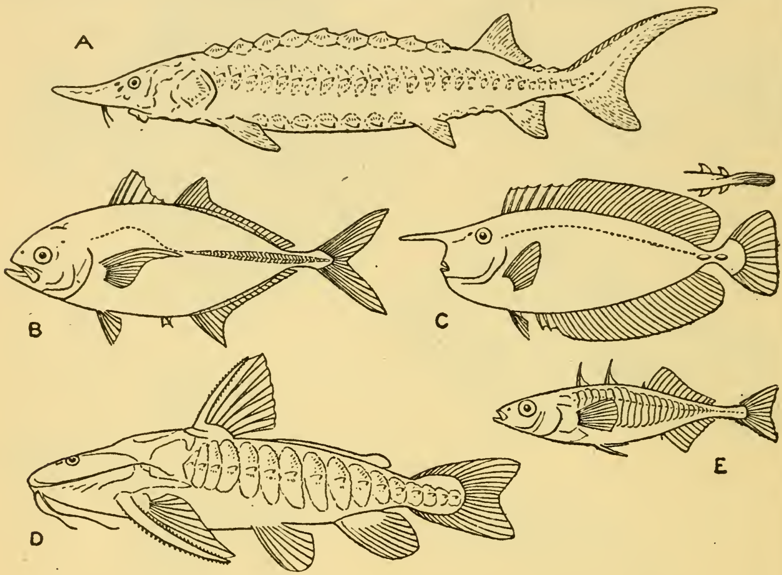


Fig. 41.—FISHES WITH SCUTES.

A. Sturgeon (*Acipenser sturio*), $\times\frac{1}{8}$; B. Pampano or Carangid (*Caranx chrysos*), $\times\frac{1}{4}$; C. Unicorn-fish (*Naseus brevirostris*), $\times\frac{1}{8}$; D. South American Cat-fish (*Megalodoras irwini*), $\times\frac{1}{4}$; E. Three-spined Stickleback (*Gasterosteus aculeatus*), $\times\frac{1}{2}$.

along the middle of either side, each of which is armed with a sharp spine and bears a superficial resemblance to the bucklers of the Sturgeons (Fig. 41D).

In the little "Tiddler" or Three-spined Stickleback (*Gasterosteus*) scales are wanting, but there is a series of large plates along each side, which in some specimens extends from the head to the tail, but in others is reduced to two or three plates behind the gill-opening (Figs. 28f; 41E). The Stickleback is equally at home in salt or in fresh water, and there seems to be some definite connection between the salinity of the water and the development of the plates. As far as the British Isles are concerned, individuals from inland waters nearly always exhibit the reduced number of plates, whereas examples from

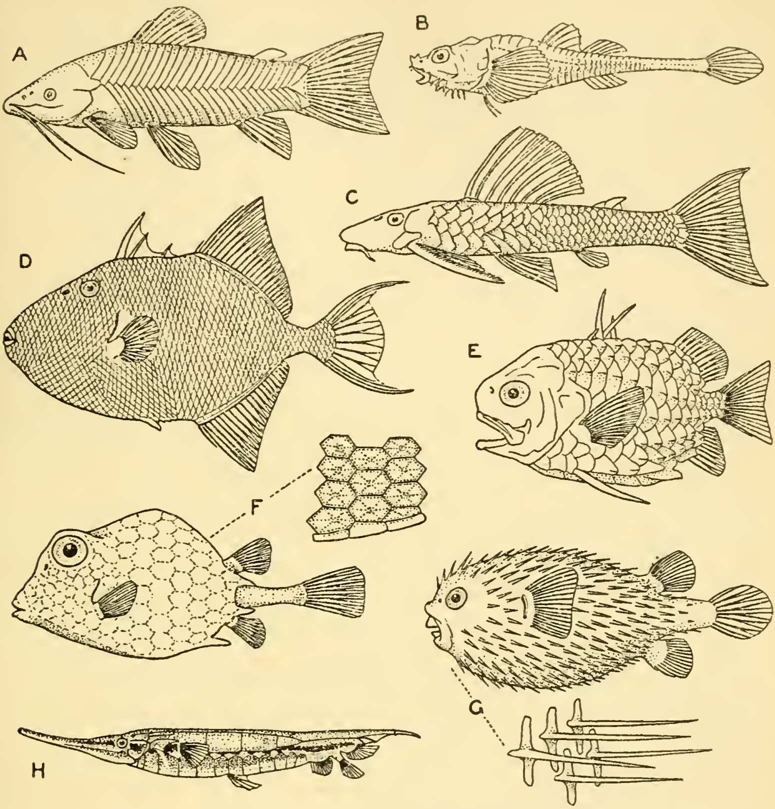


Fig. 42.—ARMOURED FISHES.

A. Hassar or Cascadura (*Callichthys littoralis*), $\times \frac{1}{4}$; B. Pogge or Armoured Bullhead (*Agonus cataphractus*), $\times \frac{1}{4}$; C. Mailed Cat-fish (*Plecostomus garmani*), $\times \frac{1}{5}$; D. Trigger-fish (*Balistes capriscus*), $\times \frac{1}{4}$; E. Pine-cone Fish (*Monocentris japonicus*), $\times \frac{1}{4}$; F. Trunk-fish (*Lactophrys trigonus*), $\times \frac{1}{4}$; G. Porcupine-fish (*Diodon hystrix*), $\times \frac{1}{8}$; H. Shrimp-fish or Needle-fish (*Aeoliscus strigatus*), $\times \frac{1}{2}$.

the sea are fully armed, intermediate types occurring in estuarine waters. Individuals from still more southerly localities may lack plates altogether.

It has been seen that the past history of fishes reveals a story of gradual improvement in heavy armour, followed by a definite decrease in its strength, and those Bony Fishes which have returned to the mail of their ancestors (although of a totally different structure) may now be considered. As a general rule, these are sluggish creatures, which have sacrificed speed and agility and have come to depend on their armour for protection from their enemies. The South American Cat-fishes, known as Hassars or Cascaduras (*Callichthys*), have the body completely encased in mail, made up of a double row of broad overlapping shields on each side. The arrangement of the shields is metameric, there being one pair to each vertebra or muscle segment. Allied to the Hassars are the Mailed Cat-fishes or Loricariids (*Loricariidae*), a large and varied family confined to the rivers of Central and South America. The body is protected above and on the sides by series of bony plates (Fig. 42C), the chest and abdomen being either naked or covered with much smaller plates. The plates on the sides have a metameric arrangement, and may be more or less sharply keeled or variously armed with small spines set in sockets (Fig. 42C). These smaller spines are of special interest, for when examined microscopically they are seen to be formed of dentine capped with enamel; thus, they are essentially similar in structure to the dermal denticles of the Selachians, and this represents another of the rare examples of the course of evolution having been reversed. The Mailed Cat-fishes are sluggish creatures, spending most of their time attached to stones or other objects at the bottom of a stream, and the bony armour provides them with an efficient protection against enemies. In some very closely related fishes from the mountain streams of the Andes (*Cyclopium*), where the absence of carnivorous fishes renders armour superfluous, the scutes have disappeared and the skin is quite naked (Fig. 93). Among other Bony Fishes with the body more or less completely cuirassed with bony shields, the Sea Robins of deep water (*Peristedion*), and the curious little Pogge or Bullhead (*Agonus*) found round our own coasts (Fig. 42B), may be mentioned.

Among the members of the large and diverse order of fishes known as Tube-mouths (*Solenichthyes*) there occur several interesting modifications of the scaly covering. In the Snipe-fishes (*Macrorhamphosus*), for example, each scale consists of a bony basal plate, rhomboid in shape, which is produced into a curved and backwardly directed spine, containing a definite pulp-cavity, reminiscent of that of the Selachian denticle. In the remarkable Shrimp-fishes (*Centriscidae*) the whole head and body is strongly compressed, and is completely encased in a transparent bony cuirass with a knife-like lower edge. This is made up of a number of thin plates, fused with the underlying ribs in much the same way as the carapace of a tortoise (Fig. 42H). In the Pipe-fishes (*Syngnathidae*) the scales are replaced by a series of jointed bony rings, encircling the body from behind the head to the tip of the tail. Similar rings surround the prehensile tail of the Sea Horse (*Hippocampus*), but in the immobile trunk region they take the form of plates which are roughly cruciform in shape, and are interlaced with one another to form a complete outer skeleton. The edges of these plates are not infrequently produced into pointed spines or rounded knobs (Fig. 5E).

The bottom-living Bat-fishes (*Ogcocephalus*) have the upper surface of the body studded with spines or tubercles, not unlike the scales of the Snipe-fishes in structure, but lacking the pulp cavity, the projecting spine being solid (Fig. 40D). Similar tubercles are sometimes found in the deep-sea Angler-fishes or Ceratioids, but these fishes mostly have a naked skin. In the Trigger-fishes (*Balistes*) the rough scales covering the body are like those of the Bat-fishes, the basal plate often being rhomboid in shape, with the outer surface roughened or armed with one or more small spines (Fig. 42D). In the File-fishes (*Monacanthus*) the spines are more numerous, and are set so close together as to give the skin the appearance of velvet. In the allied family of Trunk-fishes (Box-fishes, Coffer-fishes, Cuckolds) a complete and solid coat of mail again occurs. The scales are represented by large six-sided plates, united with one another to form a strong, bony box, from one end of which projects the mouth and from the other the naked tail. This box may be three, four, or even five-sided, and one or more of its edges may be armed with strong spines (Figs. 5B; 42F). A West Indian species (*Lactophrys tricornis*), with two long spines projecting forward from the forehead, is appropriately named the Cow-fish. The little Pine-cone fish (*Monocentris*), although pertaining to a totally different order of fishes, is another form in which the thick scales unite to enclose the body in a sort of box (Fig. 42E).

The Surgeon-fishes (*Teuthidae*) of tropical seas derive their name from the presence of a lancet-like spine on either side of the fleshy part of the tail. When not required this is retracted into a sheath in the skin, but can be quickly turned outwards and forms an effective weapon when the fish lashes its tail from side to side.

In the Puffers or Globe-fishes (*Tetrodontidae*) the scales are replaced by small, movable spines, which stand erect when the body is inflated with air. The Porcupine-fishes and Burr-fishes (*Diodontidae*) have an even stronger protection, the roots of the long, stout spines coming into contact with one another and providing a more or less continuous coat of mail. In some species these spines are two-rooted and movable, so that they can be laid back flat or erected at will; in other forms they are three-rooted and fixed (Fig. 42G).

The Lung-fishes (*Dipneusti*) are the sole living representatives of a once large and important group of fishes, in which the scales have a structure different to those of all other Bony Fishes. The primitive members of this group had a covering of ganoid scales, which must have been derived from plates similar to those of the Palaeoniscids, but the cosmine layer has a special regular structure and the ganoine is reduced to a thin superficial covering. Of the existing forms, the Australian genus (*Epiceratodus*) has large, thin, overlapping cycloid scales, whereas in the African (*Protopterus*) and South American (*Lepidosiren*) forms the scales are very much smaller, completely embedded in the skin, and more or less separated from one another (Fig. 99).

With few exceptions, the scales of Bony Fishes have a regular arrangement, and within certain limits both their size and disposition is constant for any given species. For this reason, a count of the number of scales is often of some importance in identifying any particular fish. Generally, the scales are arranged in obliquely transverse series, and the number of these series is counted along the middle of the side from behind the gill-opening to the base of the caudal fin. In estimating the number of scales across the body (*i.e.* the number of longitudinal rows) they are usually counted in one of the transverse series, as a rule that which runs from the commencement of the dorsal fin downwards and forwards to the lateral line, and from thence downwards and backwards to the pelvic fin (Fig. 43). Thus the scale formula for a particular species may be written: $44\text{-}47\,\frac{6\text{-}7}{9\text{-}10}$. This means that there are from 44 to 47 scales in a longitudinal series from the head to the tail, 6 or 7 between the origin of the dorsal fin and the lateral line, and 9 or 10 between the latter and the base of the pelvic fin. The Salmon (*Salmo salar*) and Trout (*S. trutta*) of our own country provide an example of the importance of scale-counts in distinguishing closely related species. These fishes are extremely similar in most characters, and although there are a number of points which enables an expert to tell them apart, by far the most reliable method consists in counting the number of scales on the tail, a sure means of identifying almost any specimen. In the Salmon the number in an oblique series from the hinder edge of the adipose fin downwards and forwards to the lateral line varies from 10 to 13, but in the Trout this number ranges from 13 to 16.

Mention may be made here of the so-called hybrid between the Pilchard (*Sardina*) and the Herring (*Clupea*), specimens of which turn up from time to time. At first sight this fish appears to have about 30 rows of scales along one side of the body, and more than 50 on the other. This is not, of course, a genuine hybrid, and the explanation of the abnormality is that the scales of the Pilchard are unequal in size, the oblique rows being

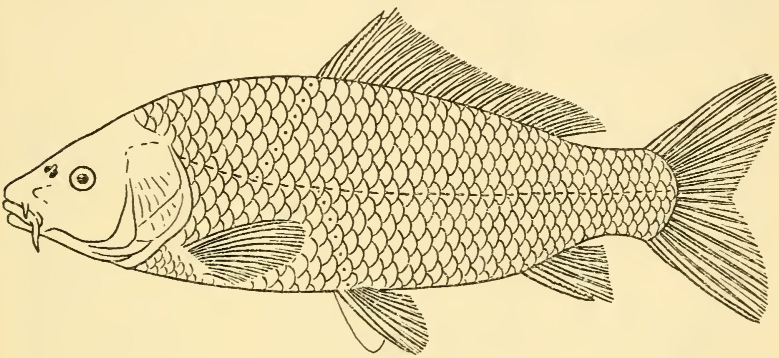


Fig. 43.
Carp (*Cyprinus carpio*), $\times \frac{1}{6}$.
To show arrangement of scales.

alternately of larger and smaller scales, the latter being quite concealed by the former in normal fish. In the so-called hybrid all the scales of one side of the body are equal in size and regularly arranged, while those of the other are large and small as usual.

In many Bony Fishes there is an enlarged and somewhat modified scale in the angle where the upper edge of the pectoral fin joins the body, and often a similar axillary or accessory scale in the outer angle of the pelvic fin. It usually takes the form of a pointed dagger-like process, sometimes stiff and hard, sometimes quite soft and flexible. As a rule, it is present in the more generalised forms, but is lacking in the more specialised fishes. Again, it is often well developed in actively swimming forms, and absent or much reduced in those living at or near the bottom, a fact which suggests that it is in some way connected with the locomotor activities of the fish. In the Salmon and Trout it is surrounded by definite fatty tissue, and is supported at its base by a splint of bone connected with the outermost ray of the pelvic fin.

The lateral line, a conspicuous feature of most Bony Fishes, will be dealt with in detail in the chapter devoted to sense organs (*cf.* p. 198), and it will suffice to point out here that it consists of continuous grooves or canals in the head and body containing special sensory organs; at intervals these grooves communicate with the exterior through pores or by little tubes which run outwards through the scales (Fig. 79d). It is these pores or modified tube-bearing scales which form the characteristic external line, generally running from behind the head to the base of the caudal fin, and not infrequently continued on to the fin itself. It may run more or less straight along the side as in the Trout (*Salmo*) or Carp (*Cyprinus*); it may be curved upwards to follow the line of the back as in the Perch (*Perca*), or downwards and parallel with the line of the belly as in the Roach (*Rutilus*) or Bream (*Abramis*). In the Parrot-fishes (*Scaridae*) and others (Fig. 44a) it is disconnected, the upper portion ending abruptly below the soft dorsal fin, and the lower portion commencing again below it and running backwards to the tail in the usual manner. In the Greenlings (*Hexagrammidae*) of the North Pacific (Fig. 44b) there may be several lines on each side of the upper part of the body. In the Tongue Soles (*Cynoglossidae*) there may be one, two or three lateral lines on the upper surface of the body and one, two or none on the lower, in addition to a complicated system of lines on the head (Fig. 44f). The continuation of the lateral line system on to the head occurs in most fishes, but where it is formed of deep-seated canals running along the surface of, or even perforating the bones, it is externally quite inconspicuous in this region. In many fishes, notably in the Flat-fishes (*Heterosomata*), the line runs straight from the tail to the tip of the pectoral fin, and then forms a more or less well-defined arch above the fin itself (Fig. 44e). In certain groups (Gobies, Cyprinodonts) the surface structures of the lateral line are entirely wanting. In the Sharks it is represented by a simple groove protected by overlapping shagreen denticles.

It is sometimes of considerable importance to be able to determine the age of a particular fish, and especially of those fishes which form the national food supply; this can be carried out, in some fishes at least, by what is known as scale-reading.

The discovery, made some years ago by Mr. H. W. Johnston, that every Salmon carries its own life-history clearly written on each one of its scales, has proved to be of incalculable value to scientific men, and this method of age-determination has since been applied to a number of other species, generally with success.

It has already been shown how the scale of a typical Bony Fish develops in the dermis and gradually grows until it comes to overlap the one lying immediately behind it (p. 90). This

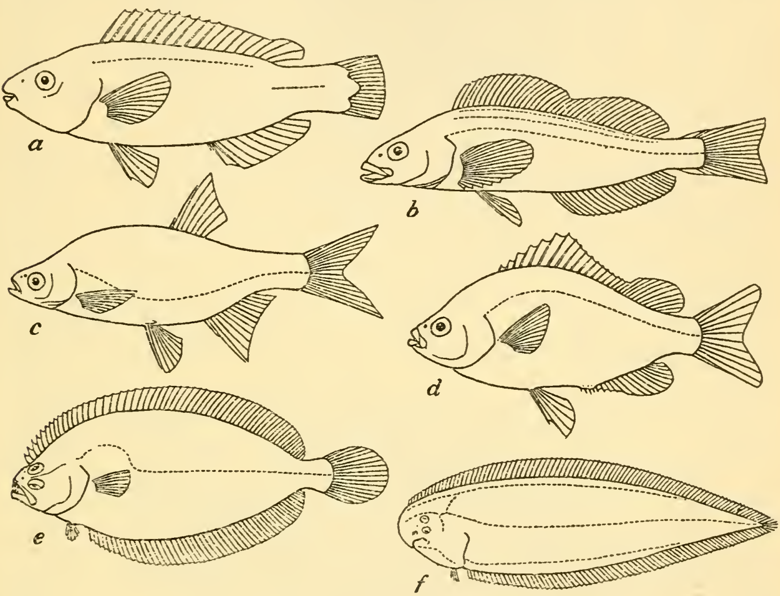


Fig. 44.—LATERAL LINES.

a. Parrot-fish (*Scarus emblematicus*), $\times \frac{1}{8}$; b. Greenling (*Hexagrammus stelleri*), $\times \frac{1}{2}$; c. Bream (*Abramis brama*), $\times \frac{1}{4}$; d. Viviparous Perch (*Hysterocarpus traski*), $\times \frac{1}{4}$; e. American Flounder (*Paralichthys dentatus*), $\times \frac{1}{8}$; f. Tongue Sole (*Cynoglossus versicolor*), $\times \frac{1}{4}$.

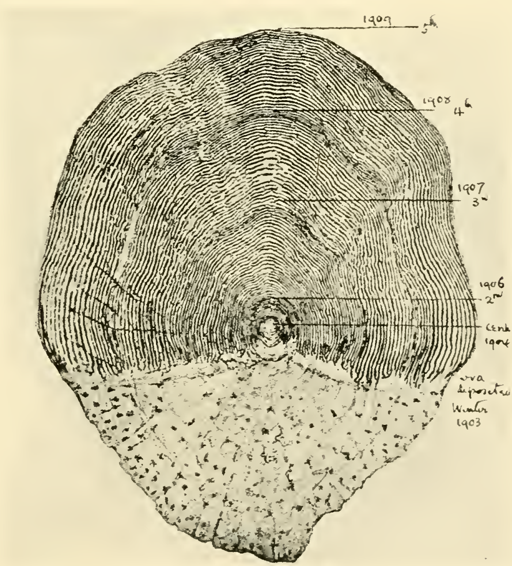
growth goes on throughout life, but seems to be retarded as the fish becomes really old. As mentioned above, the number of scales in any species remains constant throughout the life of the fish, so that as the fish grows the scales must inevitably increase more or less proportionally in size. Now, if the scales of a Salmon be examined under a low-power microscope or hand lens, it will be observed that each one is made up of a number of rings arranged concentrically like the rings on a target. Some of these rings are seen to be well separated, others closer together, recalling the rings of growth exhibited by a cross-section of the trunk of a tree. They represent the new material manufactured by the tissues of the skin, and added to the scale from time to time. But since a fish grows unequally at different seasons of the year, this irregular growth is duly reflected in the scales. In spring and summer, when food is plentiful and the fish grows rapidly, the scales increase in size by the addition of a large number of rings well separated from each other; when growth slows down in autumn or almost ceases in winter the rings added become fewer in number and much closer together. This check in growth once a year enables us to determine the age of any fish by counting the number of winter "zones"; that is to say, of areas of close rings.

A glance at the accompanying figures of Salmon scales (Pl. I) will give an idea of the manner in which this method is applied. The first represents the scale of a 5-lb. Grilse, caught in the River Wye in July when returning from the sea to spawn. The centre of the scale (Fig. A) shows clearly the two years spent in the river from the time of hatching until it descended to the sea as a Smolt, *i.e.* the two years' Parr life; this is followed by a number of well-separated rings representing the first summer in the sea, after which is a winter zone, followed in turn by an area representing half a second summer in the sea. It may thus be deduced that the age of this fish when caught was three and a half years. The second (Fig. B) was taken from a large spring fish of 22-lb. weight, caught in April, and shows two years' river life and three years' sea life. At the end of a winter's growth an irregular scar will often be seen running right round the scale. This is known to scale-readers as the "spawning mark," and is due to the following cause: after spawning the girth of the fish greatly decreases, and the outer edges of the scales become much frayed and worn; when it again reaches the sea scale-growth recommences, but it does not take place in such a way as to repair the eroded parts, and the line of junction between the old and the new growth is necessarily irregular.

From time to time the scales of a fish tend to wear off or to become otherwise dislodged, a not infrequent occurrence in such forms as the Salmon (*Salmo*) and Herring (*Clupea*). When this happens, new scales, known as replacement scales, are formed to take the place of those lost. Naturally these are of no value for scale-reading purposes, the concentric rings in the centre of the scale being absent.

A.

A. Scale from grilse caught in the River Wye, July 14th, 1909; 5 lbs., male, 24 inches long, showing 2 years in river and $1\frac{1}{2}$ years in sea. × about 12.



B.

B. Scale from large spring-fish, April 7th, 1909; 22 lbs., male, $38\frac{1}{2}$ inches long, showing 2 years' river and 3 years' sea life. × about 11.

Plate I.

SCALES OF THE SALMON (*Salmo salar*).

CHAPTER VI

MOUTHS AND JAWS

Form of mouth in Cyclostomes, in Selachians. Jaws of Selachians, of Bony Fishes. Form and position of mouth in Bony Fishes. Modifications of lips. Weevers and Star-gazers. Gar Pikes, Gar-fishes, and Half-beaks. "Sword-fishes." Tube-mouths. Fishes with protractile mouths. Flat-fishes.

THE importance of the part played by hunger and the consequent need for food in the daily life of a fish is obvious, and is reflected in the form of the mouth, jaws, teeth, and so on, structures which present more diverse modifications than any other organ of the body. As will be explained in the present chapter, such modifications may generally be shown to be more or less intimately associated with the mode or conditions of life, the manner of obtaining food, and the nature of the diet itself.

The Cyclostomes (Lampreys and Hag-fishes) differ from all other fishes in having a rounded, funnel-like mouth placed at the end of the head, which, although supported by special cartilages, is entirely devoid of true biting jaws. The mouth of the Lamprey (*Petromyzon*) acts as a sucker, by means of which it attaches itself to other fishes, devouring them by sucking their blood and rasping off their flesh with the horny teeth on the muscular piston-like tongue (Fig. 45A). At one time the absence of jaws was regarded as the result of degeneration consequent upon the adoption of semi-parasitic habits, but a detailed examination of some very ancient extinct forms now known to be ancestral to the modern Cyclostomes has shown that these also lacked true jaws (*cf.* p. 344). The Lamprey is able to strike its suctorial mouth against the skin of its prey, and becomes so firmly attached that it is rare indeed for the victim to shake off its persecutor before succumbing from loss of blood. The amazing strength of the sucker may be tested by allowing a Lamprey in an aquarium to attach itself to the hand or arm, and it will be found almost impossible to detach the fish without lifting it from the water. While engaged in feeding the Lamprey is carried about by its victim, and it is by no means uncommon for one of these pests to steal a ride on a Salmon or other fish when it wishes to ascend a river for spawning purposes. The sucking mouth is also used to anchor it to stones on the river bed, and it is of interest to note that the name Lamprey refers to this habit, being derived from the

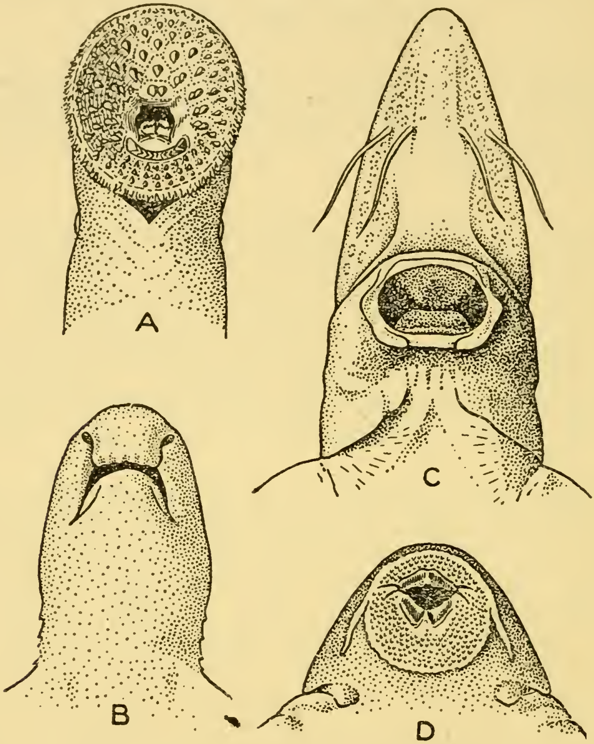


Fig. 45.—INFERIOR AND SUCTORIAL MOUTHS.

A. Opened mouth of the Sea Lamprey (*Petromyzon marinus*), × $\frac{1}{3}$; B. Lower surface of head of Spotted Dog-fish (*Scyliorhinus caniculus*), × $\frac{1}{3}$; C. The same of Sturgeon (*Acipenser rubicundus*), × $\frac{1}{3}$; D. The same of Mailed Cat-fish (*Plecostomus guacari*), × $\frac{1}{3}$.

mediaeval Latin *Lampreda*, a corruption of the older *Lampetra*, from *lambere*, to lick, and *petra*, a stone. In the Hag-fishes (*Myxinidae*) there is no distinct funnel, and the almost terminal mouth is surrounded by short barbules or tentacles.

Among the existing Sharks the mouth is nearly always crescentic in shape, and placed on the under side of the head

(Fig. 45B), but in the primitive Frilled Shark (*Chlamydoselachus*) the wide mouth occupies a completely terminal position (Fig. 32C). In other Sharks the position of the mouth seems to have been brought about by the forward prolongation of the front part of the head above the jaws to form a snout or rostrum, a modification clearly designed to gain increased speed. From the position of the mouth it is generally assumed that a Shark is obliged to turn over on to its side or back in order to engulf its food. This, however, is by no means always so, and, although it may turn over when taking food at the surface, as in the case of a lump of meat thrown overboard from a ship, it has frequently been observed to maintain its normal position when seizing living prey, and to push the snout out of the water in order to bring the jaws into play.

In the sluggish, ground-living Rays (*Hypotremata*) the mouth is nearly always well under the head, and generally takes the form of a straight slit (Figs. 14B; 107). Although for the most part a rather inactive creature, a Ray (*Raia*) will display great activity when a small fish or crustacean comes within its reach. Owing to the position of the mouth it is unable at once to seize its prey, but darts rapidly over it, covers it with its body and enlarged pectoral fins, and devours it at leisure. The large Rays known as Sea Devils (*Mobulidae*) differ from the remainder in living more or less in the open sea, and the mouth, in some of them at least, lies nearly at the end of the head. These fishes are remarkable in having the front parts of the pectoral fins prolonged forward to form a pair of fleshy appendages having the appearance of horns (Fig. 13A). They are known as the cephalic fins, and the part played by these structures in obtaining food differs somewhat in the various species. The Smaller Devil-fish (*Mobula*) is in the habit of swimming about in shallow water near the shore in shoals of three to five in number. The "horns" are normally kept tightly curled up to a sharp point, but no sooner is a shoal of small fishes sighted than the Rays swing round in a semi-circle, and rush their intended meal to the beach; at that instant the cephalic fins flash open, and meeting below the mouth form a funnel through which the fishes are conveyed to their jaws. The great Sea Devil (*Manta*), on the other hand, is a more or less solitary feeder, and swims along slowly near the surface, turning from one side to the other with the cephalic fins in constant movement, and actually using these appendages to throw the food into the mouth.

Except in the Lampreys and their allies, the mouth of a fish is always supported internally by structures known as jaws. In order to understand the origin of these jaws it is necessary to consider again the half-hoops of cartilage or branchial arches, which in the Selachians lie in the side walls of the pharynx between the internal openings (*cf.* p. 35). There is little doubt that the earliest fishes possessed a series of these arches, all of them connected with gills, and that after a time the first two pairs became specially modified (Fig. 46A). The first pair was transformed into biting jaws, consisting of an upper portion known as the pterygo-quadrate cartilage (*ptq.*), and a lower portion known as Meckel's cartilage (*mk.*). In some Sharks living to-day this first or mandibular arch still exhibits traces of its original character, and may lie in front of a gill-cleft and be associated with vestigial gills; in the remainder it has lost all trace of its branchial origin, and only the manner of its development provides a clue as to how it came into being. The second or hyoid arch has been much less modified, and is not very unlike the branchial arches which lie behind it. Its normal function is to provide a support for the tongue, but in most fishes it has acquired the secondary task of suspending the mandibular arch from the cranium (Fig. 46A; *hym.*).

Examination of the skull of the Spotted Dog-fish (*Scyliorhinus*) shows that each upper jaw is connected with its fellow in front below the cranium, and that the two halves of the lower jaw are similarly bound together. Further, the upper jaw is attached to the cranium by a muscular ligament at about the middle of its length, and the hinder ends of both jaws are slung from the back part of the cranium by the intervention of one of the segments of the second arch, namely, the hyomandibular cartilage (Fig. 46A). In the Comb-toothed Sharks (*Hexanchidae*) the mode of suspension is somewhat different, the upper jaw being not only joined to the cranium by a process at the middle of its length, but also has another direct articulation with that part of the cranium which lies behind the eye-socket or orbit. Being relieved from taking part in the suspension of the jaws, the hyomandibular cartilage is here reduced to a relatively slender rod, and below is connected with the remainder of the hyoid arch. Yet another type of suspension is found in the Bull-headed Sharks (*Heterodontidae*); the jaws are slung from the cranium by the hyomandibular, but the upper jaw fits into a deep groove in the cranium and is firmly attached to it by strong ligament. In the Chimaeras (*Holocephali*) this condition is carried still further, the upper jaw being completely fused with the cranium, and the supporting element of the hyoid arch is reduced to a mere vestige (Fig. 56A).

In the class of Bony Fishes the primary upper and lower jaws have become so much modified as to be scarcely recognisable in the adult fish, but the early development of the mandibular and hyoid arches throws considerable light on the manner in which the changes have taken place. The skull commences

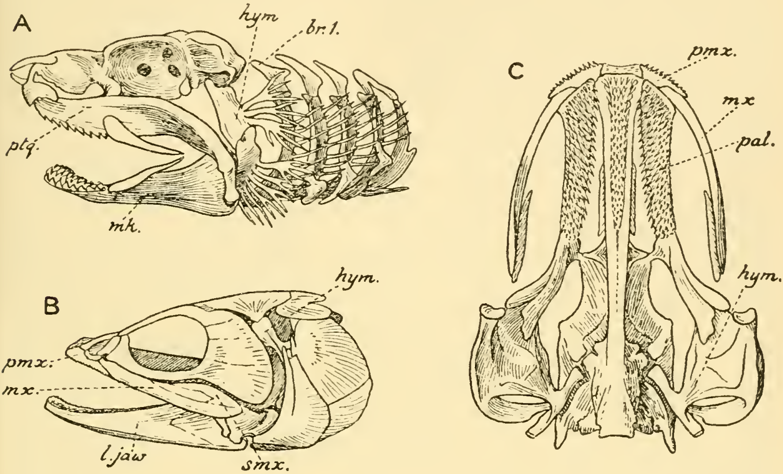


Fig. 46.—CARTILAGINOUS AND BONY JAWS.

A. Lateral view of skull of Spotted Dog-fish (*Scyliorhinus sp.*), × $\frac{1}{3}$; B. The same of Ten-pounder (*Elops saurus*), × $\frac{1}{2}$; C. Lower surface of skull of Pike (*Esox lucius*), × $\frac{1}{4}$.

*br.*1., first branchial arch; *hym.*, hyomandibular; *l. jaw*, lower jaw; *mk.*, Meckel's cartilage; *mx.*, maxillary; *pal.*, palatine; *pmx.*, præmaxillary; *ptq.*, pterygo-quadrate; *smx.*, supra-maxillary.

as a simple cartilaginous box, with a series of visceral arches all more or less similar in form. As growth proceeds, the first pair of these arches takes on the form of the jaws as seen in the Dog-fish, and these are suspended from the cranium through the intervention of the hyomandibular. Soon afterwards the cartilages are replaced by bones, these being of two kinds, cartilage bones which eat into and take the place of the original cartilage, and dermal bones which arise as entirely new structures by the deposition of lime salts in the dermal layer of the skin. It will be unnecessary to deal with the disposition and manner of development of the several bones here, nor are their technical names of great importance; for such details reference must be made to any good text-book of zoology. The chief point of interest lies in the later history of the bones developed in connection with the primitive pterygo-quadrate cartilage. These never function as an upper jaw, but, together with certain dermal bones developing in the skin of that region, form a bony palate or roof to the mouth, losing practically every trace of their original nature. These palatine and pterygoid bones are firmly united with the cranium in front, and behind are generally suspended by the hyomandibular bone, the condition being essentially the same as in the Dog-fish. The primitive lower jaw or Meckel's cartilage becomes entirely invested or surrounded by bones, but retains its mobility as well as its original function. To replace the primary one, an entirely new upper jaw has arisen in Bony Fishes, made up mainly of two bones on each side developed as dermal structures in the upper lip. These bones, which articulate with the skull in front, are known as the praemaxillary and maxillary, and the latter is sometimes provided with one or two small bones attached to its upper edge, the supramaxillaries. In the more generalised fishes the praemaxillaries are much shorter than the maxillaries, which are provided with teeth and form part of the border of the mouth (Fig. 46B). In many forms, however, the praemaxillaries nearly or quite exclude the toothless maxillaries from the gape, and the latter merely act as a kind of lever for the protrusion of the former (Fig. 65). The two praemaxillaries generally meet in the middle line, but in some species (*e.g.* the Pike) they are well separated (Fig. 46C), and in the Eels (*Apodes*) they are altogether wanting.

In a typical Bony Fish the mouth is placed at the end of the head, and the upper and lower jaws are equal in length, but this is by no means always the case, and considerable variations both in size and position are found in certain fishes. In some the mouth lies on the under side of the head, as in the Sharks, its inferior position usually being due to the forward prolongation of the forepart of the head to form a rostrum. In the Sturgeons (*Acipenser*), for example, the snout is particularly massive, varying in shape and length in the different species, and is provided with a transverse row of tentacles or barbels on its lower surface (Fig. 45B). The mouth itself is small and circular, completely devoid of teeth in the adult fish, and is capable of being protruded to a remarkable extent. The

Sturgeon feeds largely on small invertebrates, rooting up the mud or sand with its snout, feeling for the prey with its sensitive barbels, and finally sucking them up by means of its funnel-like mouth. Its diet not infrequently includes small fishes, and a large Sturgeon will rapidly engulf large numbers of "minnows" unsuspiciously engaged in depositing their spawn. The related Paddle-fish or Spoonbill (*Polyodon*), found only in the rivers of the southern states of North America, has a comparatively wide mouth armed with small teeth. The rostrum, forming no less than one-fourth of the entire length of the fish, is a thin, flat, spoon-shaped blade, the outer surface of which is more or less sensitive (Fig. 47G). This fish lives entirely on mud and the minute organisms contained therein, the snout being used for stirring purposes, whilst the food is strained from the water by the exceptionally long and close-set gill-rakers.

A mouth which is semicircular in outline and placed on the under side of the head, is characteristic of a large number of fishes habitually living in mountain streams or torrents (*cf.* p. 239). In many Indian species of the Carp tribe (*Cyprinidae*) the jaws are much strengthened, and their edges have become sharp and cutting. One fish, which lives on very fine weeds stripped from the rocks and stones of the river-beds, has the jaws encased in a strong covering of horny substance. In many of the Cat-fishes (*Siluroidea*) of these regions the mouth, together with the much modified lips, forms a broad, flat sucker by means of which the fish is able to cling to a stone or other fixed object when resting. In the Mailed Cat-fishes (*Loricariidae*) of South America the sucker-like form of the mouth is well shown, the lips being greatly enlarged, reflected outwards, spread in circular form round the mouth, and often fringed with membranous tentacles of various sizes (Fig. 45D). The mouth itself is provided with small, weak jaws, and armed with feeble teeth, the food consisting of putrifying organic substance or the minute creatures contained therein.

Apart from those cases in which they are adapted for taking part in the formation of a sucking apparatus, the lips of fishes do not exhibit many striking modifications. In the Wrasses (*Labridae*) they are particularly thick, a feature from which the German name of *Lippenfische* given to the members of this family is derived. In certain species of Cichlids (*Cichlidae*) the central portions of both upper and lower lips are prolonged to form freely projecting fleshy lobes (Fig. 47D). It is of interest to note that this peculiar modification, which may be connected in some way either with the diet or with the method of feeding, has arisen quite independently several times. Each of the large African lakes, Victoria, Nyassa, and Tanganyika, contains some hundred or so species of Cichlids which are found nowhere else, and each lake boasts a species with modified

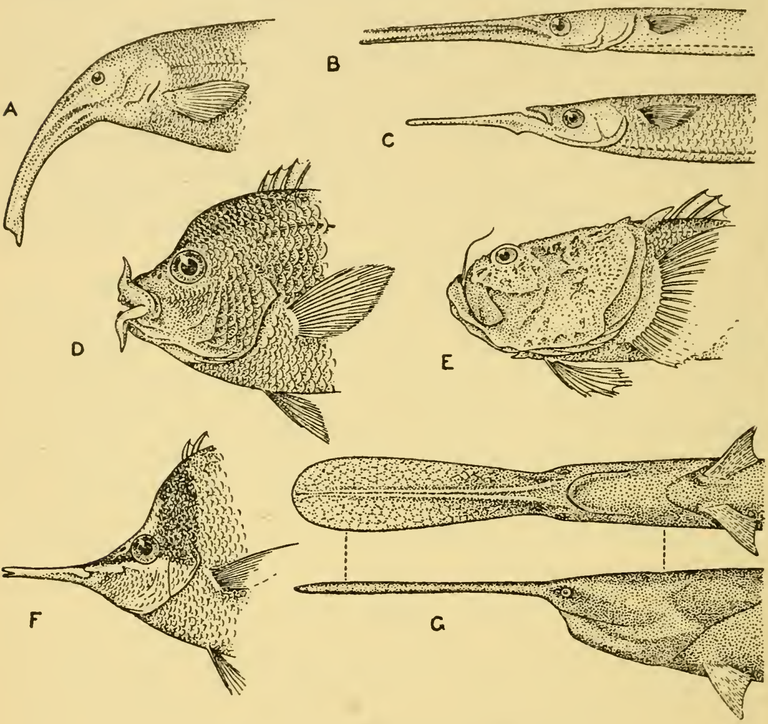


Fig. 47.—DIFFERENT KINDS OF MOUTHS.

A. Head of Elephant Mormyrid (*Gnathonemus elephas*), $\times \frac{1}{2}$; B. Of Gar-fish (*Tylosurus longirostris*), $\times \frac{1}{4}$; C. Of Half-beak (*Hemirhamphus unifasciatus*), $\times \frac{1}{2}$; D. Of Thick-lipped Mojarra (*Cichlasoma lobochilus*), $\times \frac{1}{2}$; E. Of Star-gazer (*Zaleoscopus tosae*), $\times \frac{1}{4}$; F. Of Butterfly-fish (*Chelmo longirostris*), $\times \frac{1}{2}$; G. Of Spoonbill or Paddle-fish (*Polyodon spathula*), $\times \frac{1}{4}$.

lips. The same feature occurs again in the Thick-lipped Mojarra (*Cichlasoma*) of Lake Nicaragua in Central America, and there can be little doubt that similar conditions in each case, or perhaps the adoption of similar feeding habits, has independently brought about the development of the same peculiarity in quite unrelated fishes. In many fishes the lips are highly sensitive, assisting in the search for food, and may be provided with special folds or ridges, or with numerous tiny papillae abundantly supplied with small nerves.

In the Weever-fishes (*Trachinus*) and Star-gazers (*Uranoscopus*) the lower jaw is longer than the upper and directed obliquely or even vertically upwards, so that the opening of the mouth is more or less on the *upper* surface of the head. The Weevers are fairly active fishes, but spend a good deal of time buried in the sand with only the head exposed, from which position they are able to pounce on the small fishes and crustaceans forming their normal food (Fig. 58A). It has been suggested that the brilliantly lustrous and mobile eyes of this fish serve to lure the intended meal within reach of its jaws, it being well known that fishes are attracted by shining or highly coloured objects. The Star-gazer (Fig. 47E) is a less active fish, with a stout, clumsy body and a box-shaped head, flat on its upper surface and bounded in front by the vertical lower jaw. It lacks the ability to chase and seize the small fishes on which it feeds, and, therefore, resorts to cunning to obtain a meal. A Mediterranean species is in the habit of burying itself deeply, until only the small, mobile eyes are projecting, and the upper part of the mouth-opening appears as a cleft in the sand. When thus hidden and immovable, the Star-gazer is difficult to see, having the general appearance of a brownish grey stone almost concealed by sand, its presence being betrayed only by the slight movements connected with respiration. At times it protrudes from its mouth a little red filament, which represents a membranous process of the valve of the lower jaw. This is made to move about on the sand, crawling, wriggling, contracting and expanding—in short, imitating to perfection the movements of a small worm. There can be little doubt that this serves as a bait to lure small fry within reach of the concealed jaws of the Star-gazer, and the deception is facilitated by the soft, dusky light of the shallow waters in which it usually operates. Another species from the coast of West Africa uses a broad membranous flap, gleaming white in colour, for the same purpose.

In most predaceous fishes with large mouths the bony jaws are strong structures, but in many deep-sea forms, and particularly among the members of the suborder known as "Widemouths" (*Stomiatoidea*), they are relatively feeble and even somewhat flexible (Fig. 91), although armed with a fearsome array of large, pointed teeth. These fishes prey mainly on their own kind, and it is not unusual to find a specimen which has swallowed another fish several times its own bulk. Such a meal is made possible by the mobility of the lower jaw, the two halves of which are very loosely bound together, and can be readily pulled apart in order to enlarge the gape. The Great Swallower (*Chiasmodon*), a curious deep-sea fish remotely related to the Perches, is another form with a capacity for dealing with out-sizes in meals, and here again are the same flexible and distensible jaws (Fig. 91A). Indeed, the action of swallowing is carried out, not, as is usual with fishes, by means of the muscles surrounding the gullet, but by the action of the jaws as in the snakes. Actually, they do not so much swallow the victim, as draw themselves over it. In the rare Gulpers (*Lyomeri*) of the oceanic depths the mouth is literally enormous (Fig. 91C), and both mouth-cavity and throat are capable of

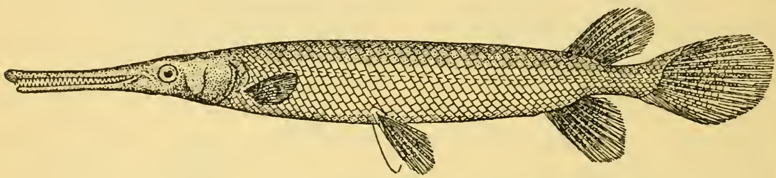


Fig. 48.

Long-nosed Gar Pike (*Lepidosteus osseus*), $\times \frac{1}{8}$.

immense distension, whilst the deep-sea Angler-fishes or Ceratoids possess similar expanding maws.

In the Gar Pike (*Lepidosteus*) of North America, and in the marine Gar-fishes (*Belonidae*) and Sauries (*Scombresocidae*), both the jaws are prolonged to form a more or less lengthy "beak," armed with sharp, unequal teeth. This is another example of convergent evolution, for in spite of the similarity of their jaws the two groups of fishes are quite unrelated. The Gar Pikes (Fig. 48) are more or less solitary feeders, and subsist largely on a diet of fresh-water crayfishes and small fishes of all kinds. The Alligator Gar Pike (*L. tristoechus*), abundant in the rivers around the Gulf of Mexico, and attaining a length of twenty feet or more, is very destructive to food fishes, and causes a great deal of damage to the nets of fishermen, who kill it without mercy. It is not even good eating itself, the flesh being rank and tough, and unfit even for dogs. If one of the Long-nosed Gar Pikes (*L. osseus*) in the tank at the Zoological Society's Aquarium be observed on the feed, it will be seen to move slowly in the direction of a group of "minnows," looking for all the world like a drifting log of wood. Placing its jaws in a suitable position, and carefully sighting its victim, the Gar gives a sudden, convulsive, sideways jerk of its head, at the same time endeavouring to grip the prey between its jaws. It seems to be possessed of infinite patience, for many are the preliminary manœuvres and tentative snaps before the body of the little fish is finally transfixed by the teeth. When this is accomplished the victim is gradually worked round into a convenient position, and unless it has again escaped during this process, is finally swallowed, generally head first.

The Gar-fishes (Fig. 47B) and Sauries, on the other hand, are equally voracious, but feed in large shoals, pursuing and capturing their prey whilst skimming along at the surface of the water, frequently transfixing the eyes or bodies of smaller fishes with their ram-like "beaks." Small fishes form the main item in their diet, but almost any animal substance is eaten. Some of the larger species of Gar-fish, perhaps five or six feet in length, may even be dangerous to man. The well-known Skipper or Saury (*Scombresox saurus*) of our own south-western coasts is an avowed enemy of the Pilchard, and should the two fishes be enclosed in the same net great damage is done to the "catch."

In the curious Half-beaks or Balaos (*Hemirhamphidae*), related to the Gar-fishes and found in all tropical seas, only the lower jaw is produced, and forms a long, spear-like projection, to which a bright red membrane is usually attached (Fig. 47C). The teeth are minute and the diet is purely a vegetable one, consisting largely of green seaweed. It is of interest to note here that in both the Gar-fishes and Half-beaks the jaws are of equal length and are not drawn out in the young. In the young Gar-fish the jaws soon begin to lengthen, and for a time the lower jaw is longer than the upper, and the little fish resembles a Half-beak. The upper jaw soon increases further in length, however, and in the adult fish is longer than the lower (*cf.* p. 336).

In the grotesque Snipe Eels (*Nemichthyidae*) both the jaws are prolonged and not infrequently curved in opposite directions, the one upwards, the other downwards (Fig. 32G).

In the tribe of Sword-fishes (*Xiphiidae*), Spear-fishes, and Sail-fishes (*Istiophoridae*) only the upper jaw is prolonged, forming in the first named a long, flattened, sword-like weapon, and in the others a rounded, tapering spear of varying length

(Fig. 6). The teeth in the jaws are small and numerous, extending forward on to the lower surface of the sword. The Common Sword-fish (*Xiphias*) is widely distributed in all warm seas, and grows to a length of fifteen to twenty feet. Its food seems to consist largely of fishes, and it is said to split large forms like the Bonito and Albacore with the sword, or to strike with lateral movements among a shoal of small fishes, afterwards devouring the stunned and wounded victims. Instances of men being attacked and wounded have been recorded, and in Daniel's *Rural Sports* it is stated that "in the Severn near Worcester, a man bathing was struck and absolutely received his death wound from a Sword-fish." Many are the tales told of ships damaged or even sunk by the attacks of these fishes, but in most of the stories no attempt has been made to discriminate between Sword-fishes, Spear-fishes, and Sail-fishes, all of which have similar habits. There can be no doubt that they sometimes succeed in piercing the bottom of a boat, and, being unable to carry out the necessary reversing movements, are compelled to break off the sword in order to get away. In the museum of the College of Surgeons is a section of the bow of a whaler in which is impaled a sword a foot in length and five inches in circumference, which had penetrated through thirteen and a half inches of wood; in another specimen of ship's timber in the British Museum the transfixed sword has been thrust through no less than twenty-two inches. Another case on record concerns the ship *Dreadnought*, which suddenly sprang a leak on its voyage from Ceylon to London, and on examination it was found that a hole about an inch in diameter had been neatly punched in the copper sheathing of the vessel. When a claim was duly made, the insurance company denied their liability, holding that the damage had been caused by some agent other than a fish, but when the case was taken to court the jury returned a verdict that the damage had been brought about "by contact with some substance other than water," and added a rider that it was probably caused by a Sword-fish. It is open to grave doubt, however, whether these attacks on ships are deliberate, although it is freely stated that, since Sword-fishes have been described as attacking Whales in company with Killers, the fish merely mistakes the ship for a Whale. It seems more probable that the occurrences are no more premeditated than, say, a head-on collision between two powerful motor-cars, and may be due to similar causes, namely, an inability to apply the brakes in time. It has even been suggested that the sword has not been evolved as a weapon at all, but merely represents an extreme case of stream-lining, the pointed rostrum acting as an efficient cutwater.

In some fishes the anterior part of the head is drawn out, but the mouth itself remains small and is placed at the extremity of a long, tube-like beak. Among the Mormyrids (*Mormyridae*) of the fresh waters of Africa, for example, a number of diverse modifications of the snout are encountered. In the Elephant Mormyrid (*Gnathonemus*) this takes the form of a curved, trunk-like structure, at the tip of which is the tiny mouth armed with few but relatively large teeth (Fig. 47A). This remarkable appendage is used for inserting between stones or into the mud in search of small crustaceans and the like which form the principal food. These fishes live mostly in more or less muddy water, and the eyes are consequently small and often much degenerated. In some species the lower lip is provided with a fleshy mental appendage, which may be globular in shape or take the form of a membranous tassel; this is sensitive, and acts as an organ of touch, aiding in the search for food and compensating for the imperfect vision. Similar modifications of the snout and jaws are found among the Gymnotids of South America. In the tribe of Butterfly-fishes (*Chaetodontidae*), nearly all inhabitants of coral reefs, many of the species have the mouth placed at the end of a straight, tubular snout, and this is used for poking into crevices and holes in the coral in search of prey (Fig. 47F).

The members of the large and varied order of Tube-mouths (*Solenichthyes*) all agree in having the snout prolonged to form a rigid tube-like "beak," with a small mouth at its extremity (Fig. 49A). The jaws themselves are quite short, and in order that they may be articulated with the hinder part of the skull in the usual manner the suspensory part of the hyoid arch, the hyomandibular bone, is drawn out into a long, rod-like structure. The Trumpet-fishes (*Fistulariidae*) and their allies have some minute teeth in the mouth, but these are wanting in all the other members of the order. The Pipe-fishes (*Syngnathidae*) live almost entirely on small crustaceans, and when searching for food they swim about slowly in a most curious manner, holding the body now in a vertical and now in a horizontal position, and indulging in wriggles and contortions of every conceivable kind. The head is in constant movement, the long snout being poked into clumps of vegetation or into any other situation

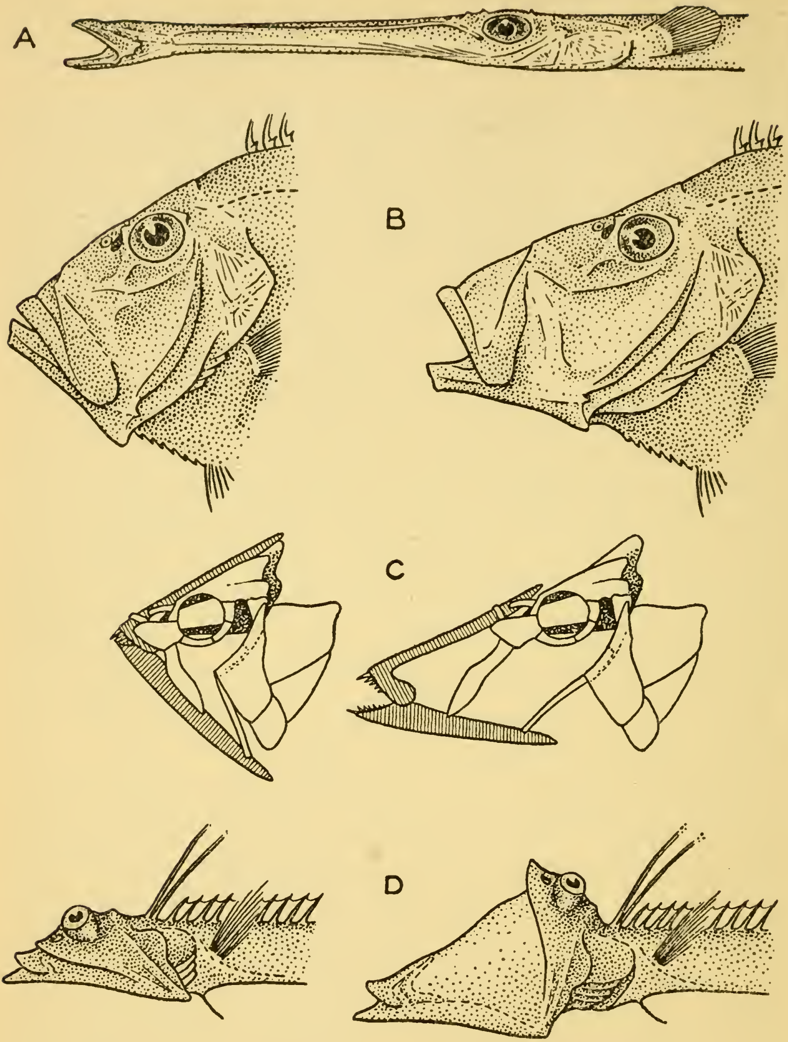


Fig. 49.

A. Head of Flute-mouth or Tobacco-pipe Fish (*Fistularia tabacaria*), × $\frac{1}{6}$; B. Head of John Dory (*Zeus faber*), with the mouth retracted and protruded, × $\frac{1}{3}$; C. Skull of Large-mouthed Wrasse (*Epibulus insidiator*), with the jaws retracted and protruded, × $\frac{1}{3}$; D. Head of *Stylophorus chordatus*, with the mouth retracted and protruded, × $\frac{3}{4}$.

where the prey is likely to be encountered. The actual manner of feeding is remarkable, the tube-like "beak" acting as a kind of syringe, the prey being drawn in rapidly by inflating the cheeks. The Sea Horses (*Hippocampus*) have a similar diet, which seems to be obtained in a like manner. The fish will approach a small crustacean in a leisurely manner, peer at it for a second or two, and then, having placed its snout in a convenient position, suddenly engulf the meal.

In a number of fishes the mouth is described as protractile; that is to say, it can be protruded or withdrawn at will. In the Sturgeon (*Acipenser*) the funnel-like mouth is thrust downward by a forward or backward swing of the suspensory bones of the hyoid arch, but in most other fishes the protrusion is accomplished by the praemaxillaries of the upper jaw sliding on certain bones of the front part of the skull, the small maxillaries acting after the manner of levers. In many members of the Carp tribe (*Cyprinidae*) the mouth is especially protractile, and in the Bream (*Abramis*), for example, forms a sort of tube when protruded. The John Dory (*Zeus*), with its large and very protractile mouth and mournful expression, has an interesting method of hunting the small fishes on which it feeds. Its deep and clumsy body is unsuited for chasing prey, but when swimming upright in mid-water its excessive thinness makes it quite inconspicuous, and when placed end-on towards the victim it is almost invisible and excites no alarm. In this way it is able to approach gradually until within striking distance, when the jaws are shot forward with great rapidity (Fig. 49B). During the preliminary manœuvres the whole attitude of the Dory is one of suppressed excitement, and the eyes are kept fixed intently on the prospective victim. Among the Wrasses, one tropical form known as *Epibulus* has the mouth even more protrusible than that of the John Dory. In the latter only the upper jaw is thrust forward, but in *Epibulus* the lower jaw is also moved, the bone to which it is articulated being long and movable, a condition quite unlike that of the other Wrasses in which it is quite short and firmly fixed (Fig. 49C).

The order of fishes (*Allotriognathi*), including the Opah (*Lampris*), Deal-fish (*Trachypterus*), and Ribbon-fish (*Regalecus*) contains some strange and very diverse forms, but all agree in the mechanism of the jaws. In other fishes with protractile mouths only the end of the maxillary bone moves forward when the mouth is opened, the other end being fixed, but in the members of this group the maxillary of each side is thrust forward as a whole, the movement of the lower jaw pulling it away from the head. Included in the same order is a remarkable deep-sea fish to which the name of *Stylophorus* (referring to the whip-like prolongation of the lower lobe of the caudal fin) is applied. This fish was first described in 1791, but it is only in recent years that the discovery of well-preserved specimens has made it possible to elucidate its anatomy. The mouth is extraordinarily protractile, and when protruded appears at the end of a long funnel-like pouch (Fig. 49D). A point of particular interest lies in the fact that the different parts of the jaws are so arranged that in order to thrust the mouth forward the fish must throw the head upwards and backwards. "We may imagine this little fish," writes Dr. Regan, "not more than twelve inches long, swimming in the Atlantic two or three hundred fathoms below the surface, peering ahead into the semi-darkness, and stealthily approaching its prey, which must be quite small, accurately judging when it is within striking distance, and then suddenly throwing back its head and thrusting out its mouth to effect the capture."

Among the Flat-fishes the characteristic asymmetry is extended to the mouth and jaws in many forms. In *Psettodes*, the most primitive member of the group, the jaws are more or less of the same size, and the teeth almost equally developed on the coloured and on the blind side. The same condition is found in the Halibut (*Hippoglossus*) and in certain other species, which are in the habit of leaving the bottom and swimming strongly in active pursuit of other fishes. In other forms, however, of which the Plaice (*Pleuronectes*) and the Dab (*Limanda*) will serve as examples, the mouth is much twisted, being more developed and armed with a greater number of teeth on the lower or blind side. This modification is connected with different habits, these fishes being less active, keeping constantly at or near the bottom, and feeding mainly on shell-fish and other ground-living invertebrates. In the Soles (*Soleidae*) and Tongue Soles (*Cynoglossidae*), which are even more specialised, the jaws and teeth are extremely feeble on the upper side of the fish, and the mouth is twisted almost completely on to the under surface. The Sole (*Solea*) is a retiring fish, burrowing into the sand and seldom moving, except at night. It is provided with special sensory organs on the lower surface of the head, and, according to Dr. Cunningham, hunts for worms or shrimps by tapping the ground gently with the side of its head, biting with the lower corner of its mouth. A study of the early development of these fishes reveals the fact that they commence life with normal symmetrical mouths, but that soon after the larva is hatched the jaws become twisted towards the future blind side.

CHAPTER VII

TEETH AND FOOD

Teeth of Cyclostomes and Selachians. Succession of teeth in Sharks and Rays. Different kinds of Shark dentition. Man-eating Sharks. Thresher Shark. Nurse Sharks and Bull-headed Sharks. Teeth of Rays. Dentition of Chimaeras. Teeth of Bony Fishes. Pharyngeal teeth. Depressible teeth. Feeding habits of Pike, Caribe or Piraya, Blue-fish, Lancet-fish, Barracuda. Canine teeth: *Chauliodus, Cynodon.* Dentition in fishes with mixed diet. Archer-fish. Plankton feeders. Wrasses. Parrot-fishes and Plectognaths. Cyprinids. Stromateoids. Unusual meals. A remarkable "Shark story."

The mouths of Cyclostomes are armed with horny, tooth-like structures, but are devoid of true teeth. The inner surface of the funnel-shaped mouth of the Lamprey (*Petromyzon*) is studded with conical yellow "teeth," and at its centre, placed above and below, are two horny plates with jagged edges, formed by the enlargement and fusion of several smaller teeth (Fig. 45A). Similar plates are found on the muscular protrusible tongue, which works like a piston and rasps off the flesh of the fishes on which the Lamprey preys. In the Hag-fishes (*Myxinidae*) the tongue is very powerful, and, apart from a single tooth on the roof of the mouth, the comb-like lingual plates represent the only dental armature. When worn out, the teeth of the Cyclostomes are replaced by new ones developing beneath those actually in use.

Certain problematical fossils known as Conodonts from the Cambrian, Silurian, and Devonian rocks have been regarded by some authorities as the lingual teeth of extinct Lampreys, but they are of a very different structure, and may not belong to vertebrate animals at all.

It has been remarked (*cf.* p. 86) that the teeth of Selachian fishes are essentially similar, both in structure and mode of development, to the dermal denticles covering the body, and a study of an unhatched embryo of a Dog-fish provides undeniable evidence in support of this statement. The outer skin is continued over the edges into the cavity of the mouth itself, and the close-set, spiny denticles form a continuous undifferentiated series (Fig. 50A). It is only as growth proceeds and the lips are formed that this continuity is broken, the denticles in the region of the jaws becoming enlarged and taking on the distinctive characters of teeth, while those on the outside of the body remain more or less unchanged. As in the case of the denticles already described, each tooth consists mainly of a bony substance known as dentine, with an internal pulp cavity and an outer covering of enamel. Thus, the teeth

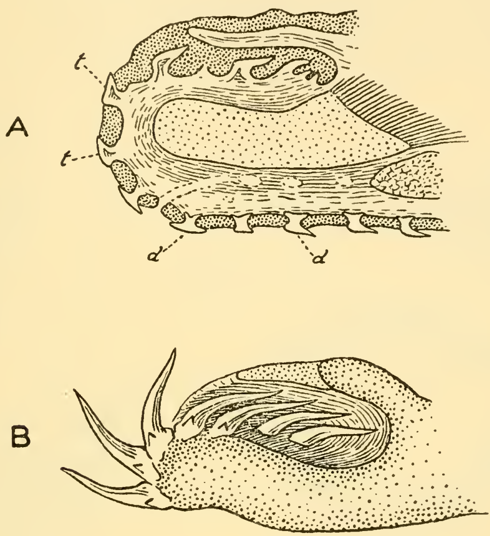


Fig. 50.

A. Cross-section through the lower jaw of an embryo Spotted Dog-fish (*Scyliorhinus sp.*), showing the gradual transition from dermal denticles (*d*) on the outer surface to teeth (*t*) on the inner surface. The dotted area in the centre represents the cartilage of the lower jaw. Greatly enlarged. (After Gegenbaur); B. Cross-section through the lower jaw of Sand Shark (*Odontaspis taurus*), showing succession of teeth, $\times \frac{1}{2}$.

of all fishes, and indeed of all higher vertebrates, including man himself, owe their origin to the modification of the dermal armour of the skin, and the teeth are to be found in their simplest form in the Selachians.

There is no firm attachment of the teeth to the jaws in these fishes, and they are simply embedded in the gums. Nor does a Shark or Ray retain the same teeth throughout the greater part of its life, but as those in use become worn and useless they are replaced by new ones. An examination of the mouth of a Sand Shark (*Odontaspis*) reveals the fact that there is more than one row of teeth in each jaw, but, whilst those of the row in actual use stand erect on the edge of the jaw, the others lie flat against its inner surface (Figs. 50B; 51A). These reserves lie in a shallow cavity closed by membrane, the rows packed closely together one upon the other, those of the lower jaw with the points directed downwards, those of the upper jaw in the opposite direction. A closer study of these teeth shows that they are in different stages of development, those of the row nearest to the edge of the jaw being most perfect. As the

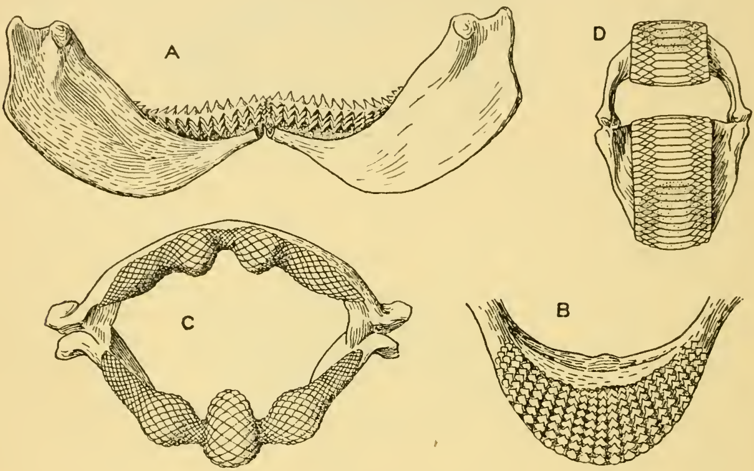


Fig. 51.—TEETH OF SHARKS AND RAYS.

A. Inner view of lower jaw of Blue Shark (*Carcharinus dussumieri*), $\times \frac{1}{4}$; B. Lower jaw of Nurse Shark (*Ginglymostoma sp.*), $\times \frac{1}{4}$; C. Jaws of Guitar-fish (*Rhina ancylostoma*), $\times \frac{1}{6}$; D. Jaws of Eagle Ray (*Myliobatis aquila*), $\times \frac{1}{4}$.

functional teeth are lost those of the next series move upward, and the whole phalanx is thus constantly marching onward throughout life, a row of teeth doing duty for a time, only to be duly cast off in its turn and replaced by its successor. In certain Sharks and Rays several series of teeth are in use at the same time (Fig. 51B-D), but the replacement takes place in exactly the same manner.

In size and form the teeth of Sharks exhibit great diversity, ranging from long, slender, awl-like structures to large, flat, triangular teeth (Fig. 52). Not infrequently the teeth of the upper jaw are quite unlike those of the lower, and different types of teeth may occur in the same jaw. In the primitive Comb-toothed Sharks (*Hexanchidae*) the teeth of the upper jaw are for the most part provided with a large central cusp or point with several smaller cusps on either side, but in the lower jaw each consists of several pointed cusps, graduated in size, all inclined in the same direction, and supported on a long basal plate (Fig. 52c). Teeth with three or more cusps probably owe their origin to the fusion of several of the primitive single teeth. In certain Sharks the denticles covering the body tend to be aggregated together in groups, perhaps three in a row, forming a plate armed with a like number of spines, and it seems likely that similar fusions have taken place in the jaws, but always of denticles lying side by side. In the Great White Shark or Man-eater (*Carcharodon*), one of the most formidable of all the Sharks, the teeth are very powerful, flattened, triangular in shape, and with the edges finely serrated (Fig. 52a). This Shark grows to a length of about thirty feet, but, judging from the large size of some fossil teeth of a similar kind which have been discovered, Man-eaters of truly colossal size must have inhabited the seas in past times. A tooth six inches in length must have belonged to a Shark at least ninety feet long, and such monsters probably survived until comparatively recent times, for the *Challenger* Expedition dredged some of their teeth from the bed of the Pacific Ocean. The Tiger Shark (*Galeocerdo*), another large species found in nearly all warm seas, has teeth of a very peculiar shape, each one being flat and sickle-shaped, with a fluted edge suggesting that of a patent bread-knife, and with a triangular point at the summit which projects obliquely outward (Fig. 52b).

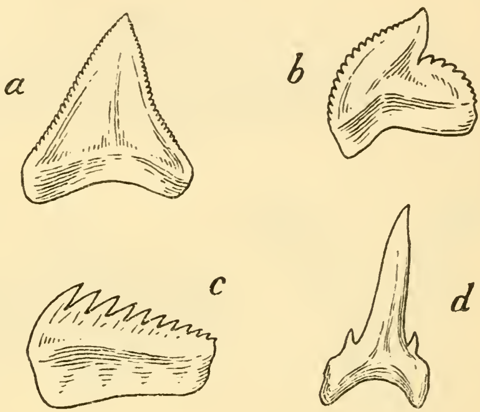


Fig. 52.—SHARK TEETH.

a. Tooth of Great White Shark or Man-eater (*Carcharodon rondeleti*), $\times \frac{1}{3}$; b. Of Tiger Shark (*Galeocerdo tigrinus*), $\times \frac{2}{3}$; c. Of Comb-toothed Shark (*Hexanchus griseus*), $\times \frac{2}{3}$; d. Of Sand Shark (*Odontaspis taurus*), $\times \frac{2}{3}$.

So characteristic is the form of the teeth in many Sharks that it is often possible to identify a species from one or two teeth alone, and in the case of many extinct forms these are the only parts of the fish which remain, all the rest of the skeleton having disappeared. Further, in those species in which the dentition is of more than one type, it is possible to state whether a certain fossil tooth belonged to the upper or the lower jaw, and whether it occurred in the front or at the side of the jaw. The curious Elfin or Goblin Shark (*Scapanorhynchus*) was first known from some teeth occurring in Upper Cretaceous strata, but a living specimen of this supposedly extinct form was

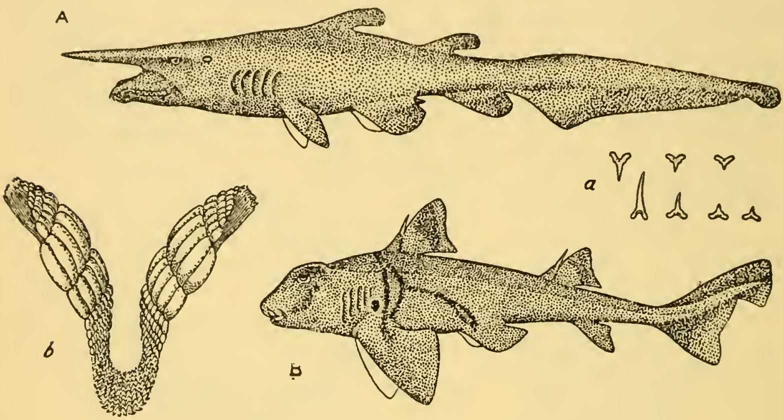


Fig. 53.—ELFIN AND PORT JACKSON SHARKS.
A. Elfin or Goblin Shark (*Scapanorhynchus owstoni*), $\times \frac{1}{30}$ (*a*, isolated teeth of same); B. Port Jackson Shark (*Heterodontus phillippi*), $\times \frac{1}{20}$ (*b*, lower jaw of same).

found off the coast of Japan in 1898. It is remarkable for the long, blade-like snout, separated from the jaws by a deep cleft, and the teeth are of a characteristic pattern (Fig. 53A, *a*). Recently the known distribution of the species was further extended in an interesting manner. A "break" occurred in one of the deep-sea telegraph cables lying at a depth of 750 fathoms in the Indian Ocean, and on its being brought to the surface the damage was found to have been caused by a fish which had left one of its teeth embedded in the cable; this tooth, which had broken off short, was identified as belonging to an Elfin Shark.

All the Sharks so far mentioned are active predaceous forms, and although they feed mainly on other fishes, the diet is sometimes more mixed. Porpoises, water birds, turtles, pieces of other sharks, crabs, and fishes of all kinds have been taken from the stomachs of Tiger Sharks, and Professor Jordan has described a Man-eater (*Carcharodon*) with a good-sized Sea Lion in its stomach. The Hammer-headed Shark (*Sphyrna*), which seems to feed almost entirely on other fishes, includes the fearsome Sting Ray (*Trygon*) in its diet. A specimen which had been feeding on these Rays was afterwards captured, and, in addition to the half-digested remains in the stomach, no less than fifty "stings" (the serrated tail-spines) were found embedded in different parts of the Shark's anatomy, and particularly in the region of the mouth and throat.

According to Linnaeus, the famous Swedish naturalist, it was the Man-eater Shark that swallowed the prophet Jonah, but this is only one of the many animals which have been credited with this feat. "Jonam Prophetum," he writes, "ut veteris Herculem trinoctem, in hujus ventriculo tridui spateo baesisse, verosimile est." The question as to whether or no Sharks will attack and devour man is one which has been much debated. Most Sharks eat only living food, but not a few will turn scavenger at times, often following a ship for days in the hope of food being thrown overboard. Human corpses which have been partially eaten by Sharks after death must be responsible for a good many of the tales of men killed by these creatures. It is a popular fallacy that all fierce-looking sharks are "man-eaters," but as a matter of fact very few can be definitely proved guilty of this practice. It is true that authentic cases are on record in which a large Man-eater or Blue Shark has attacked and even killed a man, but it is fairly certain that this was because he happened to be handy, as it were, and the Shark more than usually hungry. The common statement that a man's leg was bitten off by a Shark "as though it were a carrot," betrays a complete ignorance of the strength of the apparatus required to perform such an amputation. As Dr. Lucas remarks: "The next time the reader carves a leg of lamb, let him speculate on the power required to sever this at one stroke—and the bones of a sheep are much lighter than those of a man." Statements that men have been cut in two "at a single bite" are equally absurd.

Most Sharks appear to chase and seize their prey as occasion offers, and in a more or less haphazard manner, but some may employ more systematic methods. The Sand Shark (*Odontaspis*), for example, a species common on the Atlantic coast of North

America, has been described as operating in shoals, forcing a school of Blue-fishes into a solid mass in shallow water, before rushing in and seizing the prey. The Thresher or Fox Shark (*Alopias*) feeds largely on Herrings, Pilchards, and Mackerel. It swims round and round a shoal of these fishes, thrashing the water with its long tail (Fig. 32A) and thus driving the prospective victims into a compact mass, when they form an easy prey. A Thresher feeding in shallow water on the coast of Carolina has been described as "throwing the fish to its mouth with its tail, and . . . one fish, which it failed to seize, was thrown a considerable distance clear of the water." Sometimes a pair of Sharks work together at this organised fishing.

In the Nurse Sharks (*Ginglymostoma*) and the Hounds (*Mustelus*), which include in their diet a large percentage of shell-fish and crustaceans in addition to smaller fishes, there is a different kind of dentition. The teeth are small, pointed or flattened, and adapted for grinding and crushing rather than for cutting. They are arranged in pavement fashion, and all or most of the rows are in use at the same time (Fig. 51B). These are comparatively sluggish Sharks, feeding for the most part at or near the bottom of the sea. The Port Jackson Shark (*Heterodontus*), a member of the family of Bull-headed Sharks (Fig. 53B), has a remarkable dentition, and provides an example of a form with more than one type of tooth in the same jaw. The teeth in the front of the jaws are like small cones, but farther back these gradually pass into teeth which have the form of "pads" or nodules of varying size (Fig. 53B). As might be supposed, this curious dentition is used for grinding and crushing purposes, the food consisting almost entirely of shell-fish.

In the Guitar-fishes (*Rhinobatidae*), Saw-fishes (*Pristidae*), Rays (*Raiidae*), Sting Rays (*Trygonidae*), and their allies, the teeth are nearly always small, generally blunt, and arranged in pavement fashion with several rows in use at once. Being ground-feeders the food generally includes a high percentage of molluscs, crustaceans, and other armoured creatures like the sea-urchins, so that the dentition is of the crushing and grinding type. In one of the Guitar-fishes, known as *Rhina*, the tooth-covered jaws present a curious shape, the upper jaw being alternately hollowed and swollen, and the lower being provided with corresponding bumps and depressions to fit into the upper jaw (Fig. 51C). In an allied form (*Rhynchobatus*) the jaws are much less wavy in outline, a single swelling in the lower jaw fitting into an indentation in the upper, whilst in the more typical Guitar-fishes (*Rhinobatus*) the mouth forms a straight horizontal slit. In some of the Rays and Skates, of which the common Thornback Ray (*Raia clavata*) will serve as an example, the teeth are actually different in the two sexes, those of the male being pointed and those of the female flat. It has been argued that this difference in the form of the teeth indicates a corresponding difference in the food or some sort of co-operation between the sexes in procuring it, but this is purely supposition and is not supported by any evidence.

The dentition of the Eagle Ray (*Myliobatis*) is very specialised, the teeth being quite flat and arranged like paving stones in the form of a mosaic work, those in the centre of the jaws having the form of long hexagonal bars, and those at the sides being much smaller but also six-sided (Fig. 51D). In the large Spotted Eagle Ray (*Aetobatis*) these side teeth are wanting, and the dentition consists of a single row of long bars arranged one behind the other from before backwards in each jaw. The food seems to consist almost entirely of oysters and clams, and the crushing power of the jaws is truly remarkable. "I have found in these Rays," writes Mr. Coles, "clams which with their shells on must have weighed more than three pounds, and to crack which a pressure of perhaps a thousand pounds would be required." In the Sea Devils (*Mobulidae*), on the other hand, with their fish diet, the teeth are very small, numerous, and have the form of flat tubercles.

The Chimaeras (*Holocephali*), although allied to the Sharks and Rays, present a totally different dentition. Instead of the ordinary teeth, the jaws are armed with three pairs, two above and one below, of large flat plates, studded with hardened points or "tritors" (Fig. 56A). In one or two species these points are absent, and the tooth plates bear a marked resemblance to the horny "beaks" of turtles. With such a specialised dentition one might reasonably expect the food to be of a very definite nature, but actually the diet is a very mixed one and ranges from seaweeds to other fishes, including also worms, echinoderms, molluscs, and crustaceans. They are themselves preyed upon by other fishes, adult Chimaeras being found in the stomachs of Greenland Sharks, and the young are eaten in large numbers by the Cod and its allies.

In the Selachians teeth are developed only in the jaws, but in the Bony Fishes they may be present on the tongue, on the roof of the mouth, or in the throat. The arrangement may be quite irregular, or they may be placed in one or more regular rows parallel with the edges of the jaws, or in rather broad bands or patches (Fig. 46C). All the teeth are, as a rule, more firmly attached than those of the Selachians, although in certain fishes some or all of them are freely movable. Very rarely, as in certain Characins (*Characidae*, etc.), and in the File-fish (*Monacanthus*) and Trigger-fish (*Balistes*), they are implanted in sockets in the bone. The succession is much more irregular, new teeth being formed at the bases of the old ones or in the spaces between them. In size and form they present an extraordinary diversity, the type of dentition being intimately associated with the nature of the food.

The teeth on the tongue (lingual teeth) are borne by the lower elements of the hyoid arch, whilst those inside the mouth are connected with the bones of the primitive upper jaw (*i.e.* the paired palatines and pterygoids) and with certain other bones developed beneath the floor of the cranium (Fig. 46C). The pharyngeal or gill-teeth in the throat are connected with the inner margins of the branchial arches. As a rule, the lower ones are borne on a pair of bones known as the lower pharyngeals, lying behind and parallel with the lower limbs of the last arch, and representing the remains of a once complete branchial arch (Fig. 54B). The upper pharyngeals are toothed bones representing the upper elements of the preceding arches. In a number of Bony Fishes the lower pharyngeals are united to form a single plate-like bone, often of characteristic form (Fig. 54A). In the majority of cases the pharyngeal dentition may be said to be inversely proportional to the extent of tooth development in the jaws; that is to say, if the jaws are strongly armed with teeth the pharyngeal teeth are feeble or absent, and *vice versa*.

A large number of Bony Fishes are piscivorous (fish-eaters), the stronger preying on their weaker brethren. The teeth of such fishes are generally strong, and may be acutely pointed as in the Cod (*Gadus*), Perch (*Perca*), and Bass (*Morone*), serving not only to seize but also to tear and dismember the prey. The Pike (*Esox*) has a large mouth which fairly bristles with teeth, those on the praemaxillaries being small, while those on the sides of the lower jaw are strong and erect, being used for seizing the victims; those on the roof of the mouth are slender and pointed, arranged in three parallel bands, and instead of being firmly joined to the bones are attached thereto by fibrous or elastic ligaments (Fig. 46C). These teeth on the palate are directed backwards towards the gullet, and can be depressed in order to facilitate the entrance of the prey; at the same time, however, as they cannot be pressed in the opposite direction, they effectively prevent any chance of escape. Similar depressible teeth are found in the Angler-fish or Fishing Frog (*Lophius*), and in many of the deep-sea forms, such as the Ceratioid Anglers, Wide-mouths (*Stomiatoidea*), Gulpers (*Lyomeri*), etc., which habitually seize and devour fishes larger than themselves (Figs. 31, 91). In a few of these creatures the teeth are even luminous, although the advantage to the fish in thus exhibiting its formidable dentition is a little doubtful. The Pike is almost unsurpassed in greediness and ferocity, and

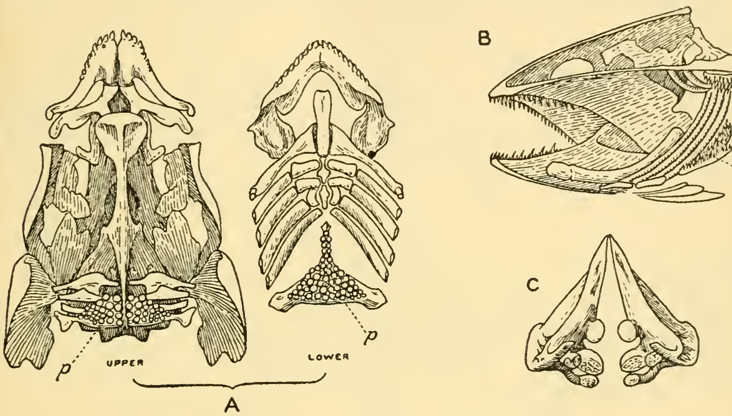


Fig. 54.—PHARYNGEAL TEETH.

A. Ventral view of skull and dorsal view of hyo-branchial skeleton and lower jaw of Wrasse (*Labrus sp*.), showing position of pharyngeal bones, $\times \frac{1}{2}$; B. Vertical section of skull of Bow-fin (*Amia calva*), showing position of pharyngeals, $\times \frac{1}{4}$; C. Lower pharyngeals of Carp (*Cyprinus carpio*), $\times \frac{1}{2}$.

when on the feed nothing comes amiss to its insatiable maw. It has been estimated that a Pike will consume in a single day its own weight of food, so great is its appetite and so rapid its digestion. Fishes are its normal diet, and these are seized crosswise and swallowed head first. Its method of feeding is to lurk within a clump of vegetation, or to lie motionless in the water looking like a moss-covered log. As soon as a victim comes within reach he is overwhelmed with a sudden rush and disappears in a smother of foam. Water-birds, frogs, and voles are also devoured, and instances are on record of human beings being attacked by hungry Pike. Cases of cannibalism are by no means rare, the Pike being one of the few fishes which will habitually devour its younger or weaker brethren. Trout are not above eating their own young, but, as a general rule, a fish may be said to be safe from the members of its own species. The Coal-fish (*Gadus virens*) has been observed to feed on the fry of the Cod, a closely related species. According to Professor Sars, "they surround the fry on all sides, and by drawing the circle closer and closer they drive them into a dense mass, which they then proceed by a sudden manœuvre to chase upwards towards the surface." The wretched fry then find themselves attacked from above and below by the voracious Coal-fishes and by hordes of screaming sea birds.

Another fish which is renowned for its ferocity is the Caribe

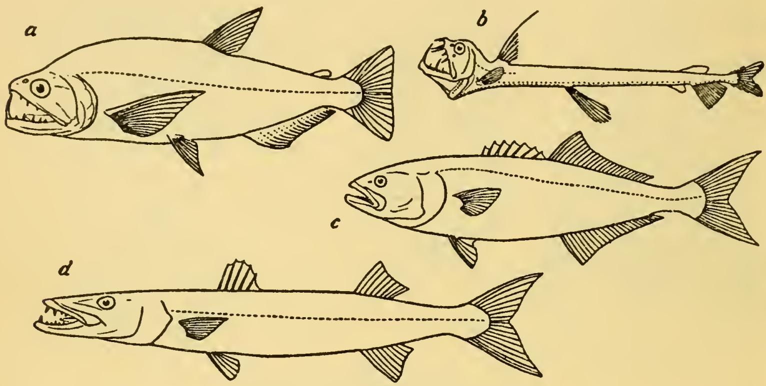


Fig. 55.—CARNIVOROUS FISHES.

a. *Cynodon scomberoides*, $\times\frac{1}{8}$; b. *Chauliodus sloanei*, $\times\frac{1}{5}$; c. Blue-fish (*Pomatomus saltatrix*), $\times\frac{1}{8}$; d. Barracuda (*Sphyraena barracuda*), $\times\frac{1}{5}$.

or Piraya (*Serrasalmus*) of the rivers of South America, a truly ugly-looking creature with a deep, blunt head with remarkably short and powerful jaws, armed with sharp cutting teeth (Fig. 56c). They are encountered in swarms, and are able to cut off a mouthful of flesh as cleanly as with a pair of scissors. Their normal diet consists of smaller fishes, but any animal unlucky enough to fall into the water where they abound is immediately attacked and cut to pieces in an incredibly short time, the smell of blood attracting them in their hundreds. Human beings bathing or wading in the rivers have been attacked and severely bitten or even killed by these ferocious pests, and a case is on record in which a man and his horse who fell into the water were subsequently discovered with all the flesh neatly picked off the bones, although the man's clothes were undamaged. They do not attain to any great size, the largest scarcely exceeding a length of two feet, but their lack of inches is amply made up for by their voracity, fearlessness, and numbers.

For sheer ferocity and cold-blooded, murderous habits the Blue-fish (*Pomatomus*), a silvery blue-backed fish, not unlike the Bass in appearance, is probably unique (Fig. 55c). This species is found in the warmer parts of the Atlantic, swimming

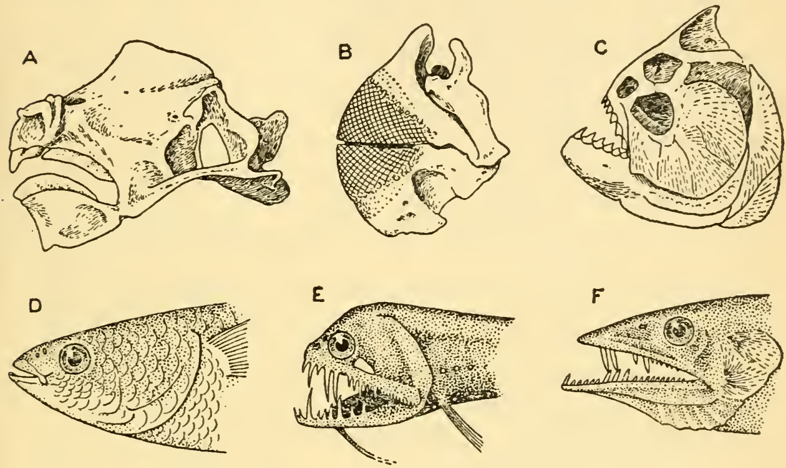


Fig. 56.—JAWS AND TEETH.

A. Skull of Rabbit-fish (*Chimaera monstrosa*), $\times \frac{1}{3}$; B. Jaws of Parrot-fish (*Pseudoscarus sp.*), $\times \frac{1}{4}$; C. Skull of Caribe or Piraya (*Serrasalmus ternetzi*), $\times \frac{1}{4}$; D. Head of Grey Mullet (*Mugil auratus*), $\times \frac{1}{2}$; E. Head of Wide-mouth (*Haplostomias tentaculatus*), $\times \frac{1}{2}$; F. Head of Lancet-fish (*Alepidosaurus ferox*), $\times \frac{1}{4}$.

in large companies near the surface, and reaches a weight of fifteen pounds. "The Blue-fish has been well likened to an animated chopping machine," observes Professor Baird, "the business of which is to cut to pieces and otherwise destroy as many fish as possible in a given space of time. . . . Going in large schools in pursuit of fish not much inferior to themselves in size, they move along like a pack of hungry wolves, destroying everything before them. Their trail is marked by fragments of fish and by the stain of blood in the sea, as, where the fish is too large to be swallowed entire, the hinder portion will be bitten off and the anterior part allowed to float away or sink.

It is even maintained with great earnestness that such is the gluttony of this fish, that when the stomach becomes full the contents are disgorged and then again filled." It has been estimated that as many as one thousand million of Blue-fishes occurs annually in the summer season on the Atlantic coasts of the United States, and, allowing a ration of ten fish per day to each Blue-fish, no less than 10,000,000,000 fish are thus destroyed each day, whilst about 1,200,000,000,000,000 are accounted for in a season lasting only one hundred and twenty days. This estimate applies only to adult fish, and if we take into account the young Blue-fishes, which vie with their parents in the work of butchery, the total will be very much greater. They seem to pay particular attention to the Menhaden (*Brevoortia*), sometimes driving shoals of them to the shore where they may be seen piled up in rows.

Among other ferocious fishes may be mentioned the Lancet-fish (*Alepidosaurus*), found in the depths of the oceans, a swift, scaleless fish with powerful jaws armed with knife-like teeth (Fig. 56F). A specimen has been described from the stomach of which was taken "several octopods, crustaceans, ascidians, a young *Brama*, twelve young Boar-fishes (*Capros*), a Horse Mackerel, and one young of its own species." Another one from Alaska had no less than twenty-one Lump Suckers (*Cyclopterus*) in its stomach. In spite of its small size, the ubiquitous Stickleback (*Gasterosteus*) is remarkably bold and greedy, being especially destructive to the spawn and young fry of other fishes. In five hours a single Stickleback is said to have devoured seventy-four young Dace, each about a quarter of an inch long, and two days afterwards it swallowed sixty-two.

Other fish-eaters, such as the well-known Barracudas (*Sphyraena*), have the powerful jaws armed with flattened, sharp-edged, dagger-like teeth (Fig. 55d). These fishes are found in nearly all tropical and subtropical seas, and the larger kinds grow to a length of eight feet or more, and attain a weight of about one hundred pounds. In form they bear a marked likeness to the Pike, but this resemblance is purely superficial. The large fishes seem to be generally solitary in their habits, although the young congregate in shoals. The large species found in the West Indies, known as the Picuda or Becune, is much more feared by the inhabitants than any Shark, since it is not only extremely ferocious, but also utterly fearless. Further, it is much more liable to attack man without provocation than the Shark, and will not hesitate to molest bathers, whilst the ease and rapidity with which the slender body slips through the water make its approach very difficult to detect until too late. The Sieur de Rochefort, writing more than two hundred and fifty years ago, observes in his *Natural History of the Antilles*:

> "Among the monsters greedy and desirous of human flesh, which are found on the coasts of the islands, the Becune is one of the most formidable. It is a fish which has the figure of the Pike, and which grows to six or eight feet in length and has a girth in proportion. When it has perceived its prey, it launches itself in fury, like a blood-thirsty dog, at the men whom it has perceived in the water. Furthermore, it is able to carry away a part of that which it has been able to catch, and its teeth have so much venom that its smallest bite becomes mortal if one does not have resource at that very instant to some powerful remedy in order to abate and turn aside the force of this poison."

Sir Hans Sloane (1707) observes that the Barracuda feeds on "Blacks, Dogs, and Horses, rather than on White men, when it can come at them in the water." Père Labat (1742) records that it prefers a negro to a white man, and further, that it will sooner attack an Englishman than a Frenchman! His explanation, however, that the hearty, meat-eating habits of the Englishman as compared to the daintier feeding of the Frenchman produces a stronger exhalation in the water to attract the nostrils of the Barracuda, savours more of national prejudice than of scientific accuracy. The normal food of the Barracuda consists almost entirely of other fishes, and it has the interesting and somewhat cold-blooded habit of herding shoals of its intended victims in shallow water, keeping a constant guard over them until its previous meal has been digested and it is once more hungry.

In many Bony Fishes the teeth at the front end of the jaws are much larger than those at the sides, forming strong fangs or canine teeth, the usual purpose of which is to seize the prey. Occasionally, one or more canine teeth are found on the sides of the jaws, or, as in certain of the Wrasses (*Labridae*), at the two angles of the mouth. In some of the Gobies (*Gobiidae*) and Blennies (*Blenniidae*) there is a pair of very long and curved canines in the lower jaw, situated inside the mouth and behind the ordinary teeth. In the formidable-looking, deep-sea fish known as *Chauliodus* all the teeth take the form of long, curved fangs, but the pair at the front of the lower jaw are extraordinarily long, and in order to strike upwards effectively with these the fish is obliged to throw the head sharply backwards (Fig. 55b). The accompanying figures illustrate the way in which, when the mouth is closed, these fangs slip up the side of the snout, *outside the jaws*. The teeth of *Chauliodus* are slightly barbed at their tips, but in many deep-sea fishes, as well as in certain of the Sea Perches (*Serranidae*) and Flat-fishes (*Heterosomata*), the barbs are strongly developed and the teeth are definitely arrow-headed. A fresh-water fish from the rivers of South America known as *Cynodon* has a pair of very formidable canines at the front of the lower jaw, but instead of slipping outside the jaws when the mouth is shut these are received into special deep sockets in the palate and may even penetrate the upper jaw (Fig. 55a). Little is known of the feeding habits of this fish, but it is clear that in order to bring the canine teeth into play it must be necessary to open the mouth to an extraordinary extent.

So much for the fish-eaters. In fishes with a more mixed diet, including all kinds of invertebrate animals (molluscs, crustaceans, worms, and the like), and in the vegetarians, the teeth may be chisel-like (incisors), blunt and crushing, slender and brush-like, small and jagged, or absent altogether, according to the nature of the food. This diversity in the dentition is found, not only in the jaws, but also in the throat teeth and in those on the roof of the mouth. In the Flounder (*Flesus*), for example, the lower pharyngeals are united to form a triangular plate, and the associated teeth are mostly in the form of bluntly pointed cones, the teeth in the jaws being also conical; in the Plaice (*Pleuronectes*), on the other hand, most of the pharyngeal teeth are blunt crushing molars and the jaw teeth chisel-like. A study of the food of the two fishes shows that the Plaice includes a much higher percentage of shell-fish in its diet, and the crushing pharyngeal teeth are admirably suited for such food. Many of the Sea Breams (*Sparidae*) live on a similar diet, and the teeth are pointed in the front of the jaws and molar-like on the sides, being designed respectively to break and grind up the shell-fish. The Wolf-fish (*Anarrhichas*) has a group of long curved canines anteriorly in each jaw, and in the hinder part of the lower jaw a double row of rounded molars: the roof of the mouth is provided with three double rows, the middle ones flat and those at the sides pointed. Among the Cichlids

(*Cichlidae*) of the Great Lakes of Africa all kinds of dentitions have been evolved in course of time: the vegetarians have bands of small, notched teeth in the jaws, sometimes with an outer series of chisel-like incisors for cutting weeds, the fish-eaters have the large mouth armed with strong, pointed teeth, and those which live largely on molluscs have strong, blunt, pharyngeal teeth.

Many fishes habitually include in their diet large numbers of larvae of aquatic insects, and flies, gnats, and the like, flying near the surface of the water are also seized and devoured, some fishes displaying great agility in leaping out of the water and securing the prey at a single snap. The Archer-fishes (*Toxotes*), found on the coasts and in the rivers from India to the Pacific, derive their name from the curious manner in which they obtain the insects on which they feed (Fig. 57). Observing a fly hovering near the surface or settled on weeds or grass, the Archer carefully approaches, and, taking careful aim, squirts a drop or two of water from its mouth at the victim, which falls in the water and is soon secured. Their aim is very accurate even at a distance of three feet.

Many fish, of which the familiar Herring (*Clupea*) is an example, are plankton feeders; that is to say, they live exclusively on the swarms of microscopic organisms, both animal and vegetable, swimming at or near the surface of the sea and constituting what is known as the plankton (*cf.* p. 407). Like the land vertebrates, all fishes are ultimately dependent on the material and energy supplied by plants for their existence, and these plants in their turn are dependent on the rays of the sun to turn non-living materials into living substances. For example, the little crustaceans known as Copepods feed on the microscopic plants called Diatoms, the plankton-feeding fish devour the Copepods, and are themselves eaten by more powerful fishes. That the plankton provides a sufficiency of nourishment is proved by the fact that the huge Basking Shark (*Cetorhinus*) is able to subsist exclusively on such a diet (*cf.* p. 43). Diatoms likewise form an important part of the food of bottom-living animals like the molluscs, echinoderms, and worms, so that fishes feeding on these invertebrates are again dependent in the long run upon the vegetable kingdom. As might be expected from the nature of the food, the teeth of the Herring (*Clupea*) are small and feeble, and the food is strained from the water by the filtering mechanism provided by the slender gill-rakers (*cf.* p. 42). The Hickory Shad (*Dorosoma*) of

America, a member of the same family, feeds mainly on mud, and the mouth is small and quite toothless. The Grey Mullets (*Mugil*) may eat small molluscs, or scrape the green seaweeds

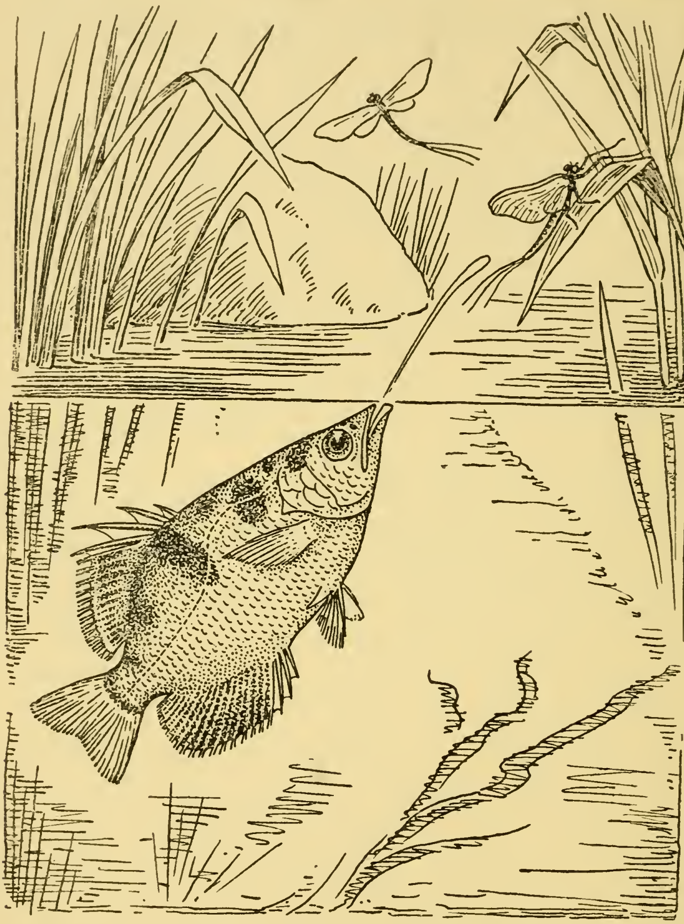


Fig. 57.

Archer-fish (*Toxotes jaculator*), $\times \frac{1}{3}$.

from the surfaces of stones or the wooden piles of piers and harbours, but their diet consists largely of decomposed animal and vegetable matter contained in mud. The numerous gill-rakers provide a sieve-like apparatus, and the dentition is represented merely by a fringe of minute bristles (Fig. 56D).

In most of the Wrasses (*Labridae*) the jaws are armed with strong conical teeth, and the lower pharyngeals are joined together to form a plate of characteristic shape studded with blunt teeth (Fig. 54A), a dentition well adapted for dealing with crabs and molluscs. The allied Parrot-fishes or Parrot Wrasses (*Scaridae*) have the pharyngeal teeth forming a flat pavement, the convex surface of the upper plate fitting closely into the concave surface of the lower. In the jaws rows and rows of tiny teeth grow up, but they remain fused together, forming sharp-edged plates set in the short jaws, the whole apparatus recalling the beak of a parrot (Fig. 56B). Most of these fishes are vegetarian, biting off pieces of seaweed with their "beaks" and grinding them up between the pharyngeal plates, but others break off lumps of coral in order to obtain the microscopic life contained therein, or prey upon hard-shelled molluscs of the Limpet kind. The common Mediterranean species, the famous *Scarus* so much esteemed by the ancient Greeks and Romans, is almost entirely a vegetable feeder, and the sliding movements of the pharyngeals when engaged in crushing pieces of weed led classical writers like Aristotle and Pliny to affirm that this fish "chewed the cud."

A similar but even more complete fusion of the teeth in the jaws is found among the members of the order of fishes known as Plectognaths. In the Globe-fishes or Puffers (*Tetrodontidae*) the teeth unite to form sharp-edged plates, one on each side above and below, and in the Porcupine-fishes (*Diodontidae*), feeding mainly on hard corals and molluscs, the teeth are joined to form a single plate above and below, sharp at the edge, but with a broad, crushing surface within. The small mouth of the huge oceanic Sun-fish (*Mola*) is armed with a similar beak-like dentition, but here the diet is composed largely of other fishes. In the Trigger-fish (*Balistes*), also pertaining to this order, each jaw is provided with eight strong, chisel-like teeth, which are used to bore holes in the shells of oysters, mussels, etc., in order to get at the soft parts. Curiously enough, the related File-fish or Leather Jacket (*Monacanthus*) has a somewhat similar set of teeth, although the diet is here said to be a vegetable one.

The members of the family of Cyprinids (*Cyprinidae*), including such well-known forms as the Carp, Gold-fish, Tench, Roach, Dace, Barbel, Bream, and Minnow, are distinguished by having toothless mouths, but the pharyngeal teeth are well developed and highly specialised. These are the leather-mouthed fishes of Izaak Walton. "By a leather-mouth," he writes, "I mean such as have their teeth in their throat, as the chub or cheven, and so the barbel, the gudgeon, the carp and divers others have." The teeth are borne on a pair of strong, sickle-shaped lower pharyngeal bones (Fig. 54C), and, instead of meeting the upper pharyngeals as in other fishes, they bite against a horny pad at the base of the skull. The teeth are arranged in one, two, or three rows, the principal row containing four to seven teeth, the others one to three. The form of the individual teeth varies greatly in the different species, being pointed, hooked at the tips, serrated, spoon-shaped, molar-like, etc., according to the nature of the diet. As a general rule the carnivorous species have hooked or pointed teeth, the vegetarians grinding molars. Sometimes the diet is a mixed one, and the Carp (*Cyprinus*), although mainly a vegetable feeder, will also eat worms, shrimps, insects, and smaller fishes, and it is said that the Barbel (*Barbus*) will not refuse any sort of animal or vegetable substance. Not a few species subsist largely on a diet of mud, from which they are able to extract sufficient nutriment in the form of decaying animal and plant matter. The manner in which they take in a mouthful of mud, extract the nutriment by a churning movement of the jaws, and finally eject the residue, is remarkable, and must be familiar to all who have observed Gold-fish feeding in an aquarium.

In the group of marine fishes known as Stromateoids or Butter-fishes (*Stromateoidea*), whose food seems to consist mainly of polyps, crustaceans, etc., the teeth in the jaws are minute, but the gullet has a remarkable structure, forming a pouch with thick muscular walls on which a number of little teeth are developed. The Square-tail (*Tetragonurus*), living almost entirely on jelly-fishes, has a similar muscular gullet, but, as might be expected from the nature of the food, this is devoid of teeth.

Before concluding this chapter it may be of interest to mention a few remarkable "meals" which have come to light from time to time. A few years ago a number of X-ray photographs of fresh-water Eels (*Anguilla*) were taken, and among the curious objects seen in the stomachs were bones of water birds and voles, pieces of wood and metal, a steel spring, and a piece of lead pencil. The Wels or Glanis (*Silurus*) of Europe normally feeds on fishes, frogs, and crustaceans, but a case is on record of a child being swallowed whole by one of these large Cat-fishes, and they are said to drag down and devour birds swimming at the surface. The Cod (*Gadus*) is another mixed feeder, and among the strange objects which have been taken from the stomach may be mentioned a bunch of keys dropped overboard from a trawler, a hare, a partridge, a black guillemot, a long piece of tallow candle, and from a specimen captured in 1626 and sent to the Vice-Chancellor of Cambridge, "a work in three treatises." Many of the deep-sea Angler-fishes (*Ceratioidea*) habitually seize and devour fishes larger than themselves, and this greediness frequently leads to the death of both victim and captor. Specimens have been found floating helplessly at the surface of the sea, each of which had neatly coiled away in its stomach a fish more than twice its own size. The captured fish was probably seized by its tail, and in its struggle to escape must have carried the Angler upwards: owing to the arrangements of the teeth, the latter was unable to release its hold and was forced to go on swallowing until it finally arrived at the surface, its meal completed, but thoroughly exhausted by the battle. The Common Angler (*Lophius*) of our own coasts does not rely entirely on its angling for food, but when hungry approaches ducks and other water birds from below and drags them down.

Finally, mention may be made of the following almost incredible "Shark story," which is vouched for by Mr. Frank Cundall, the Secretary of the Institute of Jamaica:

> "In the eighteenth century an American privateer was chased by a British man-of-war in the Caribbean Sea, and, finding escape impossible, the Yankee skipper threw his ship's papers overboard. The privateer was captured and taken into Port Royal, Jamaica, and the Captain was there placed on trial for his life (Mr. Cundall says 'for violation of the Navigation Laws'). As there was no documentary evidence against him he was about to be discharged when another British vessel arrived in port. The Captain of this cruiser reported that when off the coast of Haiti a shark had been captured, and that when opened the privateer's papers had been found in the stomach. The papers thus marvellously recovered were taken into court, and solely on the evidence which they afforded the Captain and crew of the privateer were condemned. The original papers were preserved and placed on exhibition in the Institute of Jamaica in Kingston, where the 'shark's papers,' as they were called, have always been an object of great interest.
>
> "(Signed) A. Hyatt Verrill, New York, Nov. 20, 1915."

CHAPTER VIII

VENOM, ELECTRICITY, LIGHT, AND SOUND

Poison glands in Selachians. In Bony Fishes: Cat-fishes, Weevers, Scorpion-fishes, Toad-fishes. Effects of venom. Treatment. Fishes with poisonous flesh. Electric organs: Torpedo, Electric Eel, Electric Cat-fish, Skates and Rays, Mormyrids, Star-gazers. Origin of electric organs. Nature of the discharge. Uses of electric organs. Luminous fishes. Photophores. Other light organs. Production of light. Purpose of luminous organs. Production of sound: by the air-bladder, by stridulation, by elastic spring mechanism. Sound-producing fishes.

As has been explained in an earlier chapter (*cf.* p. 68), the spines arming the gill-covers, or those which support the fins, may form useful weapons of offence or defence, and their effectiveness may be further increased by the development of poison glands in association with them. Such poison organs are more common in fishes than was formerly supposed, but they seem to be used almost entirely for defensive purposes, instead of playing a part in securing food as in the snakes. They are, for the most part, of rather simple structure, often composed merely of strips or bunches of specialised cells, and appear to owe their origin to the modification of certain portions of the epidermal layer of the skin.

Among the Selachians poison organs are found in the Spiny Dog-fishes (*Squalus*), Bull-headed Sharks (*Heterodontus*), Sting Rays (*Trygonidae*), Eagle Rays (*Myliobatidae*) and Chimaeras (*Holocephali*). Until quite recent years the presence of definite glands was denied by many, and the acute inflammation resulting from a wound caused by the tail-spine of a Sting Ray was believed to be due merely to the action of the mucous covering the spine on the lacerated flesh. Pliny alone among classical writers seems to have suspected the presence of venom in this fish. "Nothing is more terrible," he writes, "than the sting that arms the tail of Trygon (the Sting Ray of the Mediterranean), called Pastinaca by the Latins, which is five inches long. When driven into the root of a tree it causes it to wither. It can pierce armour like an arrow, it is as strong as iron, yet possesses venomous properties." It has now been shown that in the groove running along either edge of the serrated spine (Fig. 36e) is a tract of tissue, glistening white in colour, which may be difficult to detect unless cross-sections of the spine be prepared and examined under the microscope. Similar tissue has been found associated with the dorsal fin-spines of the Spiny Dog-fishes (Fig. 60A), Bull-headed Sharks (Fig. 52B), and Chimaeras (Fig. 80), and the cells of which it is composed secrete a virulent venom capable of causing painful or even dangerous wounds.

Among the Bony Fishes poison glands of a rather more elaborate structure occur in a number of forms, of which the Cat-fishes, Weevers, Scorpion-fishes, and Toad-fishes may be

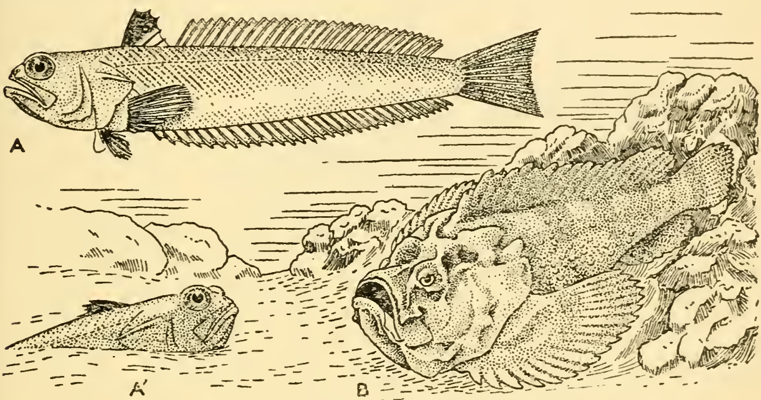


Fig. 58.—POISONOUS FISHES.

A, A′. Greater Weever (*Trachinus draco*), $\times \frac{1}{8}$; B. Poison-fish (*Synanceia verrucosa*), $\times \frac{1}{4}$.

specially mentioned. Certain Cat-fishes of the rivers of North America, known locally as Stone-cats or Mad-toms (*Noturus*, *Schilbeodes*), have the outer rays of each pectoral fin modified to form a stout, flat spine, generally serrated along one or both of its edges, and capable of inflicting nasty jagged wounds. At the base of each spine is a sac with a more or less wide opening, and this is believed to contain fluid of a venomous nature, which is poured out when the spine is brought into action.

In the Weevers (*Trachinus*), of which two species occur on our own coasts, the glands are associated with the long, sharp spine with which each gill-cover is armed, as well as with the five or six spines supporting the first dorsal fin (Fig. 58A). The opercular spine is ensheathed by an extension of the skin, only its tip projecting, and is traversed along its upper and lower margins by a deep groove. Along each groove is a pear-shaped mass of glandular tissue, the broad end of which lies towards the base of the spine (Fig. 59A). There is no canal leading from the gland, and it appears that the venom is set free by the rupture of the cells, and, flowing down the groove, is injected into the wound rather after the manner of a hypodermic syringe. It may be noted here that the name Weever is believed to be derived from an Anglo-Saxon word, *wivere*, meaning a viper.

The Poison-fishes (*Synanceidae*), belonging to the tribe of Scorpion-fishes, are confined to more or less tropical seas, and many of them are as ugly as they are formidable (Fig. 58B).

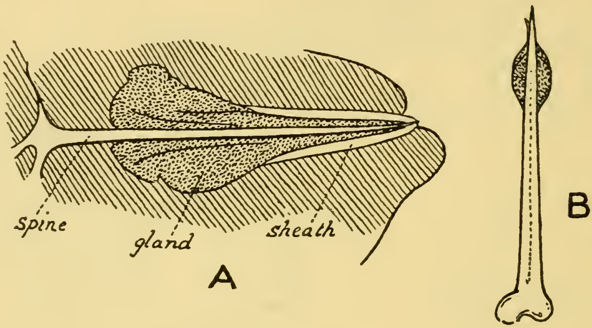


Fig. 59.—POISON GLANDS.

A. Opercular spine of Greater Weever (*Trachinus draco*) and its poison gland. (After Parker); B. A dorsal spine with poison sacs of Poison-fish (*Synanceia verrucosa*). (After Günther.)

The glands here lie under the skin at the bases of the dorsal spines, each being continued into a duct situated in the deep groove on either side of the spine (Fig. 59B). Native fishermen handle these fishes with great care, being well acquainted with their venomous nature. It sometimes happens, however, that when wading with naked feet one will step on a Poison-fish lying buried in the sand: the erect dorsal fin-spines penetrate the skin, and the venom is injected into the wound by the pressure of the foot on the bag-like glands. In the PoisonToad-fishes (*Thalassophryne*) of tropical America the glands are even more elaborate in structure, and represent the most perfect organs of their kind found among fishes. Like the Weevers, the spines on the gill-covers and the two spines of the first dorsal fin constitute the weapons, and each of these spines is hollow and perforated at either end like the venomous fang of a snake. The base of the spine is embedded in the centre of the poison gland, and the secretion is discharged through the hollow spine.

The virulence of the poison seems to vary greatly in the different fishes or even among individuals of the same species. The Sting Ray (*Trygon*) is particularly venomous, and many are the stories told of painful and even fatal wounds caused by the tail-spines of these fishes. It has been recorded that an Italian youth became extremely pale and fell down almost senseless for a few minutes from having received a very small puncture when handling a Sting Ray. Dr. Schomburgk mentions a fresh-water species of British Guiana, which was responsible for the death in violent convulsions of a colonist, whilst the two natives who accompanied him were wounded in the feet, became seriously ill, and only recovered the use of their feet after a long period of suffering. Another author gives a vivid account of how a large Spotted Eagle Ray (*Aetobatis*) which he was handling drove its "sting" two inches or more into his thigh. He suffered exquisite agonies, but, having a syringe handy, he injected a strong solution of formalin into the wound: the effect was magical, the pain stopped at once, and the wound rapidly healed. The poison of the Spiny Dog-fish (*Squalus*), although not quite so potent, is nevertheless capable of causing intense pain and discomfort. Dr. Evans describes the pain as being as severe as that from a Weever, but of a duller and more numbing character, and he cites cases of fishermen who were incapacitated for several days from a wound in the hand. Large quantities of these Dog-fishes are landed by trawlers and find a ready sale, but the two dorsal fins with their offending spines are invariably cut off soon after the fish is caught.

The venom of the Weevers (*Trachinus*) is particularly virulent, and a person who has had the misfortune to step on one of these fishes when bathing will not forget his experience in a hurry. On being "stung," the first symptom is an acute pain of a burning, stabbing character, which, if untreated, will last for several hours or even throughout the day; it is a common belief among fishermen that the pain will not subside until the next tide. So acute is the agony that men have been known to attempt to throw themselves overboard in their distress. Among other symptoms which have been noticed is a tendency to fainting, palpitations, fever, delirium, bilious vomiting, and so on, and in extreme cases heart failure may ensue. The potency of the venom may be gauged by the fact that a few drops of the fluid compounded by crushing up the poison spines will kill a guinea-pig when injected into its blood.

Dr. Evans writes that "the treatment of wounds produced by venomous fish is simple and efficacious." The injection of a few minims of a five per cent. solution of permanganate of potash (Condy's fluid) into the puncture provides immediate relief and prevents any inflammation. For the inflammation in cases which have not been promptly treated he recommends the application of cooling lotions or of hot fomentations.

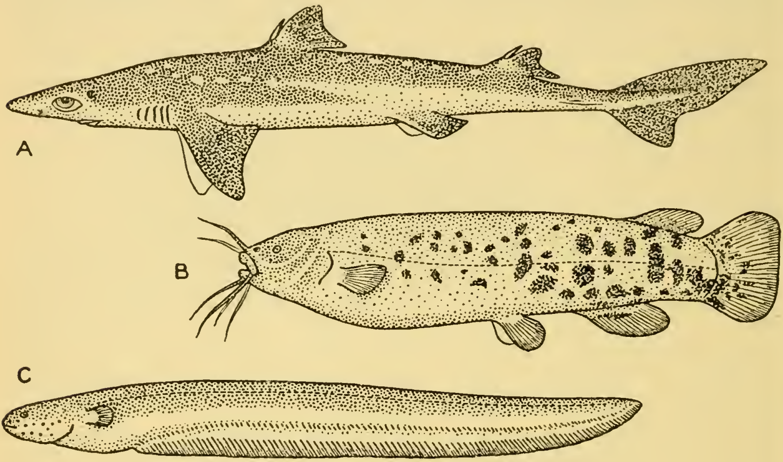


Fig. 60.

A. Spiny Dog-fish (*Squalus acanthias*), $\times \frac{1}{10}$; B. Electric Cat-fish (*Malopterurus electricus*), $\times \frac{1}{4}$; C. Electric Eel (*Electrophorus electricus*), $\times \frac{1}{15}$.

There are a number of fishes which, although without definite poison organs, have their flesh more or less permeated with poisonous substances, which takes the form of alkaloids of a particular kind called leucomaines. This may be regarded as a special form of self-protection, saving the species by poisoning its enemies! The Puffers or Globe-fishes (*Tetrodontidae*), File-fishes (*Monacanthidae*) and most of the Toad-fishes (*Batrachoididae*) are all more or less poisonous, and to eat certain species such as the Muki-Muki or Death fish of Hawaii is to invite almost certain death. The principal symptoms are paralysis and severe gastric derangement, and the poison seems to act especially on the nerves of the stomach, causing violent spasms of that organ and later of all the muscles of the body, death finally resulting from paralysis of the heart and asphyxiation. No antidote to the poison is known, and the only treatment consists in administering a strong emetic and giving suitable stimulants to prevent collapse. Such sickness is not to be confused with ordinary fish poisoning so prevalent in the tropics, which is not caused by any specific poison in the living flesh, but by the formation of other alkaloids known as ptomaines due to the action of bacteria in the decomposing tissues. These poisonous bacteria may be destroyed by cooking, but the alkaloids present in the flesh of a Puffer are not affected by the highest temperature. Other fishes, although not normally harmful, may become highly poisonous at certain seasons, and especially at the breeding season, when it is dangerous to eat the roes. Others again, like the Wrasses (*Labridae*) and Parrot-fishes (*Scaridae*), owe their poisonous properties at certain times to the food which they have been eating, having devoured poisonous mussels, echinoderms, polyps, and the like, themselves containing the deadly alkaloids. In many Eels (*Apodes*) the serum of the blood is said to be highly poisonous, but as the venom is destroyed by the gastric juices these fishes may be eaten with impunity. The futility of prohibiting as food any species suspected of causing poisoning was demonstrated by the action taken by the Cuban Government in drawing up a list of forbidden species. As fresh cases of poisoning occurred, new names were added to the list, which finally included all the best food-fishes of the West Indies!

Still more remarkable than the poisonous are the electrical properties of fishes. Among those forms provided with special organs capable of generating an electric discharge, the following are deserving of special mention: the Torpedoes, Ray-like fishes of tropical and temperate seas; the Skates and rays; the Mormyrids; the Electric Eel of the Orinoco and Amazon river systems; the Electric Cat-fish, a fresh-water species widely distributed in Africa; and the marine Star-gazers. This list includes species by no means closely related, and found both in salt and fresh water.

In the Torpedo or Electric Ray (*Torpedo*) two organs are present, lying on either side of the disc-like body, between the head and the greatly enlarged pectoral fins (Fig. 61). Each is a large, flat body, made up of a number of upright hexagonal tubes or columns, separated from one another by walls of fibrous tissue. Each column is filled with a clear, jelly-like substance, and is further subdivided by thin partitions into a number of small compartments, each containing a flat electric plate. On one side of the plate is a cluster of fine nerve tendrils, which unite and join the main nerve supplying the whole organ, and this is in turn connected with a special lobe of the brain.

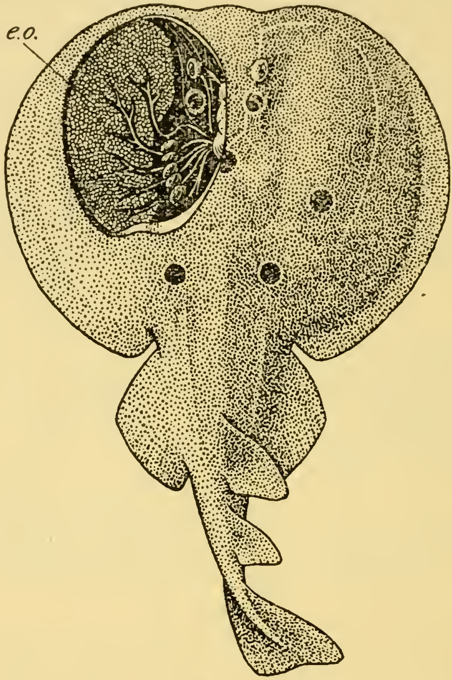


Fig. 61.

Electric Ray (*Torpedo*) dissected to show one of the electric organs with the associated nerve supply. The prismatic areas on the surface of the organ indicate the vertical columns of electric plates, of which there may be 500,000 in each organ. (After Gegenbaur.) *e.o.*, electric organ.

The side of the plate with the nerve-endings has been shown to be negative to the other side, and the current passes from the upper (positive) surface of the whole organ to the lower (negative).

In the Electric Eel (*Electrophorus*) there are two organs on each side of the tail, a large upper one and a small lower one along the base of the anal fin (Fig. 60c). Their structure is the same as those of the Torpedo, but the columns containing the electric plates run lengthwise instead of vertically, and the nerves supplying them, which may be as many as two hundred in number, arise from the spinal cord instead of from the brain. In the Electric Cat-fish (*Malopterurus*), on the other hand, the organ, instead of being made up of hexagonal columns of plates, takes the form of a sheath of gelatinous material lying between the skin and the muscles, and enveloping the whole of the trunk (Fig. 60B). The electric plates are scattered quite irregularly throughout this layer, and are placed transversely to the length of the body of the fish. There is another important difference, for here the nervous side of each plate is positive, and the hinder end of the fish is positive to the front end, the current passing from the tail to the head. On either side of the body the organ is supplied, not by a single nerve, but by a single fibre; this is much branched, each branch ending in an electric plate. The fibre itself arises from a single, enormous, lens-shaped nerve-cell, situated where the brain joins the spinal cord.

In the Skates and Rays (*Raia*), and in the Mormyrids (*Mormyridae*), the electric organs are quite rudimentary, lying on either side of the terminal portion of the tail as in the Electric Eel. They are, moreover, of comparatively feeble power, and serve merely as a protection against enemies. In the Star-gazers (*Uranoscopus*) the organs take the form of two oval areas of considerable size, placed immediately behind the eyes (Fig. 47E). These are of a complicated structure, being made up of many layers of electric plates, and are capable of giving off a shock of quite painful intensity.

How, then, have these complicated electric organs of fishes arisen? In order to answer this question it is necessary to study the development of the embryo or larval fish, and it is found that in the Torpedo, for example, each electric plate is nothing more than a transformed muscle fibre. Further, the whole organs have been derived from some of the branchial muscles, which have been relieved from their original duty of moving the gill-arches in order to take on this new function. The organs of the Electric Eel, the Skates, and the Mormyrids are similarly modified muscles, and owe their origin to the transformation of some of the lateral muscles of the tail. In the Electric Cat-fish the development of the organs has not yet been studied, as the smallest specimens so far obtained have these fully developed and capable of giving a tiny shock. There is good reason to believe, however, that the plates have arisen through the modification of certain cells in the epidermal layer of the skin. In the Star-gazers the electric organs have been shown to be developed from portions of the eye muscles, each of the plates representing a single muscle fibre.

As to the manner in which the electric discharge is actually produced, comparatively little is known. Various more or less ingenious suggestions have been made which are too complicated to be discussed here, and it must suffice to point out that the available evidence suggests that it is the nervous parts of the organs that play the most important rôle in the production of electricity. The currents created exercise all known powers of electricity, and in order to obtain the full shock it is necessary to complete the circuit by touching the fish at two points, either directly or through the medium of some conducting body: it is said that a powerful sensation may be produced by a discharge conveyed through the medium of a stream of water. It is generally stated that the fish gives the shock voluntarily, the time and strength of the discharge being completely under its control. It seems more probable, however, that quite often the stimulation produced by anything touching the skin of the fish causes a similar stimulation of the nerves supplying the electric organs by ordinary reflex action. Repeated use of the organs exhausts the fish, and a period of repose is necessary for recuperation.

There can be little doubt that the Torpedo makes use of the organs to kill or benumb its prey, and of two specimens of the Common Torpedo, taken in the estuary of the Tees, one had an Eel weighing two pounds and a Flounder of one pound in its stomach, and the other a Salmon weighing nearly five pounds, none of the victims showing any marks or blemishes on their bodies. The power of the shock seems to vary according to the number of electric plates included in the circuit, and is also dependent on the size and energy of the fish. It is usually of sufficient strength to knock down a fully grown man if he accidentally steps on one of these fishes lying buried in the sand in shallow water. The Mediterranean species was well known to the ancient Greeks and Romans, to whom it was a food-fish of some importance. Mr. Radcliffe, in his book entitled *Fishing from the Earliest Times*, has collected many of the classical references to this fish, which, in addition to serving as food, was regarded as a sovereign remedy for chronic headache, gout in the feet, and other kindred complaints. Still more amusing is the recommendation of the "brains of the

Torpedo applied with alum on the sixteenth day of the moon" as a remedy for superfluous hair!

The shock given by the Electric Eel [which, by the way, is not an Eel at all, but a member of the group of Gymnotids (*Gymnotiformes*), related to the Characins and Cyprinids] is a powerful one, and in an individual of six or eight feet in length probably exceeds in strength that given by any of the Torpedoes. Numerous are the stories told by travellers of men and their pack-beasts being knocked down through coming into contact with an Electric Eel while fording a river. The Electric Cat-fish (Fig. 60B), growing to a length of about three feet, is

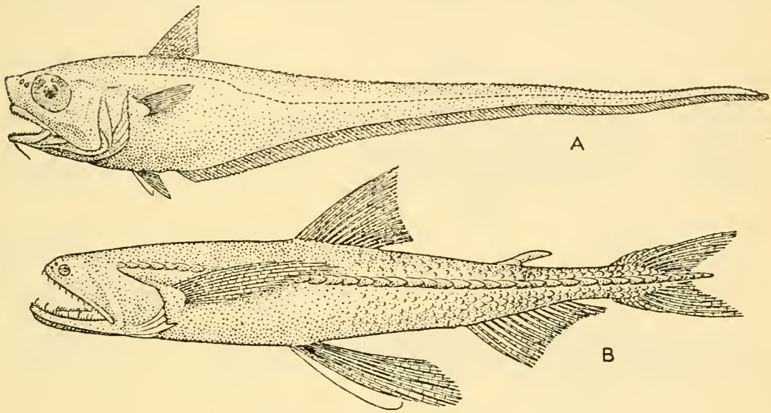


Fig. 62.—LUMINOUS FISHES.

A. Grenadier or Rat-tail (*Malacocephalus laevis*), × ¼; Bummalow (*Harpodon nehereus*), × ⅓.

sluggish in its habits and lurks in dark places. Its shock does not seem to be so powerful as that given by the forms just mentioned, but is of sufficient strength to cause considerable inconvenience to anyone handling the fish, and quite small specimens, two or three inches long, are said to be capable of giving shocks "like a succession of pricks." This species is used by the Arabs for food, and they refer to it as the Raad or Thunder-fish.

The production of light provides yet another example of transformation, for the luminous or phosphorescent organs to be described here owe their origin to the modification of certain gland-cells in the skin. These organs are of varying size and form, ranging from a simple local aggregation of gland-cells, which manufacture a luminous slime, to elaborate and powerful structures with lens and reflector. Some fishes seem to have the power of emitting light without possessing any definite light organs, but, in some forms at least, this is due to the presence of luminous bacteria in the tissues of the fish, or to the luminous properties of the slime exuded from the skin. A species of Smooth-head (*Leptoderma*) captured in the Bay of Bengal has been described as having the skin covered all over with a thick, opalescent, and uniformly luminous epidermis, and was said to glimmer like a ghost as it lay dead at the bottom of a pail of sea-water. The Bummalow (*Harpodon*), the Myctophoid fish of the Indian Ocean, which in a dried and salted condition

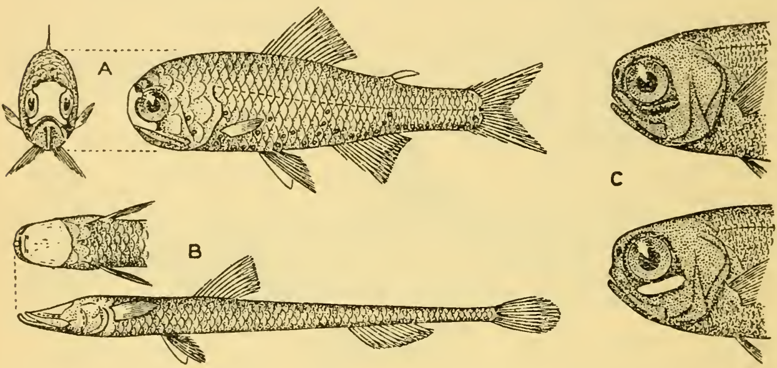


Fig. 63.—LUMINOUS ORGANS.

A. Lantern-fish (*Diaphus metopoclampus*), × 1; B. *Ipnops murrayi*, × ½; C. *Anomalops katopron*, × ½. (In the upper figure the luminous organ is retracted and therefore invisible.)

forms the well-known "Bombay Duck," is brilliantly phosphorescent all over when freshly caught, but there are no special light-producing organs (Fig. 62B).

Certain sharks, most of them inhabitants of deep water and belonging to the family (*Squalidae*) which includes our own Spiny Dog-fish, have the power of emitting light. This has been described as a vivid and greenish phosphorescent gleam, and has been shown to be due to the presence of numerous tiny light organs of very simple structure scattered over the skin. The *Spinax* of the Atlantic and Mediterranean, known to fishermen as "Darkie Charlie," has been kept alive in the Naples aquarium and the production of light carefully observed. Another form found near Ceylon was placed on the deck of a ship after capture, and continued to emit a luminous glow until its death three hours later.

Among the Bony Fishes, the members of the great group of Wide-mouths (*Stomiatoidea*), inhabitants of the open oceans, many of them descending to considerable depths, possess phosphorescent organs which may be of a much more elaborate structure. There are typically two rows of organs, or photophores, on either side of the fish, one on the belly and another parallel to it and near the lower edge of the side, but in some species additional series may be developed above these (Fig. 91). The rows generally extend continuously from behind the head to the tail, but may be interrupted in some species and confined to certain regions of the body and tail. The arrangement is metameric, that is to say, there is one set of four organs to each muscle segment or section of the vertebral column. The organs may be of a comparatively simple structure, consisting of little more than a group of gland-cells, not very different from the ordinary groups of cells in the epidermal layer of the skin from which the photophores have been derived. Some of them, however, may be more elaborate in structure, consisting of a lens set in the opening of a cup which is sunk in the skin, the walls of the cup being made up of the gland-cells which manufacture the light-giving substance: the walls may be lined with black pigment to form a reflector similar to that used in a bull's-eye lantern, and the outer skin partially projects over the surface of the lens and functions like the diaphragm or stop of a camera. In addition to the body photophores, there are others on the head and jaws, including a large and sometimes complicated organ below or just behind each eye. This organ has a backing of black pigment, and is freely movable, being rolled inwards when not required. A still more curious organ is found in a rare Berycoid fish from the Indian Ocean known as *Anomalops*. This fish has a large phosphorescent organ below the eye, placed on a movable flap, so that when light is not wanted it can be turned inwards and received into a cavity underneath the eye (Fig. 63C).

In the Myctophids or Lantern-fishes (*Myctophidae*) the photophores are fewer in number, but are larger and brighter, having the appearance of glistening jewels or small mother-of-pearl buttons. Instead of being set out in rows running from the head to the tail, they have a complicated arrangement of short rows and groups, which is, nevertheless, perfectly symmetrical (Fig. 63A). As in the Wide-mouths, the great majority of the photophores occur on the lower parts of the body, rarely on the back or upper parts of the sides. Many species have a special organ above or below the eye, and others possess a very powerful head-lamp covering the greater part of the snout (Fig. 63A). Certain patches may be developed on the head and body, especially at the bases of the fins, which, although luminous, lack the specialised structure of the photophores. One or more of these patches may be present on the upper and lower edges of the fleshy part of the tail, where they are described as "stern-chasers."

The line and bait of the Angler-fishes, representing the much modified first ray of the dorsal fin, has already been described (*cf.* p. 71). In the deep-sea members of this order (*Ceratioidea*) the bait is luminous and can be "switched on" at will, serving to attract smaller fishes within reach of the Angler's jaws. In addition to this line and bait certain species possess a much branched tree-like structure below the chin which also has luminous properties and probably acts as a lure (Fig. 31A). Other deep-sea fishes, in which one or more of the fin-rays may be drawn out to form a fine filament, have these rays tipped with small luminous bulbs. Another remarkable form, known as *Ipnops*, has the whole of the upper surface of the flattened head occupied by a pair of large organs lying beneath the transparent superficial bones of the roof of the skull and believed to be luminous (Fig. 63B). It is possible that these take the place of the eyes, which are entirely wanting in this curious and rare fish.

So far only the light organs of fishes inhabiting the open oceanic waters and descending to a fair depth have been mentioned. These structures may also occur, however, in fishes living more or less close to the shore, having been found in the common Haddock (*Gadus aeglifinus*) and in one of the Toad-fishes (*Porichthys*) of the coast of California. The latter fish, known locally as the Midshipman or Singing-fish, has no less than seven hundred photophores on its head and body, each presenting the appearance of a shining white spot. These organs are developed in connection with the complicated system of lateral lines, and many of them are associated with the sense organs. Each consists of four parts: lens, gland, reflector, and pigment, and, as usual, they are more abundant on the lower parts of the fish.

Although various theories as to the production of luminescence have been advanced, it is now generally agreed that this is due to the luminous nature of the slime secreted by the gland-cells. These manufacture a substance containing phosphorus, and this is oxidised by the oxygen supplied to the cells by the blood to produce the gleam. To put the matter into the language of biochemistry, a substance called *luciferin*, secreted by the gland-cells, is burnt to *oxyluciferin* in the presence of a ferment known as *luciferase*. In the vast majority of luminous fishes the substance is burnt within the cells in which it is manufactured, but a fish has recently been studied in which the cells secrete the material for oxidation to the exterior and it is burnt outside the cell. This fish (*Malacocephalus*), a member of the tribe of Grenadiers or Rat-tails (*Macruridae*), is taken in large numbers along the outer edge of the continental shelf from Ireland to Morocco in depths of one hundred and fifty fathoms or more, and possesses a remarkable luminous gland lying between and behind the pelvic fins (fig. 62A).

The purpose of the light organs of oceanic fishes is largely a matter for conjecture. The use of the luminous bulbs and barbels of the oceanic Wide-mouths (*Stomiatoidea*) and Anglers (*Ceratoidea*) as lures has already been described. In other fishes the emission of light is almost certainly defensive rather than offensive. In the Grenadier just mentioned, for example, it seems probable that a sudden beam of light emitted from the gland between the pelvic fins would tend to confuse an enemy and cover the retreat of the pursued in the same way as does the ink-cloud of the Cuttle-fish. The "stern-chasers" of the Lantern-fishes (*Myctophidae*) may serve a similar purpose, a sudden flash from the tail being used to dazzle or even frighten the pursuer. To explain the photophores and other organs on the head and body is rather more difficult. It is generally assumed that they enable fishes living in the depths of the ocean—the region of eternal night, as one author describes it—to seek for and detect their prey. This may be true in part, but it must be remembered that the same light which illuminates the prey renders its owner equally conspicuous and liable to be hoist by his own petard! Further, an extensive study of the fishes inhabiting the oceans shows that there is no certain connection between the possession of light organs and a life in the abyssal depths. Many fishes spending the greater part of their times at or near the surface have these organs well developed, whilst a number of forms known to live permanently at considerable depths are without them.

In considering the function of luminous organs it is important to bear in mind the following facts. Firstly, the complicated apparatus often present for concentrating the beam of light and for regulating its intensity, together with the abundant nerve supply to each organ, suggests that the emission of light can be controlled by the fish. Secondly, the position of the main organs on the sides and belly of the fish, and the presence of special organs in the neighbourhood of the eyes and jaws, provides evidence that they may be used to light up the surrounding water in front of and beneath the fish. Thirdly, and this seems to be a fact of some importance, the number and arrangement of the photophores exhibits considerable variation in the different genera and species, but, with the exception of small differences, remains constant in any particular species. Indeed, in the Lantern-fishes (*Myctophidae*) the number and pattern of the photophores provides the most important character for distinguishing the different species. Finally, there is some evidence that the colour of the emitted light may vary in different fishes. It seems probable, therefore, that the luminous organs may fulfil the same function among the dwellers in darkness or semi-darkness as do the spots and stripes of pigment in many littoral fishes, and that one of the important uses of these structures is to act as recognition marks, enabling their possessor to pick out another individual of its own kind, and thus assisting the members of a shoal to keep in touch with each other.

There is a widespread and popular belief that fishes possess no voices. This is quite untrue, for, although incapable of vocal efforts comparable to those of mammals and birds, a number of Bony Fishes produce sounds of one sort or another, and some forms are provided with special sound-producing organs. These may be associated with the air-bladder, fin-spines, vertebrae, and so on, and provide another example of the assumption of new duties by organs originally designed for a totally different function. Owing to the impossibility of an investigator remaining under water for any length of time, it is very difficult to obtain definite data on the production of sound, and, at the same time, it is by no means easy to discriminate between sounds actually due to the action of vocal organs and those of a purely accidental or abnormal nature. The simplest type of sound, for example, is that produced merely by the expulsion of air from the air-bladder through the pneumatic duct, and the grunting or gurgling noises made by fishes as they are taken from the water, including the so-called "bark" of the Conger Eel, may perhaps be ascribed to this cause. The characteristic breathing or murmuring sounds made by the members of the Carp family (*Cyprinidae*) may be similarly accounted for, but the noises of a like nature made by the Loaches (*Cobitidae*) are said to be due to the rapid expulsion of air-bubbles through the anus.

In a number of fishes characteristic sounds are made by stridulation; that is to say, by the rubbing or friction of one surface against another. For example, the Horse Mackerel (*Trachurus*), the Sun-fish (*Mola*), and certain species of Trigger-fishes (*Balistes*) produce harsh noises by grating together the upper and lower pharyngeal teeth. The Bull-head (*Cottus*) uses a portion of the gill-cover for stridulation; the Flying Gurnard (*Dactylopterus*) the hyomandibular bone; the Trigger-fish (*Balistes*), File-fish (*Monacanthus*), Boar-fish (*Capros*), Surgeon-fish (*Acanthurus*), Stickleback (*Gasterosteus*), and some of the Cat-fishes (*Siluroidea*), the spines of the dorsal, anal, pectoral or pelvic fins.

In the "Drumming" Trigger-fish (*Balistes aculeatus*) of Mauritius the noise is said to be due to the friction of certain of the bones of the arch supporting the pectoral fin against one another, and since these are more or less intimately associated with the air-bladder, the latter acts as a sort of amplifier and intensifies the sound vibrations. Professor Cunningham, who has made a special study of a species of Trigger-fish (*B. buniva*) abundant at Ascension Island, describes the production of sound as follows. "Just behind the pectoral fin is an area of skin resembling a drum, a portion of the air-bladder being immediately beneath it. . . . When the drumming sound was produced the pectoral fin was moved rapidly to and fro and the membrane of the drum could be seen to vibrate. It certainly seemed as though the sound was due to the vibrations of the drum itself, and as though these vibrations were due to the striking of the drum by the fin, but it was impossible to decide whether the friction of the internal bones of the pectoral girdle was necessary to produce the sound. . . ." Mention may be made of an Indian Cat-fish (*Callomystax*) which possesses a most elaborate stridulating organ involving the vertebral column and the dorsal fin. The sounds are produced by the scraping of the first interspinous (radial) bone of the dorsal fin between two thin ridged plates representing the hinder portion of a bony ridge formed by the fusion of the spines of the fourth and fifth vertebrae. When the fish flexes its body in a certain plane this apparatus is brought into play and harsh, grating noises are produced.

In the remaining sound-producing fishes to be discussed, the organs are for the most part of a more elaborate nature, and the noise is produced through the agency of special muscles associated with the air-bladder. In a number of Cat-fishes (*Siluroidea*) an apparatus known as the elastic spring mechanism occurs, the purpose of which is to cause the walls of the air-bladder to vibrate. The "springs" are specially modified portions of the

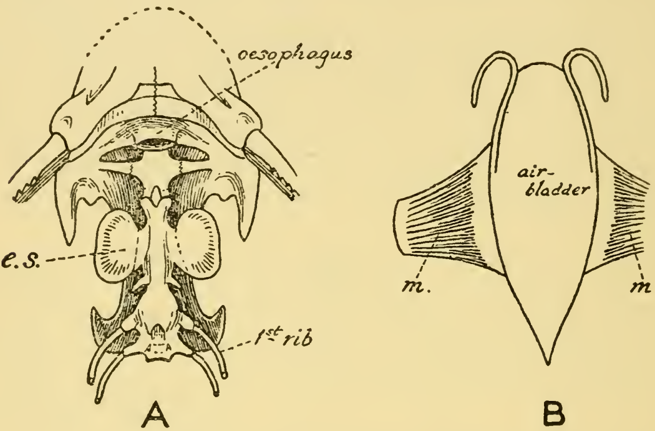


Fig. 64.—SOUND-PRODUCING ORGANS.

A. Elastic spring mechanism of a South American Cat-fish (*Auchenipterus nodosus*), showing the oval bony plates in which the elastic springs terminate, × about ½. (After Bridge and Haddon); B. Air-bladder of a Sciaenid (*Micropogon undulatus*), showing the musculo-tendinous extensions from the muscles of the body-wall, which partially invest the surface of the bladder (*m.*), × about ½. (After Sörensen.)

fourth vertebrae and their expanded ends are attached to the front part of the air-bladder (Fig. 64A). Two strong muscles run from the springs to the hinder portion of the skull, and when these contract the springs, and with them the walls of the bladder, vibrate rapidly and produce a sort of growling or humming noise. Generally, the air-bladder is divided up by internal partitions into a number of chambers all freely communicating with one another, and there can be no doubt that the sound is intensified by the vibratory movements of the gases contained in the bladder across the free edges of the partitions. In the Sciaenids or Drums (*Sciaenidae*), fishes renowned for their vocal efforts, the sounds are produced by the rapid vibration of a special muscle, which is not always attached directly to the bladder, but may run from the abdomen on either side to a central tendon situated above the bladder (Fig. 64B). The rapid contraction and expansion of the muscle (at the rate of about twenty-four contractions per second) causes the walls of the bladder to vibrate, and since this has a complicated structure, it acts as a sort of resonator and intensifies the sound. Mr. Tower, an American investigator, has performed a number of experiments on living fish which are of some interest. He found that if the bladder was deflated or removed altogether the drumming entirely ceased, but if he introduced an artificial india-rubber bladder it again commenced. In the Gurnards or Sea Robins (*Triglidae*), and in the Toad-fishes (*Batrachoididae*) the grunting noises are produced by special muscles lying in the walls of the bladder itself, which, when they contract, throw the walls into rapid vibrations. By experiments it has been shown that if either the muscle or the nerve supplying the bladder is artificially stimulated, a perfectly normal sound is produced, even when the bladder has been removed from the fish and placed on the operating table. No sound is produced if the bladder is punctured, but the introduction of a rubber balloon inside the bladder leads to a sound when the muscle is stimulated by electricity.

The actual noises produced by the different fishes present great diversity, ranging from a more or less melodious vocal effort to a mere grunt. A South American Cat-fish (*Doras*) is said to produce a sound described as a "deep, growling tone," distinctly audible at a distance of one hundred feet when the fish is out of the water. There can be little doubt that when in their native element the sounds made by fishes must travel for considerable distances, as water is a much more efficient conductor of sound waves than air. The elastic spring apparatus of the Electric Cat-fish (*Malopterurus*) causes a hissing sound, the Trunk-fishes (*Ostraciontidae*) and Globe-fishes (*Tetrodontidae*) are credited with "growling like dogs," and the little Sea Horses (*Hippocampus*) are said to utter a "monotonous sound analogous to that of a tambour, which is characteristic of both sexes, but is more intense and frequent in the breeding season." An Indian species of Horse Mackerel (*Caranx hippos*) has been described as grunting like a young pig, and a related species from Egypt (*C. rhonchus*) is known to the Arabs as "Chakoura" or "Snorter." The sounds made by the Drums (*Sciaenidae*) have been variously described as creaking, drumming, humming, purring, whistling, etc., and are quite loud enough to be audible to a person standing on the deck of a ship. It has been demonstrated that the noise can be heard when the fish is eighteen metres below the surface of the water and the ear of the observer two metres above the water. In the Malay Peninsula and other tropical countries the native fishermen make use of the sounds to locate shoals of fish, one of their number "listening in" and instructing his companions where to cast their nets. The Meagre or Weak-fish (*Sciaena aquila*), a species occurring round our own coasts, is abundant in the Mediterranean, and its vocal powers have been the subject of comment and discussion in all ages. It is not improbable that the Greek myth of the song of the Sirens which occurs in the Homeric fable arose from the sounds made by shoals of these fishes. A curious point about the Sciaenids is that some species make no sounds at all, in others only the males make a noise, and in others, again, both sexes are responsible. The drumming seems to take place especially at the breeding season, and is probably a signal for the assembling of the shoals.

In the Gurnards (*Triglidae*) the sounds are of a somewhat different nature, and have been variously described as grunting, crooning, snoring, etc. Unlike the Drums, these fishes do not make use of rapidly repeated sounds and rolls, but produce short, sharp sounds, repeated at more or less lengthy intervals. The grunts can be imitated, according to Mr. Tower, "by drawing the forefinger and thumb towards each other over the surface of an inflated rubber balloon. . . ."

CHAPTER IX

INTERNAL ORGANS

Skeleton: skull, vertebral column. Muscles. Alimentary canal: mouth, tongue, stomach, intestine, rectum. Vascular system: heart, arteries and veins, lymphatic system. Kidneys. Air-bladder.

THE parts of a fish so far described have been mostly those which can be made out without any detailed dissection, and in the present chapter the true internal anatomy, including the skeleton, digestive system, circulatory system and so on, may be studied. Space will permit of only a brief survey of the more important of these internal organs, detailed descriptions of which will be found in any of the recognised text-books mentioned in the accompanying list (*cf.* p. 435).

The skeleton, whether composed of cartilage or bone, may be regarded as the local strengthening of certain regions of the connective tissue (which itself forms a scaffolding pervading the whole body), and has clearly been developed in order to give a general support to the body, to provide a protection for the delicate brain and spinal cord, and to furnish an attachment for the powerful muscles. The skeleton of a fish, like our own, is a complicated structure, and is often referred to as the endoskeleton, in order to distinguish it from the more superficial exoskeleton of scales or scutes: as will be shown later on, however, the line of demarcation between the two is by no means as clear cut as would at first appear. Three main regions of the skeleton may be recognised: skull, vertebral column, and fin-skeleton. The last has been dealt with in a previous chapter (*cf.* pp. 57-59). The skull itself is made up of two distinct parts: the cranium, enclosing the brain and sense organs; and the visceral arches, including the upper and lower jaws as well as the series of segmented arches supporting the tongue and gills. The visceral arches have been discussed in the chapters devoted to the jaws and gills (*cf.* pp. 35, 106) and only the cranium need be described here.

To obtain a clear understanding of the general ground plan of a fish's cranium it is necessary to study it in its most primitive form, and for this purpose that of the common Spotted Dog-fish

(*Scyliorhinus*) is at once most suitable and easily obtainable. It may be objected that the skull of the Lamprey (*Petromyzon*) is even more primitive, but, although this is true of many features, there are others in which it has attained to a marked degree of specialisation along lines peculiar to this class of fishes. In order to reveal the skull of the Dog-fish it is necessary to cut away the skin and muscles of the head, and in so doing it is quite easy to cut into and damage the underlying cranium. This fact should serve to fix in the mind the most important feature of the skull, namely, that it is composed, not of bone, but of a much softer substance called cartilage. In all living Selachians the entire skeleton is cartilaginous, and this provides one of the principal characters separating them from the Bony Fishes. In some Sharks and Rays the cartilage is strengthened by the addition of calcareous or limy matter, but true bone is never developed.

The cranium of the Dog-fish (Fig. 46A) has the form of a somewhat flattened oblong box, with more or less complete floor, roof, and lateral walls, but open in front and behind. Through the posterior aperture the spinal cord emerges from the brain, and on the cartilages forming the lower edge of this opening are two prominences or condyles by means of which the cranium is articulated to the first segment of the backbone. Within the trough-like cranium lies the brain, and the various nerves as well as the associated blood-vessels pass outwards through a number of holes or foramina in its floor and walls. On the outside of the box are two pairs of prominences, hollow capsules attached to the cranium: the pair at the front end are open below and lodge the delicate organs of smell, and the other pair at the hinder end enclose the organs of hearing. Between them, on either side in the centre of the cranium, is a cavernous recess known as the orbit for the lodgment of the eyes. So much for the skull of the Dog-fish.

In the Bony Fishes there is a much more complex skull, in which true bones have to a greater or lesser extent replaced the primitive cartilage, although in some of the more generalised forms large areas of the softer substance still remain. In the Sturgeon (*Acipenser*), for example, the head is covered with a dense bony armour made up of a large number of separate and symmetrically arranged plates, but below these is a cartilaginous cranium not very unlike that of the Dog-fish. In the Bichir (*Polypterus*), another primitive form, there is still more bony matter in the skull, for, in addition to the investing armour on the surface, which contains much fewer elements than that of the Sturgeon, some of the cartilages of the cranium itself have been replaced by bone. In the more highly organised Bony Fishes the amount of cartilage in the cranium of the adult fish becomes less and less, until finally it is entirely absent as in the great majority of the members of this class living to-day.

As previously explained (*cf.* p. 107) the bones are of two distinct kinds, each with a different mode of origin, but they are so welded together to form a compact whole that in the adult fish it is often impossible to decide as to which category a particular element belongs. Firstly, there are cartilage bones, so called because the bony tissue develops in the cartilage itself and eventually replaces it. Secondly, there are dermal or membrane bones, not preceded by cartilage, but developing as new structures in the thin membranes of certain regions of the head and forming an investing sheath on the outer surface of the cranium. The bones of the roof, most of those on the floor, as well as those supporting the gill-covers, are of this nature (Figs. 46B, C; 65). The dermal bones are particularly interesting from an evolutionary point of view, representing, as they do, nothing more than much modified scales, which at some time or other sank inwards from the skin and came into intimate connection with the cranium. Many of these bones in the fish's skull persist in the higher land vertebrates, so that in reality the large frontal bones of the human skull have been derived from the bony scales on the head of a fish, which were themselves developed from dermal denticles similar to those of the Selachian skin.

The development of the skull in such a fish as the Salmon (*Salmo*) provides yet another interesting example of the manner in which the evolutionary history of any organ or organs is recapitulated during the development of the individual. The first trace of the skull as seen in the unhatched embryo takes the form of two pairs of cartilaginous plates lying below the brain, known as the trabeculae and parachordals. Later, centres of cartilage start to grow in the regions of the organs connected with the senses of smell and hearing, the cartilages in the floor grow up the sides and meet above the brain, and, later still, the capsules round the sense organs fuse with the remainder of the cranium. At this stage, which may occur as late as the second week after hatching, the cranium is still entirely cartilaginous, and is not very unlike that of the adult Dog-fish. Soon afterwards, dermal and cartilage bones begin

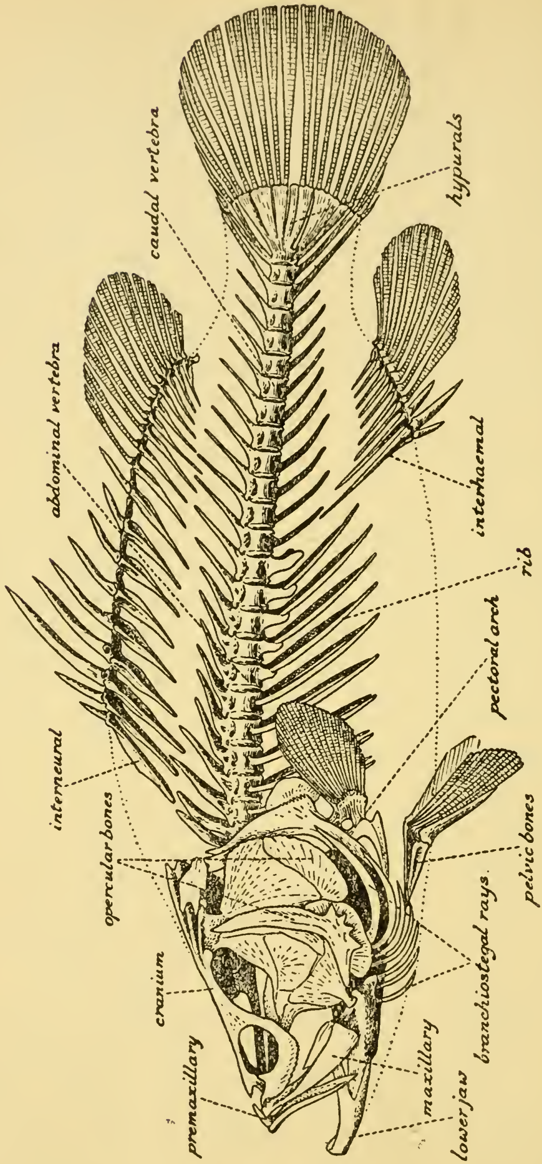


Fig. 65.

Skeleton of the Nile Perch (*Lates niloticus*), × $\frac{1}{8}$.

to develop, much of the cartilage disappears, and the skull gradually assumes the adult form. It is of interest to note that the dermal bones have become so much an essential part of the cranium that they have in some way inhibited the growth of cartilage in the regions which they will finally occupy, and during the early stages of development the brain is protected merely by connective tissue in these regions.

The series of cartilages or bones constituting the axis of the body, designed to afford protection for the delicate spinal cord and for certain blood-vessels running from head to tail, is known as the vertebral column or backbone (Fig. 65), and the separate elements are spoken of as vertebrae. It is very probable that this was the first part of the skeleton to be evolved, and, indeed, there is good reason for believing that the skull itself arose primarily through the fusion and modification of some of the anterior vertebrae. In the developing embryo of any fish the first part of the skeleton to make its appearance is not the proper backbone but an unjointed rod of gelatinous tissue, the notochord, running along the axis of the body and ending in front between the rudiments of the cartilages forming the floor of the cranium. The ancestors of the fishes probably retained this simple axial rod throughout life, but with the ever-growing need for some protection for the spinal cord, as well as for a centre for the attachment of the body muscles, the vertebral column was developed round it. During the development of the individual fish the different vertebrae arise as rings of cartilage which grow round the notochord and gradually constrict it. Later on, additional pieces of cartilage grow up to surround the spinal cord, and others are developed below as a protection for the main artery and vein. In all the higher fishes the notochord disappears altogether in the adult stage.

In the Lamprey (*Petromyzon*) the vertebral column is very simple, the notochord persisting in the adult, and merely supporting a series of isolated cartilages on either side of the spinal cord. In the Selachians it is more complicated, but is still composed entirely of cartilage. Each vertebra is a complex structure made up of a number of pieces firmly joined together. The names of all these elements need not be mentioned here, and it will suffice to point out that the body of each vertebra, the centrum, takes the form of a ring of cartilage, which is hollow in front and behind like a dice-box: on its upper and lower edges this bears an arch of cartilage, the upper or neural arch protecting the spinal cord, and the lower or haemal arch performing a like service for an artery and a vein (Fig. 66A). The lower arches are of two kinds, those in the tail region (*i.e.* of the caudal vertebrae) being complete and meeting below to form a tunnel, whilst those in the trunk region (*i.e.* of the abdominal vertebrae) project sideways as short processes to which are attached slender ribs, running outwards in the walls of the body and ending in the partitions between the segments of the body muscles. In some of the more primitive Bony Fishes, such as the Sturgeons (*Acipenseridae*) and Lung-fishes (*Dipneusti*), the vertebrae are still composed largely of cartilage, and portions of the notochord persist between the centra, as in the Dog-fish. There are, however, two pairs of

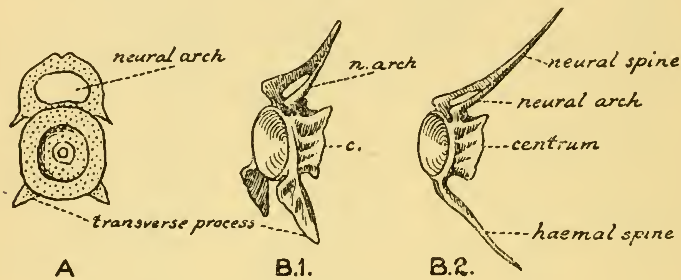


Fig. 66.—VERTEBRAE.

A. Cross-section through one of the vertebrae of Comb-toothed Shark (*Heptranchias perlo*), × ¼; B.1. Lateral view of an abdominal vertebra of Cod (*Gadus callarias*), × ¼; B.2. Caudal vertebra of same, × ¼.

additional elements not found in the Selachians: the supra-neurals, united to form neural spines, and infra-haemals, united in the tail region to form haemal spines, but in the trunk region taking the form of what are known as pleural ribs. In most of the higher Bony Fishes the vertebrae are more or less completely ossified, but have the same essential form throughout the class (Figs. 66B.1, B.2). The Gar Pike (*Lepidosteus*) is unique in the form of its vertebrae, each centrum being convex in front and concave behind. In the remaining Bony Fishes the centra almost invariably have concave surfaces at both ends, although in the Eels (*Apodes*) they may be flat or even convex in front. In a number of fishes the articulation between two vertebrae is made more effective by the development of little bony processes on the sides of the neural arches or the centra; these project backwards in one vertebra and meet a similar process projecting forwards in the next.

It is a general rule that the more deep-seated organs are far less liable to modification than the more superficial structures, such as the scales, fins, and so on. Thus, although they show a number of differences in the various orders, suborders, and families, often of considerable value in classification, the skulls of Bony Fishes, apart from the jaws, do not present many very striking modifications. This is true to some extent of the vertebral column, but here there are one or two remarkable adaptations worthy of consideration. In the deep-sea *Chauliodus*, for example, which is in the habit of throwing the head back when striking at its prey in order to bring the huge lower canine teeth into play (*cf.* p. 134), the first vertebra immediately behind the skull is enormously enlarged, being several times larger than any of those following. This serves to take the strain when the head is suddenly jerked back, and at the same time provides additional surface for the attachment of the muscles moving the head (Fig. 67D). In some of the members of the genus *Eustomias*, oceanic fishes of the suborder of Wide-mouths (*Stomiatoidea*), the anterior part of the vertebral column is unique in being incompletely ossified and with the notochord bent to form one or two distinct loops. The first vertebra is normal, but this is followed by six or seven without centra and made up of isolated bony elements. This curious modification is undoubtedly related to the violent movements of the head involved in protruding the jaws and in wrestling with large prey, the incompletely ossified and bent anterior portion giving flexibility and acting as a kind of shock absorber (Fig. 67C). It has been suggested that the opening out and closing up of the bends, and the corresponding movements of the jaws, may assist in swallowing prey. In *Stylophorus*, another oceanic form with protractile jaws, whose feeding habits have been already described (*cf.* p. 118), a similar strain due to the backward jerk of the head is provided for by a complicated system of interlocking among the first few vertebrae by means of special bony processes (Fig. 67B). Finally, in the Sword-fishes (*Xiphiidae*) and Spear-fishes (*Istiophoridae*), whose violent charges on whales and other Cetaceans have been considered in an earlier chapter (*cf.* p.114), the vertebrae have undergone some marked modifications clearly designed to give power to resist the shock of such encounters, the interlocking processes being very powerful (Fig. 67A). The changes undergone by the first two or three vertebrae in the Cyprinoids and Siluroids in connection with the so-called Weberian mechanism will be fully described in the next chapter.

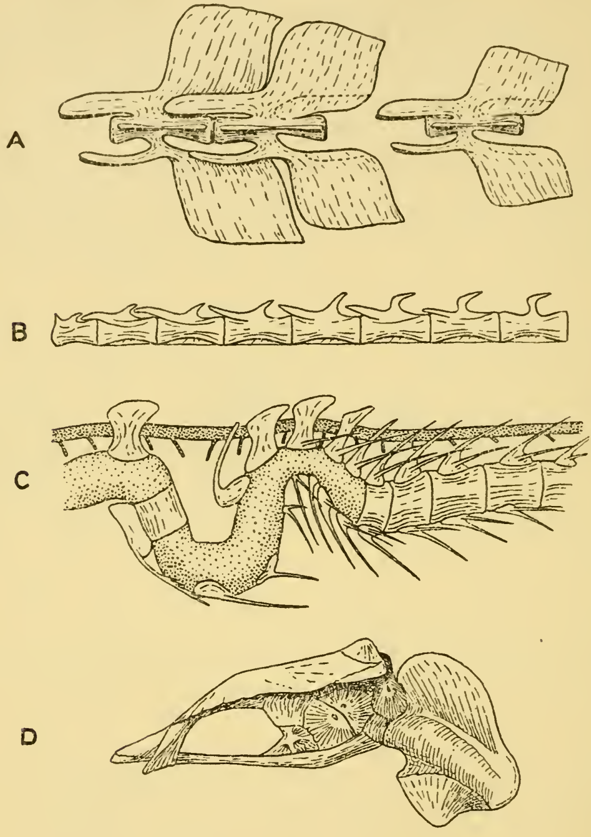


Fig. 67.—MODIFICATIONS OF VERTEBRAL COLUMN.

A. Three vertebrae from the tail of Sail-fish (*Istiophorus sp.*), $\times \frac{1}{8}$; B. First eight vertebrae of *Stylophorus chordatus*, $\times 3$. (After Regan); C. Anterior part of vertebral column and spinal cord (above) of *Eustomias brevibarbatus*. (After Regan and Trewavas); D. Skull and first vertebra of *Chauliodus sloanei*. (After Regan and Trewavas.)

Before leaving the skeleton, attention may be drawn to the curious bright green colour of the bones in the Gar-fishes (*Belonidae*), Skippers (*Scombresocidae*) and allied forms. This is unique among fishes, and remains even after cooking. There is a strong prejudice against eating these fishes on this account, but the colouring is not due to any deleterious substance and the flesh is wholesome and nutritious.

The tissue clothing the skeleton, generally known as the meat or flesh, is made up of muscles, and provides the greater part of the bulk of the body. In the higher vertebrates the muscular system is a complicated one, but in the fishes the arrangement is comparatively simple, and represents a primitive condition. The most important muscles are the great lateral bands running along the body in the trunk and tail—the muscles concerned with the locomotor movements. In the ancestors of the fishes these may have formed continuous bands running from the head to the tail, but in all living forms they are divided transversely into a series of segments, corresponding in number to the vertebrae, each of which usually has roughly the shape of an S. On either side each of these segments or myotomes is further divided into an upper and lower half by a groove running along the length of the fish. If the scales are removed from the side of a fish a number of parallel white stripes of zigzag form may be seen, representing the edges of the thin partitions between the successive myotomes. In the neighbourhood of the fins the segments are variously modified for their special duties, and in the head there is a more complicated system of muscles, each with its own particular task: one set to move the eyes, another the gill-arches, another the jaws, and so on.

As a general rule, the muscles of a fish are white or pinkish in colour, but in the members of the family which includes the Tunnies (*Thynnus*) and Mackerels (*Scomber*) they are charged with animal oils and appear deep red. The characteristic colour of the flesh of the Salmon (*Salmo*), a beautiful orange-red, is also due to the presence of certain oils. When a Salmon runs up the river after a season of abundant feeding in the sea the flesh is firm and red, and there is a good store of fat in the tissues, but as the time for breeding approaches the fat is expended on the development of the roe and the flesh becomes pale and watery. Not only the colour but also the taste of the flesh varies to some extent in different fishes. The palatability of a fish is due to the presence of some peculiar chemical substance in the muscles which gives it its characteristic flavour. There is, for example, an immense difference in the flavour of a Plaice (*Pleuronectes*) and a Sole (*Solea*), the latter being regarded by many epicures as the most tasty of all fishes. The explanation of this difference in flavour is interesting. In the Plaice, as in most other fishes, the chemical substance is present in the flesh when the fish is alive, but unless it is eaten soon after capture this soon fades away and the flesh becomes comparatively tasteless. In the Sole, on the other hand, the characteristic flavour is only developed two or three days after death in consequence of the formation of a chemical substance by the process of decomposition: thus, it forms a tasty dish even when brought long distances.

After the muscles the alimentary canal or food channel may be considered, that lengthy tube which commences at the mouth and ends at the vent or anus. The alimentary system

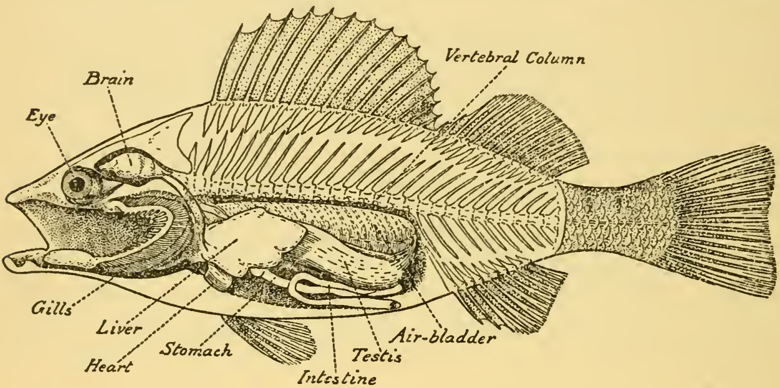


Fig. 68.—INTERNAL ORGANS.

Dissection of a Perch (*Perca fluviatilis*), showing the principal internal organs, × ⅓.

also includes the mouth, jaws, and teeth, which have been already described, and such glands as the liver, pancreas, and spleen (Fig. 68). The alimentary canal is found in its simplest and most primitive condition in the Lampreys and Hag-fishes (*Cyclostomes*), where it forms a straight tube running from mouth to vent, with the different regions scarcely indicated, but in the Selachians and in the vast majority of Bony Fishes the pharynx is followed in succession by a gullet, a stomach, an intestine, and a rectum. Commencing with the mouth, it may be noted that there is never a protrusible tongue in fishes, this organ serving merely as an organ of taste instead of being used to assist in the mastication of the food. Further, although the mouth and intestine both pour out a more or less copious supply of mucous to lubricate the food mass and assist its passage, there are no salivary glands in the mouth as in the higher vertebrates. As the food leaves the mouth it passes rapidly along the pharynx, the walls of which are perforated by the internal branchial clefts, and enters the more or less elongate gullet, from whence it is passed on to the stomach, where the processes of digestion commence. Generally, a slight constriction in the tube marks the boundary between the gullet and stomach, but in some fishes only the change in the character of the cells lining the walls serves to indicate where one begins and the other ends, although the presence of gastric glands in the walls of the stomach provides another clue. The stomach is generally somewhat larger than the gullet or the succeeding intestine, and may be U-shaped, with the concave part of the U directed towards the mouth, or may take the form of a blind sac with the openings for entrance and exist close together at the front end. Attached near the exit of the stomach may be seen in many Bony Fishes a number of blind tube-like sacs, the pyloric caeca (from the Greek *pyloros*, a gate-keeper, and the Latin *caecus*, blind). These may be very numerous as in the Salmon (*Salmo*), few in number, or absent altogether, and they also exhibit considerable variation in length and breadth. No pyloric caeca occur in the Cat-fishes (*Siluroidea*), Pikes (*Esocidae*), Wrasses (*Labridae*), Pipe-fishes (*Syngnathidae*), and others; the Sand Eel (*Ammodytes*) is said to possess a single one, the Turbot (*Rhombus*) two, other Flat-fishes three or a few more; in the Whiting (*Gadus*) one hundred and twenty have been counted, and in the Mackerel (*Scomber*) no less than one hundred and ninety-one. Their function is not yet properly understood, although they are believed to secrete special juices to assist digestion, and may also be concerned with the actual absorption of the food into the blood. Pyloric caeca are not found in any of the higher vertebrates. The walls of the stomach, although provided with a strong coat of muscles, are not, as a rule, particularly thick, but in certain Bony Fishes these are specially modified to deal with a particular diet. In many of the lakes of Ireland there is to be found a form of Trout, known locally as the Gillaroo, which subsists largely on shell-fish, and as a consequence has a remarkably thick-walled and muscular stomach. In the Grey Mullets (*Mugilidae*) and in the Hickory Shad (*Dorosoma*) of America, fishes which feed largely on decomposing vegetable and organic matter mixed with mud, a true gizzard like that of a fowl is developed. In the Mullets the walls are so thickened that the cavity inside is reduced to a mere crack, and is lined by a thick horny covering.

Passing from the stomach, the food, which is now in a liquid condition, enters the intestine, the commencement of which is generally marked by the presence of a ring-like thickening (pyloric valve) of the inner surface of the canal, or, if this is wanting, by the entrance of the ducts leading from the liver and pancreas (Fig. 68). The purpose of this section of the alimentary tract is connected with the absorption of the food into the blood, the essential process of assimilation, and the length of the intestine in a particular fish is closely connected with the nature of its normal diet. In the Sharks and Rays, and in many of the Bony Fishes feeding largely on other fishes, the intestine is straight, or at the most is thrown into one or two simple loops, but in the vegetarians and mud-eaters it is exceedingly long and variously coiled and looped, so as to pack the maximum of absorptive surface into the minimum of space. In the Grey Mullets (*Mugilidae*), for example, it is very lengthy and closely coiled; in the Stone Roller (*Campostoma*), a member of the family of North American Suckers (*Catostomidae*), it is wound round and round the air-bladder, and in the Mailed Cat-fishes (*Loricariidae*) of South America it is disposed in numerous spiral coils like the spring of a watch. Mention may be made here of two important glands pouring their juices into that part of the intestine which lies immediately behind the stomach, and which play their part in the process of digestion. These are the liver, a large irregular mass of tissue varying much in size and colour in different fishes, and generally provided with a gall-bladder as in higher vertebrates, and the pancreas, a more diffuse gland, a part of which is generally more or less embedded in the substance of the liver (Fig. 68). Sometimes the products of liver and pancreas are carried to the intestine by a common duct. Another dark red gland, the spleen, is found attached to the stomach in practically all fishes.

The rectum or large intestine, the last part of the alimentary canal, may be recognised by its straight course to the vent or sometimes by an increase in calibre. In the Sharks and Rays this develops a curious internal structure known as the spiral valve (Fig. 69). This occurs in its simplest form in the Lampreys (*Cyclostomes*), but attains its maximum development in the Selachians, where it may be very complicated and exhibits a good deal of variation in the different species. In one Shark the spiral valve has as many as forty turns, whilst in some of the Hammer-heads (*Sphyrna*) it has the appearance of a scroll. The peculiar and characteristic shape of the fossilised faeces ("coprolites"), known to have been excreted by extinct shark-like fishes, indicate that these forms also possessed a spiral valve. The function of this structure is to increase the area of absorptive surface, an end which is accomplished in the Bony Fishes by an increase in the length of the intestine. A more or less vestigial valve is found in the Sturgeons (*Acipenser*), Bichirs (*Polypterus*), Lung-fishes (*Dipneusti*), Bow-fins (*Amia*), and other primitive forms, but this disappears in all the higher Bony Fishes.

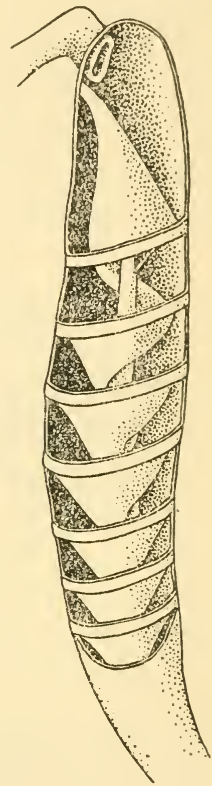


Fig. 69.

Rectum or large intestine of Ray (*Raia sp.*), opened to show spiral valve, $\times \frac{2}{3}$.

In the Selachians and Lung-fishes the rectum opens into a cloaca, which also receives the ducts from the kidneys and reproductive organs, but in all the remaining Bony Fishes it opens to the exterior by the vent or anus, lying in front of the excretory and reproductive openings. The cloaca is invariably situated near the junction between the trunk and tail regions of the body: the vent, on the other hand, varies considerably in position in different fishes, and may occupy almost any position from the primitive one at the hinder end of the trunk to one between or even in front of the pectoral fins. In the Electric Eel (*Electrophorus*) and other Gymnotid fishes the vent is actually to be found *in the throat*.

Space will not permit of a description of the elaborate and delicate structure of the lining membrane of the different parts of the alimentary canal, but it may be pointed out that this is, for the most part, designed either to prepare the food for absorption into the blood or to carry out the absorptive process itself. Like any other animal, the fish, in order to live, has to convert the food into power, and after the food is dissolved in the stomach and intestines the nutritious part is taken up by the walls of the canal, whence it passes into the blood. The elaborate intercommunicating system of arteries and veins, by means of which the nourishment is carried to the hungry cells in every part of the body, is known as the vascular system, and its principal features may now be described.

The essential organ of this system is the heart, in fishes a stout, muscular pump of comparatively simple design and small size, situated in a chamber known as the pericardium, which generally lies below the pharynx and immediately behind the gills (Figs. 68, 70), although in some of the Eels (*Apodes*) it is placed some way behind the head. The heart consists of four parts: a chamber or sinus into which the veins open; an auricle

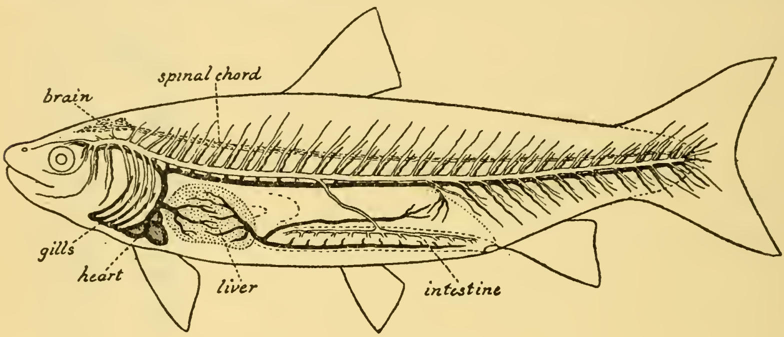


Fig. 70.

Vascular system of a typical fish. (After Grote, Vogt and Hofer.) Arteries—white; veins—black.

or atrium; a deep red, thick-walled ventricle, the rhythmical contractions of which serve to drive the blood round the body; and a bulb at the base of the main artery carrying the blood to the gills. In the Selachians and more generalised Bony Fishes this bulb is muscular, provided with special valves, and pulsates like the ventricle, but in all higher forms these structures degenerate and the walls are incapable of contraction. It is of special interest to note that in the air-breathing Lung-fishes there are traces of the beginnings of a division of the auricle and ventricle into two by the development of a partition, thus foreshadowing the four-chambered heart of the higher vertebrates. From the ventricle the blood passes through the bulb into the great ventral aorta, from both sides of which branches carry it to the fine vessels in the gills, where the respiratory exchange of gases takes place (*cf.* p. 40). Having been purified, the blood, instead of returning to the heart, is again received into a main artery—the dorsal aorta—giving off various branches which divide again and again into smaller and smaller vessels, by means of which the oxygenated blood is carried to the remotest parts of the body (Fig. 70). The blood gives up its oxygen to the hungry cells, receives their waste products, and then, loaded with impurities, makes its way back to the heart through the veins. All the large veins, with the exception of those from the liver, unite into two large vessels running across the body, and these meet together as they open into the sinus of the heart. The details of the circulation may vary somewhat in the different groups of fishes, but the essential features are as described above.

The amount of blood present in the body of a fish is a good deal less than in the higher vertebrates; it is pale in colour, and its flow through the arteries and veins is a sluggish one. Further, except in forms such as the Tunny (*Thunnus*), Albacore (*Germo*), and Sword-fish (*Xiphias*), remarkable for their great muscular activity, in which it is abundant and comparatively warm, the temperature of the blood is but little higher than that of the surrounding water. In addition to the blood-vessels, there is also the fine network of tubes known as the lymphatic system, widely distributed in the connective tissue of different parts of the body, collecting the blood plasma which oozes through the fine capillaries for the nourishment of the tissues, and carrying it back to the veins. In some fishes lymph hearts are present where the larger lymphatics open into the veins, and the Common Eel (*Anguilla*), for example, has such a pulsating organ in its tail.

Among the remaining organs occupying the interior of the body cavity are the kidneys, reproductive organs, air-bladder, and such ductless glands as the thyroid, thymus, and suprarenal bodies. These last glands are as yet little understood, and need not be further considered here. The kidneys are generally long, thin glands, dark red in colour, situated immediately below the vertebral column. Their purpose is to extract certain impurities from the blood, poisonous by-products formed by the processes of combustion constantly taking place in muscles and nerves, and to convey them to the exterior by means of urinary ducts. The reproductive organs are of two kinds, ovaries in the female, testes or milt in the male, or, as they are familiarly called, hard and soft roes (Fig. 68). These will be considered in greater detail in the chapter devoted to breeding (*cf.* p. 279).

It has been previously pointed out that the air-bladder is an organ with more than one duty, and its function as a lung (*cf.* p. 49) and as a sound-producing organ (*cf.* p. 155) has been already considered, while in the next chapter its connection with the inner ear will be described. Its original function was probably a respiratory one, but in the vast majority of Bony Fishes in which this organ is present it has discarded this duty and taken on another, namely, that of a hydrostatic organ or float, enabling the fish to adapt itself to the changing pressure encountered at different depths. The walls of the bladder are richly supplied with fine blood-vessels, and at certain areas these are accumulated to form the so-called red bodies or red glands, masses of interlacing and tightly packed arteries and veins. As far as is known, these glands occur only in those fishes in which there is no duct connecting the bladder with the gullet, and it is believed that they secrete gases into the bladder. Another remarkable structure, the oval, seems to have the power of absorbing some of the excess gas when necessary. The gas has been analysed and found to contain oxygen, nitrogen, and a small trace of carbon dioxide. These are the same constituents as are contained in atmospheric air, but the proportion of oxygen is very much greater. Further, the amount of oxygen varies somewhat in different fishes, generally being greater in marine than in fresh-water forms; it is considerably greater in fishes living at any depth, in some cases as much as eighty-seven per cent. of the whole.

The hydrostatic function of the air-bladder is to render the weight of the fish the same as the surrounding water in which it lives. In this stable condition it floats in the water without any tendency either to rise or to sink, and is able to swim with the minimum of muscular effort. It is clear that if the fish rises to a higher level the pressure of the surrounding water is diminished, the gas in the bladder expands, and the body tends to shoot upwards. To counteract this, and to restore the fish to a plane of equilibrium at the new level, gas is absorbed by the oval, or, if the bladder is connected with the gullet, some of the gas is allowed to escape through this channel. In the same way, if the fish swims downwards the hydrostatic pressure increases, the body becomes heavier and tends to sink rapidly towards the bottom, but by increasing the volume of gas in the air-bladder the necessary adjustment is attained. This power of changing the volume of gas is limited, however, and the process of secretion or absorption is by no means always a rapid one. For this reason a sudden rise or fall is dangerous to the fish, and if it ascends suddenly from a considerable depth to the surface it may be quite incapable of descending again. An interesting case of this nature is given by Mr. Semper in his book, *Animal Life*, concerning one of the White-fishes (*Coregonus*), an important food-fish of Lake Constance, known locally as the Kilch. He describes how "the fish are caught in nets and brought to the surface of the water; they come up invariably with the belly much distended, the air in the swimming-bladder, being relieved from the pressure of the column of water, has expanded greatly and occasioned this unnatural distension, which renders the fish quite incapable of swimming. Under these conditions the fish is naturally unable to live for any length of time. But the fishermen of the lake have a very simple remedy; they prick into the air-bladder with a very fine needle; the air escapes with some force, the distension subsides, and the fishes are enabled to live under totally changed conditions as to pressure, even in quite shallow water and at the surface. . . . Hence the Kilch is confined to a certain depth, because it is not capable of accommodating the tension of its swimming-bladder to the change of pressure in the column of superincumbent water." A similar experiment has been carried out on fishes in the aquarium, and individuals, floating helplessly at the surface at one moment, have resumed their normal activities as soon as the air-bladder was punctured. Sometimes when deep-sea fishes are brought to the surface by the trawl or dredge, so great is the expansion of the contained gases brought about by the rapid change in external pressure that the air-bladder is forced out through the gullet and projects from the mouth. Aristotle was aware of this phenomenon, for he writes that "very often the Synodon and the Channa cast up their stomachs (!) while chasing smaller fishes; for, be it remembered, fishes have their stomachs close to the mouth, and are not furnished with a gullet."

From the foregoing facts it is clear that a fish like a Shark, which is devoid of an air-bladder, possesses a body which is heavier than the water it displaces and tends to sink continuously, but this downward movement is overcome by a constant movement of the muscular tail and of the fins. Further, in oceanic fishes such as the Myctophids or Lantern-fishes (*Myctophidae*), requiring an exceptional freedom of movement in all directions, and habitually swimming rapidly from one level to another, the possession of an air-bladder would be of little advantage, if not an actual hindrance to the fish, and this organ has been lost by these fishes in the course of evolution. Nor do those forms living on the sea bottom require a hydrostatic float, and no air-bladder is found in the Flat-fishes, Lump-suckers, many Blennies, etc., nor is it present in those forms which spend their lives in the comparatively shallow water of mountain streams.

CHAPTER X

NERVOUS SYSTEM, SENSES, AND SENSE ORGANS

Nervous system: brain, spinal cord, nerves. Sensory and motor nerves. Olfactory organs. Sense of smell. Eyes: structure, modifications, position. Sense of sight. Auditory organs. Otoliths. Connection of air-bladder with internal ear. Weberian mechanism. Sense of hearing. Internal ear and equilibrium. Sense of taste. Of touch. Barbels. Other tactile organs. Lateral line: structure, functions. Sense of pain. Schooling or shoaling sense. Sleep. Reflex and conscious actions.

The principal organs of a fish's body have now been described, and it remains to consider the nervous system, the elaborate organisation of brain, nerves, and sense organs, unifying and co-ordinating the complex activities of the body, and placing the various parts in communication with one another and with the outside world. This has been compared to a telephone system with the central exchange represented by the brain; but although this analogy is in many respects a good one, it must not be pushed too far, for as will be shown in the following pages, there are a number of important differences between the two organisations.

As in higher vertebrates, the nervous system consists of brain, spinal cord, and nerves. In the newly formed embryo the first two are indistinguishable, and together form a simple tube, the medullary canal, lying along the upper surface of the body. That part of the tube which is to form the spinal cord soon becomes more solid through the thickening of its walls, but a minute central canal persists throughout life as a vestige of the original cavity. The anterior end of the tube in the head region enlarges to form the brain, and at the same time two transverse constrictions divide this into three hollow chambers or primary vesicles, known respectively as the fore-, mid-, and hind-brain. As development proceeds, certain parts of the walls of the vesicles become variously thickened, and others give rise to hollow outgrowths, which may be either median or paired. In this way the elaborate brain of the adult fish comes into being, the original three chambers continuing to exist as a series of linked spaces or ventricles.

It will be unnecessary to describe the brain of a fish in any detail, but a brief outline of its more important features may be given, commencing with those at the anterior end which have been derived from the original fore-brain, and proceeding backwards. At the extreme front is a pair of hollow chambers, the olfactory lobes, the inner cavities of which are in communication with the parts of the brain lying immediately behind. These lobes, centres of the sense of smell, are large in the Cyclostomes, relatively enormous in the Sharks and Rays (Fig. 71A), but in the majority of Bony Fishes tend to be reduced in size, and may be placed at the end of lengthy stalks (Fig. 71B).

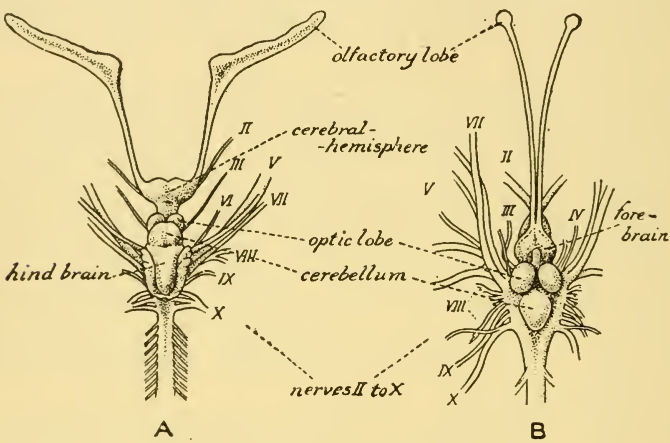


Fig. 71.—BRAINS.

A. Upper surface of brain of Ray (*Raia sp.*), $\times \frac{1}{2}$; B. The same of Cod (*Gadus callarias*), $\times \frac{1}{2}$.

In the Cyclostomes, Selachians, certain of the more primitive Bony Fishes, and in the Lung-fishes, the olfactory lobes are followed by another pair of outgrowths, the cerebral hemispheres, which may be completely differentiated into two lobes, or may coalesce to form a single cerebrum (Fig. 71A). In the Cyclostomes these hemispheres are very small, forming mere appendages of the olfactory lobes. They are rarely developed in Bony Fishes, but, instead, a bulging chamber with a non-nervous roof grows forward from the fore-brain, and from its sides the olfactory lobes are formed. In higher vertebrates the cerebrum is the centre of the more complex mental processes, such as thought and reason, but in most fishes it seems to be intimately associated with the sense of smell. Starting with fishes, and passing upwards through the amphibians and reptiles to the birds and mammals, this region of the brain becomes progressively larger, until in man it forms a very large and important part. It is of interest to note that the Selachians, so much more primitive in many other characters, have the cerebral region of the brain much better developed than in the majority of Bony Fishes. Other important parts derived from the primary fore-brain are the optic vesicles, which arise from the sides and later become transformed into parts of the eyes and their associated nerves, and the pineal body or gland, arising from the roof, which will be considered further in connection with the eyes. From the floor of the fore-brain a hollow outgrowth, the infundibulum, develops, to which is attached the pituitary body or gland, whose secretion plays an important part in the regulation of the activities of the body: at the sides of this gland are two small lobes and a tiny sac. The remaining structures, which arise inside the original fore-brain, are of minor importance and need not be detailed here.

The roof of the mid-brain bulges out to form a pair of optic lobes (Fig. 71), which may or may not be connected with the main central cavity or vesicle. They vary greatly in size in different fishes, and may cover the fore-brain and press against the cerebral hemispheres. In some of the Lung-fishes (*Dipneusti*) the two are united to form a single oval body. As their name implies, the optic lobes are associated with the sense of sight.

The principal part formed from the original hind-brain is a large single lobe, the cerebellum (Fig. 71), lying behind the optic lobes. Below this is the medulla oblongata, the cavity of which communicates with the cerebellum above and with the central canal of the spinal cord behind. In the Lampreys (*Petromyzonidae*) the cerebellum is very small, in the Hag-fishes (*Myxinidae*) it is absent altogether; in the Selachians and Bony Fishes it is very large, sometimes almost covering the optic lobes.

The brain never entirely fills the cavity of the cranium, the space between it and the membrane lining the inner surface of the cranial cavity being filled with a sort of gelatinous tissue. In a young fish it is very much larger in proportion to the size of the body than in an adult. The size of the brain also exhibits considerable variation in different fishes, although on the whole it may be regarded as relatively small. The brain of the Burbot (*Lota*) has been estimated to be $\frac{1}{720}$ of the weight of the entire fish, that of the Pike (*Esox*) $\frac{1}{1305}$, whilst in some of the Sharks it is relatively still smaller. It is a remarkable fact that the Mormyrids of tropical Africa have a brain which is a good deal larger in proportion to the size of the body than in any other fish, that of *Mormyrus*, for example, being between $\frac{1}{52}$ and $\frac{1}{82}$ of the weight of the entire fish, or twenty-five times greater than that of the Pike.

There is little more to add concerning the spinal cord, which is very uniform in structure throughout the Selachians and Bony Fishes. It usually extends the whole length of the body, but is much shorter in some of the Globe-fishes (*Tetrodontidae*) and their allies. In the huge Sun-fish (*Mola*) it is remarkably reduced, being actually shorter than the brain: in a specimen two and a half metres long and weighing about a ton and a half the cord was only fifteen millimetres in length.

The nerves may be divided into two categories, spinal and cranial, the former having their origin in the spinal cord, the latter in the brain. The spinal nerves are metamerically arranged, that is to say, their number is the same as that of the vertebrae, through or between which they pass out. The cranial nerves consist of ten pairs, which may be briefly described (Fig. 71). The first or olfactory nerve is a purely sensory one, and controls the sense of smell, connecting the nasal organ with the olfactory lobe. The second or optic nerve (II) is likewise sensory, and supplies the eye. In the Cyclostomes each optic nerve runs from the optic lobe direct to the eye of the same side; in the Selachians the two nerves are fused together to form an optic chiasma; and in the Bony Fishes the two cross each other below the brain immediately after leaving the optic lobes, the nerve from the left lobe going to the right eye and *vice versa*. The third, fourth, and sixth are motor nerves, and their function is to supply and stimulate the muscles which move the eyes. The third or oculomotor (III) starts from the lower surface of the brain, the fourth or trochlear from the groove between the optic lobes and the cerebellum, but the sixth or abducens (VI), like the remainder of the cranial nerves, has its origin in the medulla oblongata. The fifth or trigeminal nerve (V), and the seventh or facial (VII), are mixed nerves, being partly sensory and partly motor. Both have branches which are widely distributed over the snout and jaws. The eighth or auditory (VIII) is another sensory nerve and supplies the organ of hearing. The ninth or glosso-pharyngeal (IX) is mixed, and has a branch which forks over the first gill-cleft and another long one running forward to the region of the palate. Finally, the tenth or vagus (X), another mixed nerve, is a complicated one, which not only gives off forked branches to the remaining gill-openings, but the main stem passes along the alimentary canal and sends nerves to its muscles and to those of the heart, whilst another stem, which separates from the nerve soon after it leaves the brain, supplies the whole of the sensory system of the lateral line.

Microscopically, a nerve is not the simple structure that it appears to the naked eye, but is made up of an enormous number of very fine fibres lying together side by side like the separate wires of a telephone cable. Each of these fibres may be of considerable length and is about one-tenth of the thickness of a human hair. Actually, they are nothing more than fine processes drawn out from star-shaped nerve cells situated in the brain or spinal cord, the tissue of these organs being made up entirely of cells of this nature. Any comparison of the nerves with the wires of a telephone system is inevitably inaccurate, for, whereas the telephone wires carry messages in one direction only, each nerve contains fibres of two kinds, one carrying messages or nervous impulses outwards, the other inwards. The first or motor fibres carry impulses to the various muscles, causing them to contract; to the glands, causing them to secrete their special products; or to the stomach and intestines, to accelerate or retard the processes of digestion. The sensory fibres, on the other hand, carry nervous impulses to the brain or spinal cord from the sense organs, conveying warning of cold, hunger, pain, fear, and the like. As soon as these messages, which generally follow some change in the conditions of the outside world, are received, motor impulses are promptly sent back along the nerves, and by an appropriate contraction or expansion of certain muscles, matters are quickly adjusted. The manner in which the various actions of the body are co-ordinated by the central nervous system will be dealt with in due course, and for the present it must suffice to point out that every muscle-fibre is supplied by its own nerve-fibre, one end of which forms a nerve cell in the brain or spinal cord and the other terminates in a cluster of fine branches spread out over the surface of the muscle-fibre. Every muscle is in turn made up of a large number of separate fibres, and is served by its own nerve, which controls its every action. When it is considered that to perform the simplest movement, the waving of a fin or the opening of the mouth, the co-ordinated action of a whole group of muscles is required, some idea will be gained of the vast number of nervous impulses continually going backwards and forwards from sense organs to brain and spinal cord, and from the brain and spinal cord to the muscles and glands.

In their general plan the sense organs of a fish are not unlike those of higher vertebrates, nostrils, tongue, eyes, and ears all being developed; but whereas certain senses of special importance to an animal living in a liquid medium are greatly accentuated, others are very feebly organised. Further, it is possible that fishes possess at least one extra sense unknown to land vertebrates.

The sense of smell resides in the nasal or olfactory organs, but, unlike the higher vertebrates, the nostrils or nasal openings are never (or scarcely ever) used for breathing purposes. Typically, each nasal organ consists of a somewhat deep pit lined with special sensitive tissue, and in order to provide the maximum of sensitive surface, the lining is generally puckered up into a series of ridges which may be parallel to each other or arranged in radiating fashion like a rosette (Fig. 72B′). The Cyclostomes are unique in possessing a single nostril on the upper surface of the head (Fig. 72A, A′), which in the Lampreys (*Petromyzonidae*) leads into a blind nasal sac, but in the Hag-fishes (*Myxinidae*) actually communicates with the roof of the mouth. In the Sharks and Rays the olfactory organs are invariably large, and, like the mouth, are placed on the lower surface of the head (Figs. 14B; 45B). The single opening of each organ is guarded by valvular flaps, provided with their own cartilages and moved by special muscles. In certain Sharks and Dogfishes deep oro-nasal grooves connect each organ with the angle of the mouth on the same side. In the majority of Bony Fishes these grooves are wanting, but in the Lung-fishes (*Dipneusti*) they have been converted into short canals, and the nasal pits communicate with the mouth by true internal nostrils, thus foreshadowing the condition found in higher vertebrates, where they are used for inhaling air for breathing purposes. In Bony Fishes both nasal pits are divided into two separate portions, each with its own opening to the exterior (Fig. 72B). The position of the nostrils varies considerably in different fishes; in some the anterior nostril is widely separated from the posterior, in others the two are almost in contact. Occasionally, as in the Cichlids (*Cichlidae*) and in certain Wrasses (*Labridae*), the nasal organs each have only a single external orifice. In some of the Eels (*Apodes*) the anterior nostril is situated on the upper lip (labial position) and in many of the Globe-fishes (*Tetrodontidae*) there are no actual apertures but a pair of solid nasal tentacles.

Most of the oceanic Ceratioid Angler-fishes with line and bait have small eyes and normal nostrils (Figs. 31, 91B), but certain forms (*Lipactis*, *Rhynchoceratias*) have the lure altogether wanting, and the eyes and nostrils are more or less enlarged,

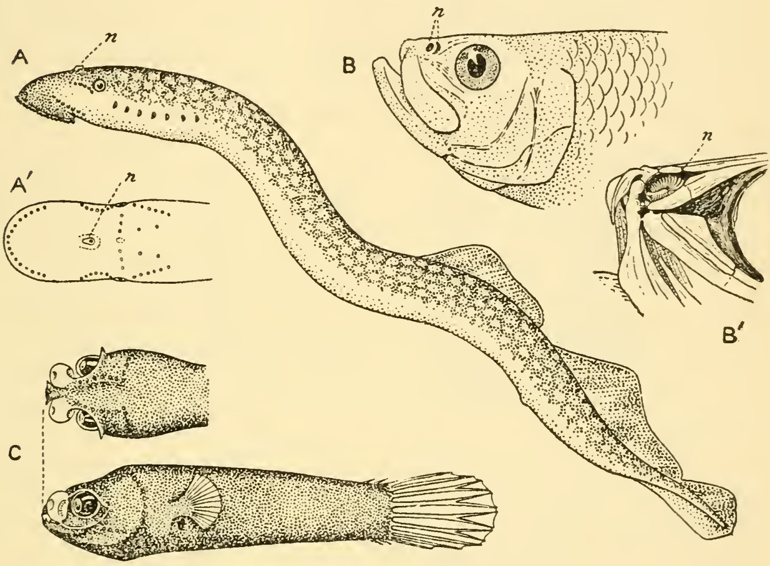


Fig. 72.—NOSTRILS AND NASAL ORGANS.

A. Sea Lamprey (*Petromyzon marinus*), $\times \frac{1}{8}$; A′. Upper view of head of same ; B. Head of Herring (*Clupea harengus*), $\times \frac{1}{2}$; B′. Front part of head dissected to show nasal organ. (After Derscheid) ; C. *Aceratias macrorhinus*, $\times$ about 2 ; *n*., nostril.

perhaps indicating that they seek their food by smell and sight (*cf.* p. 315). In the genus *Aceratias* (Fig. 72C) the lure is again absent, the eyes are directed forwards, the snout is shortened in relation to the stereoscopic vision (as in man), and the olfactory organs are relatively enormous. They are, however, developed on a somewhat different plan, one nostril being at the end of a tube.

There can be little doubt that the sense of smell in fishes is relatively acute, as has been proved by numerous experiments. The large nasal organs of Sharks are said to enable them to "scent actively as well as to smell passively," and it is well known that the smell of flesh or blood, or of a decaying carcase will attract them to it from some distance away. The Caribe or Piraya (*Serrasalmus*), the ferocious Characin-fish of the rivers of South America (*cf.* p. 130), is irresistibly attracted by the smell of blood, and woe betide the animal unfortunate enough to be bitten by one of these pests, for hundreds more will rush to the spot with incredible rapidity. As long ago as 1653 Izaak Walton wrote the following in his *Compleat Angler* with reference to the sense of smell in fishes. "And now I shall tell you that which may be called a secret. I have been a-fishing with old Oliver Henly, now with God, a noted fisher for Trout and Salmon; and have observed that he would usually take three or four worms out of his bag, and put them into a little box in his pocket, where he would usually let them continue half an hour or more before he would bait his hook with them. I have asked him his reason, and he has replied: 'He did but pick the best out to be in readiness against he baited his hook the next time'; but he has been observed, both by others and myself, to catch more fish than I, or any other body that has ever gone a-fishing with him, could do, and especially Salmons. And I have been told lately, by one of his most intimate and secret friends, that the box in which he put these worms was anointed with a drop, or two or three, of the oil of ivy-berries, made by expression or infusion; and told that by the worms remaining in that box an hour, or a like time, they had incorporated a kind of smell that was irresistibly attractive, enough to force any fish within the smell of them to bite."

Mention may be made of a number of careful experiments conducted by Mr. Gregg Wilson at Plymouth at the end of the last century, with a view to ascertaining the respective parts played by the sense of smell, sight, etc., in obtaining food. He concluded that "fish that are not *very hungry* habitually smell food before tasting it," but, when really ravenous, Pollack would bolt clams that had been saturated with alcohol, turpentine, chloroform and other unpleasant substances without any hesitation. He also states that in many cases the fish actually search for the meal by sight alone, and then test the quality of what they have found by smelling it. Some blind specimens of Pollack, however, were able to find their food by smell alone, and there are doubtless other forms which do this habitually, especially those dwelling in muddy or foul water, where the eyes would be of little use. The Cod (*Gadus*) is generally believed to feed more at night than in the day-time, and may rely largely on its olfactory sense. Mr. Gregg Wilson has shown that the Dab (*Limanda*) is normally a sight-feeder, but under experimental conditions, if a number of worms were placed in a small wooden box with minute apertures to allow the water to pass in and out considerable excitement was immediately produced, and the fish hunted eagerly in every direction. "When water in which many worms had lain for some time was simply poured into the tank through a tube that had been in position for several days, and by a person who was out of sight of the dabs, the result was most marked. . . . Yet there was nothing visible to stimulate the quest."

From the above and other sources of evidence it may be concluded that the sense of smell plays a fairly important part in the daily life of a fish, and although as a general rule this is not the only sense upon which it relies to obtain a meal, if the eyes or ears should in any way fail to function it could probably be induced to search for its food by smell alone.

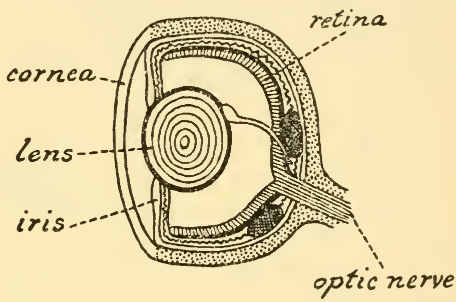


Fig. 73.

Vertical section through the eye of a Trout (*Salmo trutta*). Semi-diagrammatic. (After Parker and Haswell.)

In its general form the eye of a fish is not unlike our own, but it is necessarily somewhat modified for vision under water. The eye, as is well known, acts after the manner of a photographic camera, the two essential parts being the sensitive screen or retina at the back, and the lens at the front, which projects an image of the outside world on the screen (Fig. 73). The lens of a land vertebrate is somewhat flat and convex on both sides, but in the fish it is a globular body, the extreme convexity being a necessity under water because the substance of the lens is not very much denser than the fluid medium in which the fish lives. The space between lens and retina is filled with a transparent jelly-like substance, the vitreous humour. The transparent outer wall of the eye, the cornea, is somewhat flatter in fishes, and the space between this and the lens is filled by the watery aqueous humour. In land vertebrates the iris of the eye is capable of great contraction, and, acting like the diaphragm of a camera, regulates the amount of light allowed to enter the eye. In fishes it generally surrounds a rounded pupil, and has comparatively little power of contraction. It may be brightly coloured, red, orange, black, blue, or green.

Land vertebrates are able to accommodate the eyes to vision at varying distances (that is to say, to focus the eyes on objects both near and far away) by altering the convexity of the lens through the action of special muscles; in fishes the same end is accomplished by simply changing the position of the lens with regard to the retina. The retina itself has an elaborate structure, and is made up of numerous sensitive cells; its function is to set up appropriate nervous impulses when acted upon by the rays of light focused upon it by the lens, and thus to convey to the brain a picture of the object upon which the fish has fixed its attention. It may be noted here that as the eyes of a fish are placed on either side of the head, what is known as monocular vision is the rule, a fish being incapable of focusing both its eyes on the same object at one and the same time.

Some of the accessory structures associated with the eyes of higher animals are wanting. For example, no lachrymal glands are developed, so that a fish cannot shed a tear, nor is this necessary when the outer surface of the eyeball is kept constantly clean and moist by the surrounding water. No fishes possess true eyelids, the skin and integuments of the head simply passing over the eye and becoming transparent as they cross the orbit. At the most, these are represented by a few folds of skin at the margins of the eye, capable of little if any movement, and even when stretched to their fullest extent leaving the greater part of the eye uncovered. In some fishes, notably some of the Grey Mullets (*Mugilidae*) and Herrings (*Clupeidae*), the skin over the eyeball is thickened, and, although still transparent, covers the greater part of its outer surface, leaving a small aperture in the centre. Such forms are said to have an adipose eyelid. Some Sharks (*e.g.* the Tope *Eugaleus*) have a third eyelid known as the nictitating membrane at the front corner of the eye, which is freely movable and can be pulled down to cover the whole surface. In bottom-living forms like the Rays and Flat-fishes, the upper part of the pupil is covered by a thick dark lobe, often covered with scales, forming an effective curtain to shut off the light from above (Figs. 14B; 40).

A curious modification of the eyes is found in the Four-eyed Fishes (*Anableps*) of the rivers of Central and South America. Each eye projects well above the top of the head, and is divided into two equal parts by a dark horizontal band: each of these sections is of a different structure, the upper being adapted for vision in the air, the lower for vision under water (Fig. 74D). These fishes swim about in small shoals at the surface of the

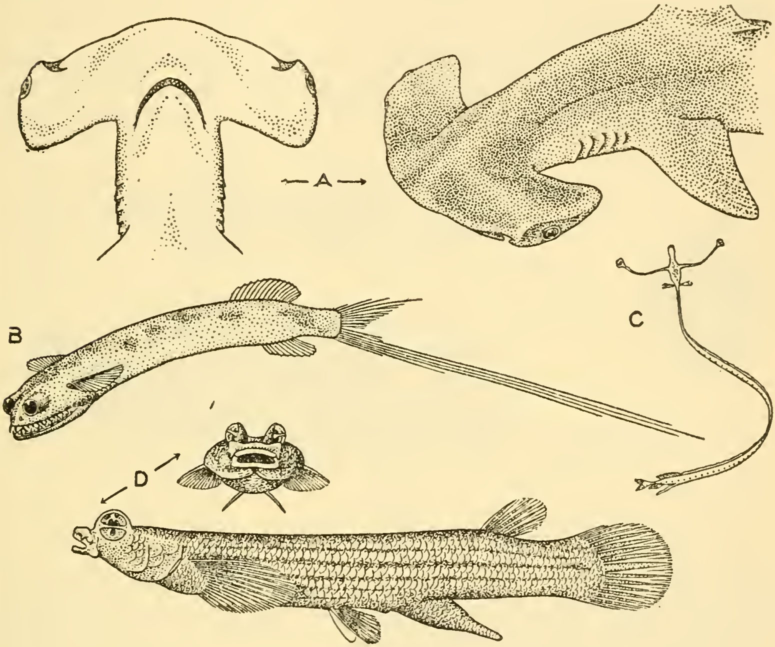


Fig. 74.—EYES.

A. Head of Hammer-headed Shark (*Sphyrna zygaena*), $\times \frac{1}{10}$; B. *Gigantura chuni*, $\times \frac{1}{2}$; C. *Stylophthalmus paradoxus*, $\times \frac{1}{2}$; D. Four-eyed Fish (*Anableps tetrophthalmus*), $\times \frac{1}{2}$.

water, and the level of the water reaches as far as the bar dividing the eye. They are thus enabled to detect, not only insects skimming over the surface or actually flying in the air, but also any swimming below the surface.

Some oceanic fishes (*e.g. Giganturidae*) are provided with curious telescopic eyes, and these generally take the form of short, protruding cylinders, each ending in a very rounded cornea (Fig. 74B). They may be directed either upwards or forwards, and as they lie parallel to one another, it is possible that these fishes are capable of binocular vision. In the rare and curious oceanic fish (*Opisthoproctus*) the telescopic eyes are directed upwards, and cannot be turned in any other direction. In the young of other oceanic forms (*Stylophthalmus*) the eyes are placed at the end of very long stalks growing out from the sides of the head (Fig. 74C). The Hammer-headed Sharks (*Sphyrna*), with the eyes placed at the extremities of lobe-like lateral outgrowths (Fig. 74A), have been already described in an earlier chapter.

In a large number of Bony Fishes there is a distinct connection between the habitual mode of life and the degree of perfection of the organs of vision. In the Cat-fishes (*Siluroidea*), for example,

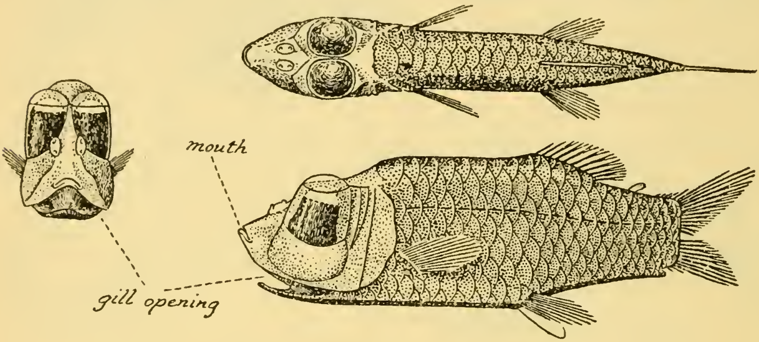


Fig. 74E.

Opisthoproctus soleatus, $\times \frac{1}{2}$.

and in other forms living in more or less turbid water the eyes are much reduced in size and efficiency, and in others (Cyprinids, Cat-fishes, Cyprinodonts, etc.), which have taken to a life in caves, wells, or subterranean streams, these organs have disappeared altogether, although the young may be born with well-developed and perhaps functional eyes (*cf.* p. 232). In the Hag-fish (*Myxine*), which is in the habit of burrowing into the body of a living fish and devouring its flesh, the eyes are quite vestigial. Among oceanic fishes the eyes vary greatly in size, and biologists have found considerable difficulty in attempting to explain the connection between the size and efficiency of the eyes and the intensity of the light at different depths. A trawl coming up from the abyssal depths will contain fishes with large eyes, side by side with others totally blind or with very small eyes. Starting at the top, fishes living at or near the surface of the sea have normal eyes, and in regions from about one hundred and fifty to five hundred metres below the surface the eyes tend to become large (Figs. 63A; 91D), a modification designed to make use of every available ray of light which penetrates thus far. It is now known that light penetrates to far greater depths than was formerly supposed, and photographic plates have been acted upon at a depth of five hundred metres, while at one thousand metres traces of light are still perceptible. At greater depths, say from five hundred to two thousand metres below the surface, the fishes tend to possess small or imperfectly developed eyes, and, as a general rule, the luminous organs also exhibit a decrease in size (Figs. 31, 78, 91). Finally, in many fishes living on or near to the sea-floor in the abyssal depths, of which the Grenadiers or Rat Tails (*Macruridae*) will serve as examples, the eyes are comparatively large and well developed, but luminous organs are absent or but feebly developed (Fig. 62A). This curious fact can only be explained on the assumption that these oceanic abysses are not completely dark, and it is probable that the invertebrate bottom animals, which are known to be luminous, emit light of sufficient strength to make objects on the bottom visible to these fishes.

Just as a man who has lost his sight tends to develop a remarkably delicate sense of touch or acute sense of hearing, fishes with eyes vestigial or absent tend to have one or other of the remaining senses accentuated in order to compensate for the loss of vision. Thus, most of the Cat-fishes (*Siluroidea*) have long, sensitive barbels or feelers, some of the blind cave-fishes have the lateral line system highly developed and covering the greater part of the head (*cf.* p. 232), and several deep-sea fishes have the rays of the paired fins prolonged to form sensitive filaments.

The position of the eyes departs from the normal in some fishes, and in bottom-living forms, such as the Rays, Anglers, and Star-gazers, instead of being placed on either side of the head, the two eyes lie close together on its upper surface. The Flat-fishes (*Heterosomata*) are unique in having both the eyes on the same *side* of the head (Figs. 8B; 40A-C). In the Mud Skipper (*Periophthalmus*), which is in the habit of leaving the water and walking about on the sand or mud, the eyes are placed on the end of more or less prominent protuberances, and can be turned in all directions, a modification of obvious advantage (Fig. 34f).

When it is considered that a fish such as the Trout (*Salmo trutta*) will show a preference for a particular kind of fly, whether natural or artificial, and will seize this with great rapidity when it is placed within his range of vision, it seems certain that, in some fishes at least, the sense of sight is a keen one. A Trout has been known to refuse a certain type of fly again and again, but when another was substituted of similar size and shape, but of different colour, this was promptly accepted. This would suggest that the Trout is sensitive to colour, but whether this is the general rule among fishes is not yet clear. Experiments have shown that the sense of sight probably plays the most important part in the search for food, but, at the same time, this is much more limited than that of a land vertebrate; and, owing to the general haziness of the water, due to the presence of organisms and other matter suspended therein, objects must appear of somewhat uncertain outline. The extreme convexity of the lens of the eye points to the fact that a fish is near-sighted, and even in the clearest water it is doubtful whether the range of vision exceeds about twelve yards, if as far as this. It is not unlikely that the fish really notices movements or changes in outline rather than actual objects.

In describing the brain, mention was made of the pineal gland or epiphysis arising from the roof of the primary fore-brain. This is particularly well developed in the Sharks, but in these and the Bony Fishes it is little more than a nervous enlargement. In the Lampreys and Hag-fishes, however, this structure bears a strong resemblance to an eye, and the external skin covering this region is partially transparent in the adult. In the fossil remains of ancestral Cyclostomes there are indications of the presence of one or two such median sense organs on the upper surface of the skull, and it is possible that these early fishes had one or two functional eyes on the upper surface of the head in addition to those at the sides.

The auditory organ or inner ear of a fish, the next of the sense organs to be considered, consists of a membranous sac or vestibule enclosed in a chamber or capsule on either side of the hinder part of the skull. Its purpose is twofold, for not only is it the seat of the sense of hearing, but it is also concerned with the maintenance of equilibrium: indeed, it is possible that the latter function is the more important of the two. Comparing the fish's ear with that of a man or other higher vertebrate several important differences are at once apparent. The human ear consists of three parts: the external, middle, and inner ear. In the fish the first two of these are entirely wanting, there being no outer meatus or trumpet, no ear-drum, and no Eustachian tube connecting the middle ear with the pharynx, and the inner ear itself is of much simpler design. The membranous sac is partially constricted into two portions, an upper chamber or utriculus, and a lower or sacculus: a small sac-like outgrowth from the latter, known as the lagena, is all that is developed of the spirally twisted cochlea, the essential

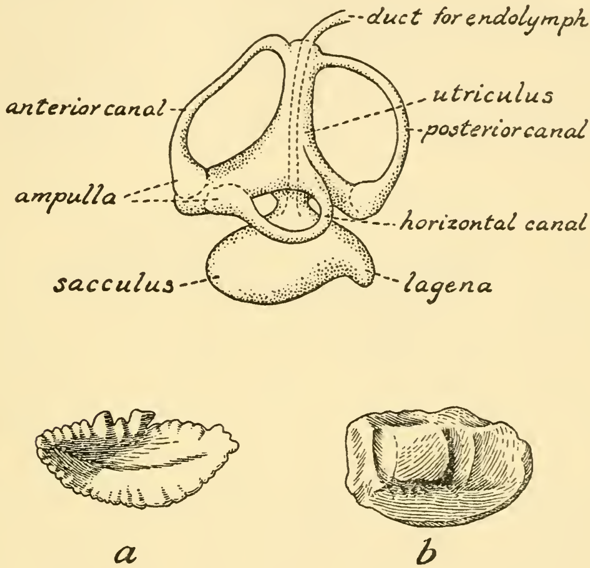


Fig. 75.—AUDITORY ORGAN OF A TYPICAL FISH.

a. Otolith (Sagitta) of Cod (*Gadus callarias*), $\times \frac{2}{3}$; b. The same of Meagre (*Sciaena aquila*), $\times \frac{2}{3}$.

seat of hearing in the higher vertebrates (Fig. 75). Connected with the utriculus are the three semicircular canals, which play an important part in the maintenance of balance, two running in a vertical direction and placed at right angles to one another, the third horizontal. At one end of each of these canals is a swelling, the ampulla. In the Lamprey (*Petromyzon*) the horizontal canal is wanting, in the Hag-fish (*Myxine*) there is a single canal with an ampulla at each end, but in other fishes all three canals are developed.

In the embryo fish the auditory organ originates as a hollow bladder, which is simply pushed inwards from the external skin, a mode of development which is exactly similar to that of the olfactory organs already described. At a later stage this bladder takes on a more complicated structure, and the tube by means of which it communicated with the exterior generally becomes closed up in the adult fish, although in Selachians a small opening on the surface of the skull is retained throughout life.

The inner walls of the utriculus, sacculus, and lagena are provided with patches or ridges of highly sensitive tissue, and the cavities of the chambers are filled with a fluid known as the endolymph: a similar fluid, the perilymph, occupies the spaces between these parts and the walls of the containing auditory capsule. In addition to the endolymph, the cavities also contain certain bodies composed of limy matter secreted by their walls. In the Selachians these take the form of small separate particles connected with one another by mucus, but in most Bony Fishes they form large, solid concretions or otoliths, a sagitta in the sacculus, an asteriscus in the lagena, and a lapillus in the utriculus. In nearly all fishes the sagitta is the largest otolith (Fig. 75*a*, *b*) and the lapillus is quite minute and of little importance: in some, however, the asteriscus is relatively enormous and the sagitta small. These otoliths or ear-stones have enamelled surfaces, and are provided with peculiar grooves and markings. They exhibit some variation in shape and size in different fishes, and as the form is fairly constant in any particular species, they are of some importance in classification. The otoliths grow by the deposition of lime in layers on the outer surface, and as the rate at which this is laid down varies at different seasons, if one is cut into thin sections and examined under a lens or microscope the layers formed in successive years are clearly visible as a series of alternately light and dark concentric rings, similar to the "zones" on a scale or the rings on a tree-trunk. Thus by a study of the otoliths it is possible to ascertain the age of any particular fish, and this method of age-determination has proved invaluable to those investigating the life-histories of our food fishes. The otoliths of the Sciaenids or Drums (*Sciaenidae*) are very large, and in ancient times were worn on a string round the neck as a preventive and cure of colic.

In some Bony Fishes the air-bladder is more or less intimately connected with the internal ear. In many marine and a few fresh-water forms there is an aperture in the hinder wall of the capsule enclosing the auditory organ, and this is closed by a fine membrane. A tube-like outgrowth from the front end of the air-bladder comes into contact with this membrane on the outer side. In some of the Herrings (*Clupeidae*), and in the Mormyrids (*Mormyridae*), the apertures in the capsule are open, and processes from the air-bladder actually come into contact with protruding outgrowths from the utriculus itself. In the Characins, Gymnotids, Cyprinids (*Cyprinoidea*), and in all Catfishes (*Siluroidea*), the connection between the air-bladder and ear is much more elaborate, and these fishes are grouped together under the name of *Ostariophysi*, derived from two Greek words meaning "a small bone" and "inflated." The connecting apparatus, known as the Weberian mechanism (after its discoverer, Professor Weber), is formed by the modification of the

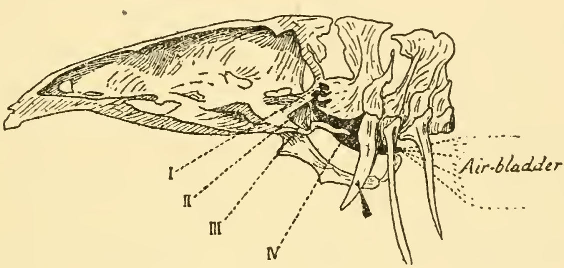


Fig. 76.

Section of the skull of Carp (*Cyprinus carpio*), showing the Weberian mechanism, $\times \frac{1}{2}$. I-IV. Weberian ossicles.

first four vertebrae immediately behind the skull, certain parts of which have become separated off and form a chain of little bones or ossicles on each side, linking up the air-bladder with the perilymph-filled spaces surrounding the inner ear. The names of these ossicles need not be given here, but it may be pointed out that the first two represent the much modified neural arch of the first vertebra, another is a portion of the second vertebra, and the last represents the modified rib of the third vertebra (Fig. 76).

The exact function of this remarkable mechanism is not yet fully understood, and it may be connected with the perception of movements in the water, or alterations in pressure, or perhaps serves to accentuate the sound waves and thus act as an accessory organ of hearing. Since the mechanism occurs almost entirely in fresh-water fishes, living in water where the range of depth is not very great, it is improbable that it is concerned with changes in pressure, and it may be concluded that it probably serves to intensify the impulses of sound waves and movements received from the surrounding water. Of its importance to the life of the fish there can be no doubt, since the elaborate Weberian mechanism is possessed by every member of the dominant group of fresh-water fishes living to-day.

Some authorities have expressed doubt as to whether fishes really hear at all, at least in the sense in which higher animals hear. Aristotle was quite certain that they are able to perceive sounds in the water, "for they are observed to run away from any loud noises like the rowing of a galley." A number of experiments have been conducted to ascertain the extent to which fishes are able to hear, but a brief survey of the more interesting of these will show the contradictory nature of the results obtained. Dr. Bateson found that loud reports or explosions made by blasting operations near Plymouth were followed by sudden movements in some fishes, whilst others seemed to be unaffected. He concluded that fishes perceive the sound of sudden shocks when sufficiently severe, but do not hear the sounds made by striking two objects together under water out of sight of the fish. Cases have been described of Carp, Gold-fish, and other fishes assembling for feeding at the sound of a bell, but Dr. Kreidl found that Trout assembled equally readily at the sight of a person even when the bell was not rung, and that they took no notice if they could not see the person ringing the bell. If, however, a stone or piece of food was thrown into the water, the fish hurried to the spot where the water was disturbed. This author agreed with Dr. Bateson that the fishes responded, not to sounds made in the water, but only to a shock such as a blow on the sides or top of an aquarium. What is even more interesting, however, is the fact that they were said still to react to similar shocks when the ear-sacs and auditory nerves had been removed. Two American investigators, however, obtained somewhat different results. They found that certain fishes responded to sounds made by a tuning fork or by a bass viol string by characteristic movements of the fins and other organs, but that when both the auditory nerves were cut these responses disappeared. Another German worker concluded that Roach, Dace, and Bleak definitely responded to sound vibrations. Mr. Radcliffe states that he and some friends, in order to test the sense of hearing in Trout, each in turn fired a gun close to the surface of the water while the others observed the result. Although the gun was fired eight, four, and three feet above a shallow stream, fired into the air or into the opposite bank in a direct line above different fishes lying either singly or in shoals from five to nine inches from the bottom, in no case did the Trout take the slightest interest, or give any sign of having either heard the shots or felt the concussion of the bullet striking the opposite bank. Sir Herbert Maxwell, however, states with equal certainty that fish in Loch Ken were disturbed every time a shooting-party half or three-quarters of a mile away discharged their guns.

On the whole, it seems most probable that the sense of hearing, if developed at all, is far from acute, and may be largely confined to the perception of disturbances in the water. The otoliths would serve to translate these disturbances into vibratory movements, which, by their action on the inner sensitive patches, stimulate the fine endings of the auditory nerve and thus convey impulses to the brain. It is difficult to understand why a number of fishes should possess an elaborate apparatus for the production of sound if their companions are incapable of appreciating the result, and it would appear that some fishes at least must be capable of perceiving sounds to a greater or lesser extent. Others are perhaps almost completely deaf, although they will react to violent shocks or disturbances in the water.

The arrangement of semicircular canals and the internal cavities of the auditory organ with their contained otoliths certainly play another part, and assist in maintaining the equilibrium of the fish. In the ampulla of each canal are highly sensitive cells, and by the pressure of the contained endolymph on these cells a movement of the head into another plane is conveyed to the brain by the auditory nerve. Similarly, if the fish were to turn over suddenly on to its side, the otoliths would press on the sensitive patches in the walls of the membranous sacs, and thus set up nervous impulses which would promptly inform the brain of the change in the inclination of the head.

Comparatively little is known about the sense of taste in fishes, but, if this exists at all, it is probably far from acute. In the first place, apart from certain forms like the Carp (*Cyprinus*) and Parrot-fishes (*Scaridae*), which appear to masticate their food with some care, most fishes swallow the food with great rapidity. Secondly, the tongue may be altogether wanting, and even when this is developed, it is unprovided with muscles and therefore immovable; further, it has no delicate membranes comparable to those of the tongues of higher vertebrates. It is true that the barbels, lips, mouth, and palate are richly supplied with tiny sense organs, but it is more than likely that these are concerned with the sense of touch rather than with that of taste. A curious cushion-like organ, richly supplied with nerves, found on the palate in the Carps and related fishes (*Cyprinidae*), may perhaps be connected with the perception of this sense.

The sense of touch seems to be highly developed, and a number of special organs have been evolved in connection with it. The whole of the epidermal layer of the fish's skin is provided with small sense organs scattered irregularly over the head, body, and fins. They are present in the Cyclostomes, Selachians, and Bony Fishes, but in the Lung-fishes (*Dipneusti*) are confined to the region of the cavity of the mouth, and there is reason to believe that they gave rise to the taste-buds found on the tongue in higher vertebrates. These dermal sense organs may take the form of tiny buds, with which are associated the fine end-branches of nerves, or of small pits with specially sensitive cells hidden away in their depths. Their function is to receive impressions or sensations from the outside world, such as a change in temperature, or a feeling of the proximity of food or of enemies, and to set up nervous impulses which convey these sensations to the brain.

Although, as already remarked, such organs are scattered over every inch of the body, they tend to be specially abundant in the organs known to be connected with the sense of touch. Of these the most important are the barbels or feelers, which may be thread-like or flattened, long or short, smooth or with corrugated or roughened surfaces. They are generally to be found in the region of the mouth, but are also developed on the lower surface of the throat and on the chin. In the Cod (*Gadus*) there is a single short barbel below the chin (Fig. 77D), in the Drums (*Sciaenidae*) there may be several in this position (Fig. 77A). In the Cat-fishes (*Siluroidea*) the barbels are always arranged in pairs round the mouth, the largest being connected with the maxillary bone of the upper jaw and freely movable at will (Figs. 34k; 41D; 77B, etc.). They vary a good deal in size and form in this group of fishes, sometimes being even longer than the fish itself. There can be little doubt that they aid in the search for food in waters which are so muddy that eyes would be of little use. In the Sturgeon (*Acipenser*), another mud-living form, the barbels are short and are arranged in a transverse row of four across the under side of the shovel-like snout, immediately in front of the protractile mouth (Fig. 45C). The related Spoon-bill (*Polyodon*) has no barbels at all, but the whole of the surface of the peculiar snout has been shown to be highly sensitive, and richly supplied with organs of feeling (Fig. 47G). In many oceanic fishes, notably in the members of the tribe of Wide-mouths (*Stomiatidae*), a single barbel is developed on the chin, which may be of a most elaborate and sometimes highly fantastic pattern, with a complicated arrange-

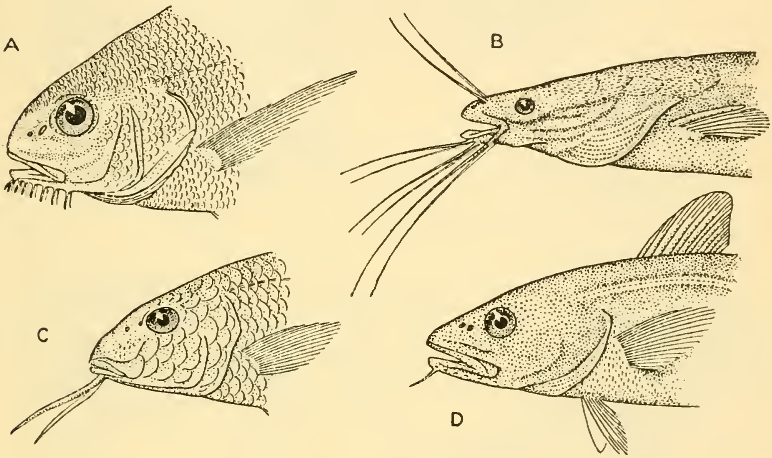


Fig. 77.—BARBELS.

A. Head of Sciaenid or Drum (*Pogonias fasciatus*), × ½ ; B. Head of African Cat-fish (*Clarias lazera*), × ½ ; C. Head of Red Mullet (*Mullus surmuletus*), × ½ ; D. Head of Cod (*Gadus callarias*), × ¼.

ment of tassels and other appendages and one or more luminous bulbs of varying size (Fig. 78). In the absence of any data as to the habits of the fishes, it is difficult to understand the exact function of these curious organs. In bottom-living fishes barbels are used to search for food in the sand or mud, but in oceanic forms living in the upper and middle layers of the ocean they obviously cannot be put to such a use. It appears probable that some simple barbels may serve as organs of touch, others may have a sensory function, receiving impressions indicating the approach of other fishes, and others, again, may act as lures.

In those fishes in which the rays of some of the fins are modified to form elongate feelers (*cf.* p. 79), these are also supplied with an abundance of tiny sense organs. They frequently occur in fishes living at considerable depths, in which the eyes are feebly developed, and undoubtedly compensate for the loss of vision. In the Southern Chimaera or Elephant-fish (*Callorhynchus*) a remarkable membranous appendage hangs

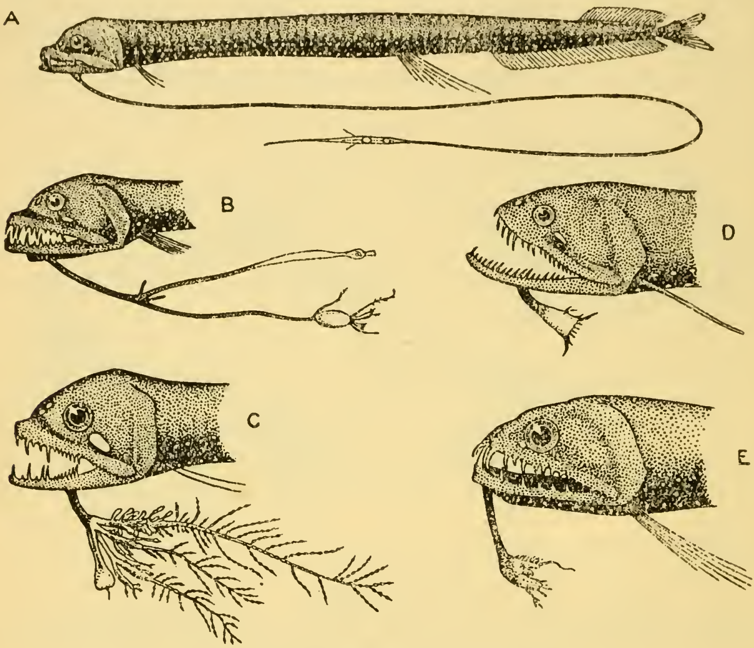


Fig. 78.—BARBELS IN OCEANIC FISHES.

A. *Eustomias bituberatus*, × ¾ ; B. Head of *Eustomias tenisoni*, × 1½ ; C. Head of *Eustomias silvescens*, × 1¾ ; D. Head of *Photonectes intermedius*, × 2 ; E. Head of *Chirostomias pliopterus*, × 1¾. (After Regan and Trewavas.)

from the snout: its exact function is a little obscure, but it is believed to be connected in some way with the sense of touch.

The last of the sense organs to be considered is the series of organs collectively known as the lateral line or mucous canal system, structures believed to be the seat of a sense peculiar to fishes. The external appearance of the lateral line in different fishes has been previously described in considering the scales (*cf.* p. 100), and it was pointed out that the series of external pores or of tube-bearing scales are only the outward and visible sign, as it were, of an underlying system of sense organs (Fig. 44). These were probably evolved, in the first place, from simple pit organs similar to those already described as being scattered all over the skin, since their mode of development is the same. The simplest type of lateral line system is found in such a primitive Selachian as the Frilled Shark (*Chlamydoselachus*), in which the sense organs lie in a row in an open groove running from the head to the tail, which is partially roofed over by the bordering denticles in the skin (Fig. 79a). In most of the other

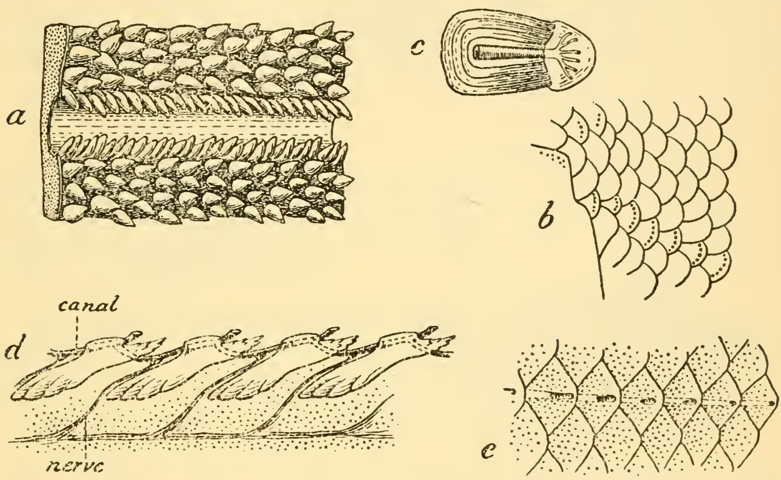


Fig. 79.—LATERAL LINE.

a. Portion of lateral line of Frilled Shark (*Chlamydoselachus anguineus*), much enlarged; b. Scales of the Bow-fin (*Amia calva*), showing apertures of lateral line tubules; c. Lateral line scale of Bow-fin (*Amia calva*), greatly enlarged; d. Vertical longitudinal section through lateral line of Perch (*Perca fluviatilis*), much enlarged and diagrammatic; e. Lateral line scales of Osteoglossid (*Heterotis niloticus*), $\times \frac{1}{2}$. (a, b, and c after Bashford Dean.)

Selachians this groove becomes converted into a tunnel sunk beneath the skin, which communicates at regular intervals with the surface by a series of pores, alternating with the sense organs developed on the inner walls of the tube. In the embryo fish these organs first appear on the surface of the skin, then sink into a groove, and finally become enclosed in a tube beneath the skin. Professor Cunningham has compared the lateral line of a Dog-fish to a tube railway, the external apertures corresponding to the stations at which the tubular tunnel communicates with the surface of the ground by means of vertical shafts.

Both the tubes and the shafts of the lateral line are kept filled with mucus, which exudes through the external pores.

In the Bony Fishes the main tube communicates with the exterior by a series of pores in the skin, or, more generally, by short canals branching off from the main tube, which perforate the overlying scales and end in pores (Figs. 79c-e). In many fishes these branch canals are themselves subdivided into a number of smaller branches, spread out over the surface of the scale, each of which ends in a minute pore: in this way the original single aperture is converted into a number of smaller ones (Fig. 79b). The sense organs of the lateral line are served by fine nerves arising from a special branch of the vagus (tenth)

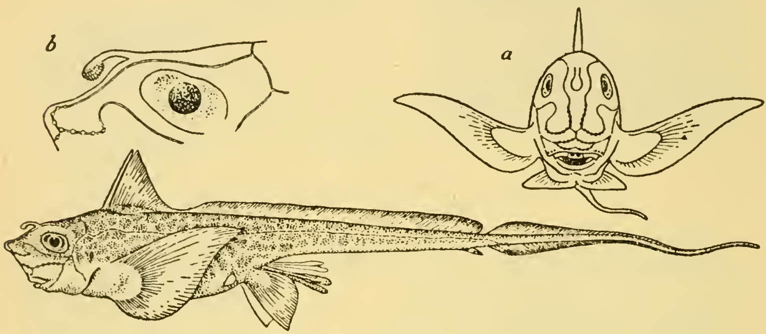


Fig. 80.

Male Rabbit-fish (*Chimaera monstrosa*), $\times \frac{1}{8}$; a. Front view ; b. Upper part of head. Greatly enlarged.

cranial nerve, running parallel to the line itself, and conveying the sensory impressions to the brain (Fig. 79d).

In the head region the canal system is continued as a series of branching tubes, which are, as a general rule, more deep-seated than those of the lateral line of the trunk region. In the Chimaeras (*Holocephali*), however, the elaborate system of branching and intercommunicating channels retains a very primitive form, with the sense organs situated in open grooves similar to that along the body (Fig. 80). The majority of Sharks and Rays are provided with a number of separate tubes on the head, running obliquely below the skin, each with its own pore above, and ending below in a swelling or ampulla containing a group of sensory cells (Lorenzini's ampullae). In the Bony Fishes the canal system rarely forms a conspicuous feature on the head, the tubes being sunk well below the skin and communicating with the exterior either by a comparatively small number of large pores or by numerous tiny apertures. In this cephalic system three main canals may be recognised: one running forward across the hinder part of the head, bending downwards below the eye and continuing on to the snout and upper jaw; another running forward above the eye and also ending on the snout region; and a third passing downwards across the front part of the gill-cover and forwards to the lower jaw. In certain regions these canals may be dilated or constricted, or they may be variously branched. The contained sense organs do not exhibit the regular arrangement characteristic of those in the trunk region, and are served by branches from the seventh cranial nerve. Often one or more of the

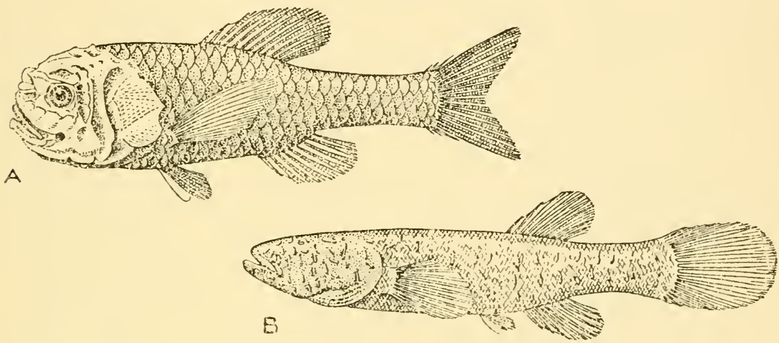


Fig. 81.

A. *Melamphaes beanii*, $\times \frac{1}{2}$; B. Kentucky Blind-fish (*Amblyopsis spelaeus*), $\times \frac{1}{2}$.

canals becomes enclosed in a tube-like bone for the whole or a part of its length; these bones, which in the young fish develop round the canal, may remain separate or become fused with neighbouring bones. In certain fishes, and especially in some living at great depths in the sea, the mucous canals are so much enlarged in certain regions of the head that the surrounding bones are excessively thin and paper-like, the whole skull being soft and spongy to the touch (Fig. 81A).

An important point about the lateral line system as a whole is its relation to the auditory organ, from which all the main channels radiate. A study of the development of the inner ear shows that this must have been at one time one of the sense organs of the lateral line, before becoming specially enlarged and modified in order to adapt it to the perception of delicate sound vibrations, and to the maintenance of equilibrium.

The lateral line system has generally been regarded as the seat of a sense akin to "feeling," but it would perhaps be more accurate to describe this sense as combining the qualities of hearing and touch. An American investigator has conducted a series of experiments on living fishes to discover exactly what part these organs play in their daily lives, and his results, although by no means conclusive, are of considerable interest. His method consisted in cutting the nerves supplying the lateral line, and then comparing the behaviour of these injured fishes with normal individuals. He has shown quite definitely that the sense organs are not stimulated by heat, light, food, electricity, salinity, or foulness of the water, oxygen, or carbon dioxide, water pressure or water currents. Nor are they sensitive to sound vibrations as are the ears. The only kind of stimuli that have any effect on the normal fish but none on an injured specimen are vibrations of low frequency (about six per second) produced by pulling an aquarium slightly to one side and then letting it go again. As a result of his experiments he concluded that "waves on the surface of the water produced by air-currents, and the disturbances made by bodies falling into the water, produce vibrations in the deeper water that stimulate the lateral line organs." It seems certain that this sense of movements in the water is peculiar to fish, or at least to aquatic animals, and probably enables them to perceive the movements of other fishes or of their prey. Further, these sense organs may serve to notify the fish of its approach to a rock or the bank of a stream, the difference in the pressure on the scales covering the mucous canals being conveyed to the brain by the nerves. As Dr. Barton has written: "This sense enables a fish to rush about in a rocky pool, swerving this way and that to avoid obstructions, for the water resistance is the greater the nearer such water is to a solid body, and one cannot but admire the marvellous muscular response, the extraordinary rapidity of co-ordination of the body of the fish, to the varying stimulation on the lateral-line sense on one or other side of its body."

That fishes are highly sensitive to electric currents has long been known, and this knowledge has been turned to practical advantage in recent years by the invention of what are known as radio fish-screens, used principally in America. They are designed to keep food-fishes within bounds, and to prevent them from straying into irrigation canals, ditches, mill-races, and other water-courses. The earlier screens were not always satisfactory, and sometimes electrocuted the fishes. Nowadays, however, by the use of a transformer and a particular voltage, a shock is produced sufficient to paralyse the fish temporarily without doing any permanent harm. As a general rule, it has been found that fish swimming in the neighbourhood of a radio screen have a sense of the direction of the danger, and attempt to steer away from the obstacle before coming within range of its effects.

The much debated question as to whether or no fishes feel pain may well be considered here. The angler will always answer it with an indignant denial, and it must be admitted that his experiences with rod and line provide some evidence for his belief. It is well known that Trout or Pike, whose mouths have been torn and lacerated by a hook, but which have succeeded in getting away before being brought to the landing net, have returned and taken a tempting bait almost immediately afterwards. There is also the classical story of the Perch hooked in the eye, which necessitated removing the organ from its socket before returning its owner to the water. The angler then baited his hook with the eye, and no sooner did his line reach the water than the bait was swallowed by the identical fish, which thus enjoyed the unique distinction of being caught with its own eye!

It would seem as though some fishes are much less sensitive than others, or at least that they lose their sensitiveness to pain under the stress of some emotional excitement. The Greenland Shark (*Somniosus*), when feeding on the carcase of a whale, is said to allow itself to be stabbed repeatedly in the head without abandoning its prey, and two Conger Eels in the act of copulation have been so insensible to other external impressions that they have been lifted together from the water by the hand. The great difficulty in deciding whether or not under normal conditions fishes feel pain lies in the fact that it is only possible to judge the matter by our own standards. We are quite certain that a barbed hook lodged in our own throat would cause us intense agony, but it is tolerably certain that a fish, with its comparatively lowly organised brain, does not feel anything nearly as acute. At the same time, the fact that all fishes possess an elaborate system of nerves and sense organs suggests that they must at times experience feelings of this nature, although it is impossible to obtain any definite information as to the extent of their sufferings.

Another sense, if it may be described as such, which is highly developed in certain fishes, is the so-called schooling or shoaling sense, the mass control which is so apparent in gregarious birds and mammals. Thus, if the hindmost individuals of a shoal are attacked, the remainder will instantly scatter in every direction, although those in front cannot possibly have seen any cause for alarm, and the feeling of danger must have been communicated to every member of the shoal with incredible rapidity. It is said that two individuals of a gregarious species, when brought close enough together to perceive each other clearly, approach to within a certain distance and then change their course so as to swim forward side by side. The usual movements of a shoal of fishes seem to be due to similar visual reactions. If some influence tends to stop the forward progress, whether it be the proximity of a rock, shallower water, or the approach of an enemy, it has been shown that the advance members of the shoal turn abruptly backwards, and a sort of "milling" movement is set up, in which the shoal turns in a circular path and continues in the new direction until some other obstacle or disruption upsets it.

Another question frequently raised concerns the habit of sleeping, and the absence of eyelids in the vast majority of fishes leads many to suppose that sleep is unknown to them. This is untrue, however, and although it is impossible for them to shut their eyes to impressions from the outside world, there can be little doubt that all fishes spend at least a part of the day or night in a state of suspended animation. This has been verified in a number of species, and it has been found possible in many cases to approach a sleeping fish and to remove it from the water with the hand. Mr. Boulenger has noted that in the aquarium at the Zoological Gardens the position adopted by a fish when sleeping varies a good deal, not only in the different groups of fishes, but in closely related species of the same genus. When suddenly disturbed by flashing an electric torch on to the tanks, some were found to be resting in a horizontal position on the bottom, others, like the Wrasses (*Labridae*), were lying at the bottom on their sides, and others were sleeping in a horizontal position but entirely surrounded by water. It was found that fish which normally sleep when darkness arrives will remain awake and active if hungry, and it is suggested that Trout taking a fly at night are hungry individuals that remain awake owing to the abnormal nocturnal activity of their insect prey. Flat-fishes such as Plaice (*Pleuronectes*) and Dabs (*Limanda*) were found just above the bottom of their tanks at night, and the suggestion has been advanced that this is the reason why the trawlers make their best hauls of marketable fish at night, since the commercial trawl does not actually drag the bottom, but the lower edge passes a foot or so above this, and in the day-time would miss the fishes lying buried in the sand. Dr. Beebe records that a young Sole (*Achirus*) may leave the bottom and on occasion actually float at the surface of the sea at night. "It undulated to the surface," he writes, "curved down to a saucer or cup-shape with the circular fin-rays above the water, and floated until I captured it. The fully expanded fins apparently made such intimate contact with the surface film that, like a vacuum cup, it remained suspended." Bat-fishes (*Ogcocephalidae*), which are also normally bottom dwellers, likewise come to the surface in the dark.

Mr. Boulenger's observations on a number of young Grey Mullet (*Mugil*) are of interest. During the hours of daylight they were observed to swim about in a massed shoal, but at night this broke up, every individual fish going to its own spot on the bottom, the members separating and facing in all directions. If disturbed, however, they rapidly returned to the surface and again adopted the mass formation.

Some indication has been already given as to the manner in which the complex activities of the fish's body are co-ordinated by the nervous system, and in concluding this chapter the matter may be considered rather more closely. Sensory impressions are received from the outside world by one or more of the organs of sense, and messages in the form of nervous impulses are flashed to the appropriate part of the brain, from which motor impulses are promptly sent back to muscles, glands, and so on, matters being at once adjusted by an appropriate movement or other activity. It is important to distinguish between two very different types of behaviour, two replies, as it were, to the impressions received from the sense organs. There is the reflex action, or, more simply, the reflex, which is quite automatic and independent of the mind. A familiar example of this action in human beings is provided by the drawing away of the hand or foot from a source of excessive heat: the movement begins, not as the result of the pain, but before consciousness of any pain has been experienced, and follows almost instantaneously upon the application of the stimulus. In the other type of action memory and consciousness are involved, and this may also be illustrated by an example of human behaviour. A man observes a ripe pear hanging from a tree and moves his arm forward to grasp it, a definitely conscious action following upon the sight of the fruit conveyed to the brain by the eye. At the same time his mouth begins to secrete saliva, his stomach to pour forth its digestive juices, and other preparations for the meal are started, all as the result of a visual impression.

The two types of action just described have different centres of control in the brain, the conscious action being controlled by the cerebral hemispheres, the seat of mind, and the reflexes by the cerebellum and other parts of the brain. As has been previously pointed out, these hemispheres are relatively small in fishes, but in higher vertebrates they become progressively larger and larger and take more and more control of the lower centres, until in man they occupy the greater part of the space allotted to the brain.

To a large extent, the fish must be looked upon as a reflex machine. That is to say, most of its movements and other activities are the result of reflex actions rather than conscious thought. A fish moves, breathes, feeds, and reproduces, but rarely thinks. The elaborate habits of courtship, and the care displayed by certain fishes in building a nest as well as in looking after the welfare of the young, suggests that some at least are susceptible to the instincts and emotions exhibited by the higher animals. Apart from rare cases of fishes trained under conditions of domestication, instances of definite thought or memory are very scarce and of more than doubtful authenticity. The combining together of two or more kinds of fish for the purpose of obtaining food or of attacking an enemy may perhaps point to a certain degree of intelligence, although it is open to question whether there is really any constructive thought or reason in the matter.

CHAPTER XI

COLORATION

Colours of some tropical fishes. Variations. Meanings of coloration. Obliterative shading. Oceanic fishes. Shore fishes. Fishes of coral reefs. Protective resemblance. Mimicry. Coloration and environment. Colour changes. Sexual differences. Warning colours. Mechanism of coloration: chromatophores, iridocytes, etc. Mechanism of colour changes. Xanthochroism. Influence of light on pigment. Coloration of Flat-fishes. Ambicoloration. Albinism.

THE pallid corpses displayed on the fishmonger's slab, or the stuffed and often faded specimens in the local museum, give but a poor idea of the colours of living fishes, and are responsible for the popular impression that in the matter of vivid hues fishes cannot challenge comparison with such creatures as the birds and butterflies. The difficulty of observing fishes in their natural surroundings is a real one, but the opening of the aquarium at the Zoological Gardens has done much to remove this, although, even here, the surroundings are necessarily to some extent artificial. Nevertheless, the beautiful colouring of many of its inhabitants has proved a revelation to visitors, and a survey of some of the fishes found in the neighbourhood of coral reefs would remove once and for all the erroneous impression that most forms wear comparatively dull liveries, an impression that has been further fostered by the fact that, with certain exceptions, the inhabitants of our own coasts and rivers are rather soberly coloured.

Many pages would be required to describe even a few of the brilliant and fantastic combinations of colour encountered in tropical fishes, but a few examples should suffice to give some idea of their possibilities. Mr. Saville Kent, who has made a special study of the fishes of the Barrier Reef of Australia, describes a Sea Perch or Grouper (*Epinephelus*) with a prevailing ground colour of brilliant carmine with a tendency to yellow on the lower parts, and with numerous ultramarine spots of brilliant intensity on the sides. Another fish (*Beryx*), belonging to the tribe of Berycoids, has the same vivid ground colour, but with various opalescent tints, chiefly reflections of blue and lilac. One of the Thread-fins (*Polynemus*) is coloured chrome yellow with some irregular darker markings, the pectoral and caudal fins are bright orange, the remaining fins yellowish, and the long filamentous rays of the pectorals bright vermilion red. A little coral-reef fish (*Amphiprion*) belonging to the family of Desmoiselles (*Pomacentridae*) has a ground colour of vivid orange, and the head and body are crossed by three broad bands of pale blue, each edged with darker blue or black; the fins are mostly of a lemon shade with narrow borders of black. A closely related species is coloured deep chocolate and the cross-bands are of bright yellow shading to orange at their margins.

Finally, there is a species of Trunk-fish (*Ostracion*) from the Barrier Reef, which for the resplendence of its hues and bizarre markings perhaps surpasses any other fish. The male and female are coloured quite differently, and were at first looked upon as distinct species. The body of the male is grass green on the sides and back, becoming lemon-yellow on the belly: the sides of the trunk and head are traversed by broad, somewhat irregular and broken bands of brilliant ultramarine blue, the edges of which are picked out by deep chocolate brown lines. Some of these blue bands are continued on to the caudal fin, where they form curled, loop-like patterns. The yellow belly is variegated by a network of pale blue lines. The caudal fin is orange or dark yellow, the remaining fins of a neutral colour and transparent. The female has a pale, pinkish-grey, or doveground colour, with local flushes of a more decided pink, and a pure yellow belly: the bands running along the body are here unbroken, and of a rich reddish-brown shade, and at the bases of the pectoral and dorsal fins they form a curious irregular spiral pattern.

In many species the general coloration, and particularly the characteristic markings in the form of bars, stripes, spots and blotches, are remarkably constant in all the individuals of a particular species, but in others there is a good deal of individual variation, and in the Trunk-fishes just described it is extremely rare to find two specimens exactly alike in the manner in which the bands on the body are arranged. Professor Jordan has described some of the remarkable colour variations found in a species of Sea Perch from the West Indies known as the Vaca (*Hypoplectrus*). Generally, the ground colour is orange, with black marks and blue lines, the fins being chequered with orange and blue. "In a second form," he writes, "the body is violet, barred with black, the head with blue spots and bands.

In another form the blue on the head is wanting. In still another the body is yellow and black, with blue on the head only. In others the fins are plain orange, without checks, and the body yellow, with or without blue stripes or spots and sometimes with spots of black or violet. In still others the body may be pink or brown, or violet black, the fins all yellow, part black or all black. Finally, there are forms deep indigo-blue in colour everywhere, with cross-bands of indigo-black, and these again may have bars of deeper blue on the head or may lack these altogether."

The apparently meaningless display of colour shades and patterns exhibited by many fishes have for the naturalist a deep, although not always obvious significance, but before dealing with this matter it is important to be quite clear as to the function of coloration. For the most part, the colours of fishes, like those of any other animal, serve to conceal their owners either from their prey or their natural enemies. This is not always the case, however, for, as will be pointed out in due course, in some fishes the colours serve a totally different purpose, and attempts that have been made to explain all types of coloration in terms of concealment sometimes press the matter to the point of absurdity. The fact remains, however, that in a very large number of fishes the particular hues and patterns adopted do tend to render them invisible, or, at least, very inconspicuous in their natural surroundings. A few examples will suffice to illustrate the general principles of these concealing colours.

A Carp (*Cyprinus*) or Roach (*Rutilus*), or almost any other fish to be found in our own rivers, exhibits a gradation of shades from silvery or yellowish-white below to a dark-blue, green, or brown above. This is known as obliterative shading, and is exactly the opposite of that which would be produced by light thrown upon the fish from above, and the general effect is to destroy the appearance of thickness and make the fish appear as a perfectly flat object. Seen from above against a background of water and the bottom of the stream coloured more or less like itself, the fish is almost indistinguishable at even a short distance, while seen from below the belly bears a close resemblance to the surface of the water and the clear atmosphere above. Many fresh-water forms depend entirely on this simple shading to bring about their concealment, but others enhance the obliterative effect by the development of darker markings in the form of bars, stripes, spots, and blotches of all kinds. The effect of such markings is twofold: they give the fish a more perfect resemblance to the ground on which it lies or the rocks and weeds among which it lurks; or, by their separate and conflicting patterns, they tend to obliterate the visibility of the form, and to break up the outline of the body against either a pale or dark background, as do the stripes on the body of a Zebra. The beautiful Angel-fish (*Pterophyllum*) of South America, a great favourite with aquarium lovers, provides an excellent example of the value of markings in concealment, its very thin, almost circular body being crossed by several deep black bars, which are continued on to the long filamentous fins (Fig. 8c). These markings harmonise very closely with the stems of the water plants among which the fish remains suspended almost motionless for hours on end, while the slowly waving fins help to perfect the deception.

With certain exceptions, of which the small Sun-fishes (*Centrarchidae*) of the rivers of North America, and some of the Cichlids (*Cichlidae*) of Africa and South America may be mentioned, fresh-water fishes are more or less soberly coloured, and even the bright hues of these forms mentioned above, so obvious when the fishes are viewed through the side of an aquarium, are largely obscured in life by the olivaceous markings and dark blotches of the upper parts. Dark spots, blotches, stripes and bars of all descriptions are profusely developed, especially in those species which habitually dwell at or near the bottom. In the few fishes living in caves, wells, and subterranean streams, where dark colours would be unnecessary and even disadvantageous, no pigments are developed, the prevailing colour being white or pale pink.

In the sea the same general principles apply. Fishes habitually swimming at or near the surface, such as the Herring (*Clupea*), Blue Shark (*Carcharinus*), Mackerel (*Scomber*), or Tunny (*Thynnus*) are coloured silvery or white on the belly and sides, and the back parts are dark green, black, or steely blue, sometimes ornamented with black spots or streaks, but as a rule more or less uniform (Fig. 82A). The water in the sea being generally bluer and clearer than that of the rivers, the olivaceous hues of the fresh-water fishes give place to these metallic shades, and seen from above against a background of dark water, or from below against a light sky, the fish is inconspicuous to its enemies, whether they be birds or other fishes. Larval fishes, swimming for the most part at or near the surface, obtain similar protection by the absence of pigments, being either transparent and colourless, or with the head and body covered with minute black dots, sometimes locally aggregated to form larger masses, whose purpose is to break up the outline of the moving body. In certain cases larval forms may bear some resemblance to the little bubbles or flecks of foam often to be seen floating on the surface of the sea.

Below the surface, fishes inhabiting the layers of water from one hundred to five hundred metres are generally of a silvery hue, although, curiously enough, a large number of species

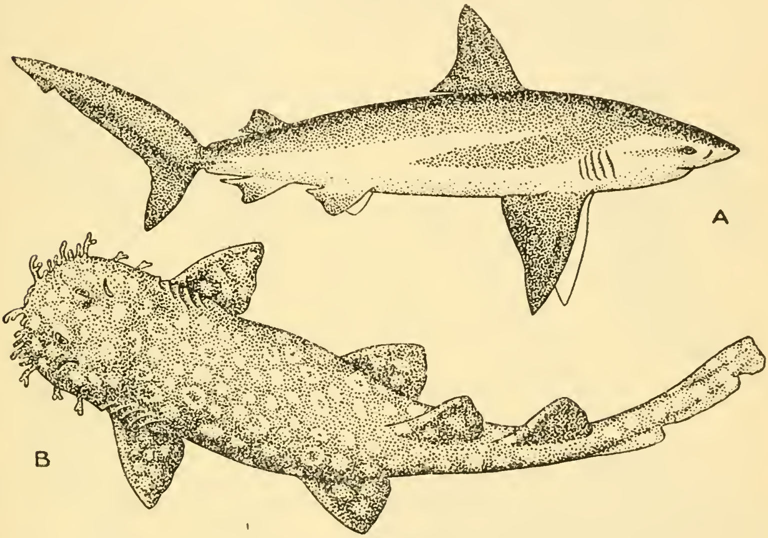


Fig. 82.—COLORATION IN PELAGIC AND BOTTOM-LIVING SHARKS.
A. Blue Shark (*Carcharinus milberti*), $\times \frac{1}{25}$; B. Carpet Shark (*Orectolobus barbatus*), $\times \frac{1}{15}$.

coloured with various shades of red also occur. It has been suggested that the prevalence of this colour in fishes living at moderate depths is in some way related to the effect of water on the light waves, but this requires further investigation. At greater depths still, five hundred to two thousand metres below the surface, where there is little or no light, the prevailing shades are brown, black or violet-black, generally quite dull, but sometimes with silvery lustres or reflections from the scales. There is also a complete absence of spots, bands, or other distinctive markings such as distinguish the fishes which dwell more or less close to the shore.

Among the littoral fishes almost every conceivable type of coloration is found, ranging from a simple and uniform grey or brown to the most vivid and bizarre combinations of colours and markings. As a rule, the spots and mottlings, when present, tend to give the fishes a general resemblance to the ground or to the rocks and weeds among which they swim. This protective resemblance is often remarkably exact, and among granite rocks we find fishes with an elaborate series of granite markings; similarly, black species are found among lumps of lava, green ones among the lighter varieties of seaweeds, olive-coloured fishes among the fucus-like weeds, and red ones among the corals of similar shades. Seen apart from their surroundings some of these fishes are difficult to explain in terms of concealing colours, but studied in their natural haunts many of the puzzling cases immediately become clear. For example, many of the Sea Perches or Groupers (*Epinephelus*) have the head and body covered all over with more or less hexagonal spots of reddish brown, separated from one another by a pale white or blue network—a reticulated pattern recalling that of the Giraffes. Lieut.-Col. Alcock in his book *A Naturalist in Indian Seas* records how he was in a boat with a native fisherman who speared one of these fishes, which, when wounded, took shelter in an adjacent clump of coral and lay concealed therein. The red spots bore a most exact resemblance to the coral polyps and the fish refused to leave its shelter and was eventually captured.

Judged from this standpoint, the vivid colours of the fishes of tropical reefs are more easily understood. Seen as museum specimens they appear as highly conspicuous objects, but observed against a background of corals and associated forms of animal life, themselves presenting a perfect riot of colour, they attract comparatively little attention. Many of these reef-dwelling forms exhibit an extraordinary variety of darker markings of every description, the pattern, however, being fairly constant in any particular species (Fig. 83). The purpose of such markings is to break up the outline of the fish and to conceal the shape. Some of the Butterfly-fishes (*Chaetodon*) have the head crossed by a dark band, often bordered with white or blue, while at the hinder end of the body is an eye-like spot or ocellus, sometimes ringed with white or yellow (Fig. 83D). They are said to be in the habit of swimming for a short distance very slowly tail first, but, if disturbed, they will dart off with great rapidity head first in the opposite direction. It has been suggested that the effect of this curious pattern tends to make a potential enemy regard the tail end of the fish as the head, and it is thus able to save itself by darting off in the direction least expected by its aggressor. When considering the colours of coral-reef fishes, however, it is important to guard against

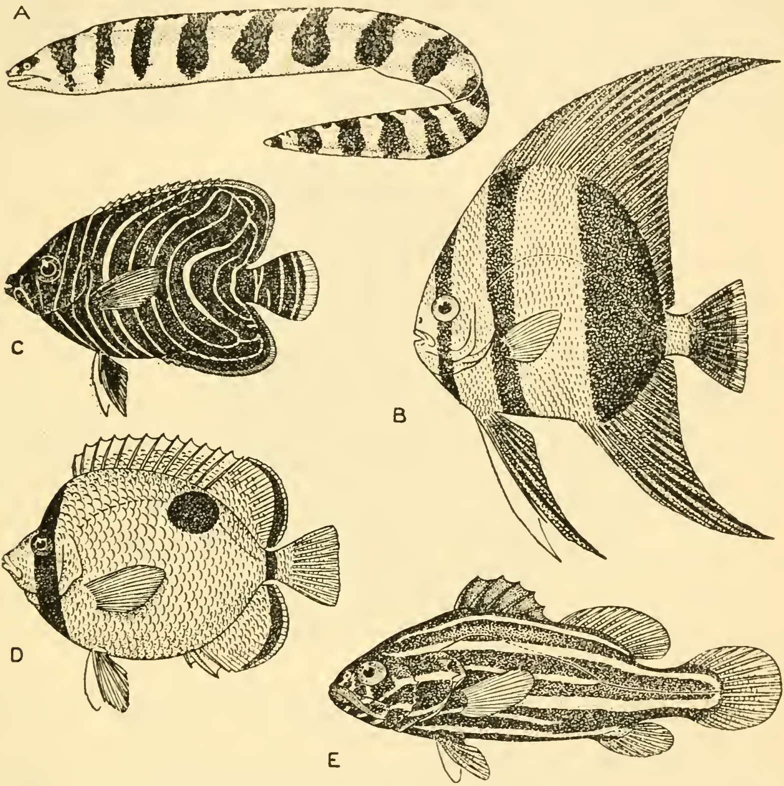


Fig. 83.—COLOUR PATTERNS IN TROPICAL FISHES.

A. Muraena or Moray (*Gymnothorax petelli*), × $\frac{1}{8}$; B. Bat-fish (*Platax orbicularis*), × $\frac{1}{8}$; C. Butterfly-fish (*Holacanthus semicirculatus*), × $\frac{1}{2}$; D. Butterfly-fish (*Chaetodon unimaculatus*), × $\frac{1}{4}$; E. Sea Perch (*Grammistes sexlineatus*), × about $\frac{1}{2}$.

the tendency to look upon *all* types of coloration as concealing, for in many regions the reefs themselves are dull greyish, and the associated forms of animal life more or less soberly coloured, but the little fishes are as vividly coloured as elsewhere. Under such conditions they cannot be protected by their liveries, and must rely on their exceptional alertness and agility, and on their ability to shelter within the clumps of coral or to bury themselves in the coral sand.

Mention may be made of a Chaetodont or Butterfly-fish (*Holacanthus semicirculatus*), in which the dark ground colour of the head and body is broken up by a series of narrow curved white stripes, the caudal fin being ornamented with markings of a similar nature (Fig. 83C). In a specimen which made its appearance in the fish-market at Zanzibar these markings on the fin bore a remarkable resemblance to old Arabic characters (Fig. 84), reading on one side of the tail "Laillaha Illalah"

Fig. 84.

Tail of a Butterfly-fish (*Holacanthus semicirculatus*), with markings resembling Arabic characters.

(There is no God but Allah) and on the other side "Shani-Allah" (A warning sent from Allah). This caused considerable excitement, and the fish, which was originally sold for a penny, eventually fetched five thousand rupees!

The most perfect examples of protective resemblance are encountered among the shore-dwelling fishes living actually on the sea bottom, and their spotted and mottled liveries imitate the background of sand, mud, pebbles, crushed coral, lava, and so on with remarkable exactitude. The Carpet Shark (*Orectolobus*), for example, has a beautiful, variegated coloration and simulates a weed-covered rock (Fig. 82B), and many of the Rays (*Raia*), Flat-fishes (*Heterosomata*), Anglers (*Lophiidae*) and other fishes, have the upper surface coloured in harmony with the ground on which they are lying. Most of the Frog-fishes (*Antennariidae*) are shore-dwelling forms, but the species of the genus *Pterophryne* live in the open sea, drifting about with the currents in masses of sargassum. The particular species of the Sargasso weed of the Atlantic is of a pale yellow colour, with small white spots and irregular brown bands, giving an almost perfect concealment in its natural habitat among the weed (Fig. 85).

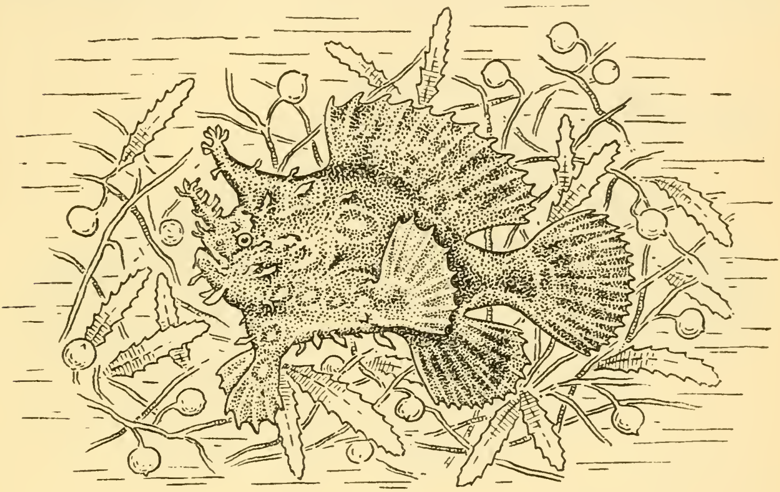


Fig. 85.

Frog-fish (*Pterophryne tumida*) in Sargasso weed, $\times \frac{1}{2}$.

In some fishes the protective resemblance is carried still further by actual mimicry, both in form and colour, of a particular inanimate object. For example, the Pipe-fishes (*Syngnathidae*), not only in their shape and colour, but also in their slowly swaying movements, bear a marked resemblance to the fronds of seaweed among which they live. The Florida Pipe-fish when among tufts of eel-grass is said to be dark green in colour, but when placed in an aquarium among pale weeds it becomes light green. Another American form is normally of a muddy brown hue, but examples collected from a tide-pool filled with red seaweeds were brick-red in colour. The grotesque Sea Dragon (*Phyllopteryx*) of Australian shores has carried mimetic resemblance to perfection, the outline of the body being broken up by the development of numerous spinous or membranous processes: some of these form leaf-like blades, and, when streaming out in the water, give the fish an almost perfect likeness to a piece of seaweed (Fig. 86). The general appearance of a Carpet Shark (*Orectolobus*) or Angler (*Lophius*), with its series of branched membranous appendages, which tend to give it a general resemblance to a weed-covered rock, has been already described, and there are a number of other bottom-living forms which feed on smaller fishes and rely on their resemblance to ordinary objects to escape detection.

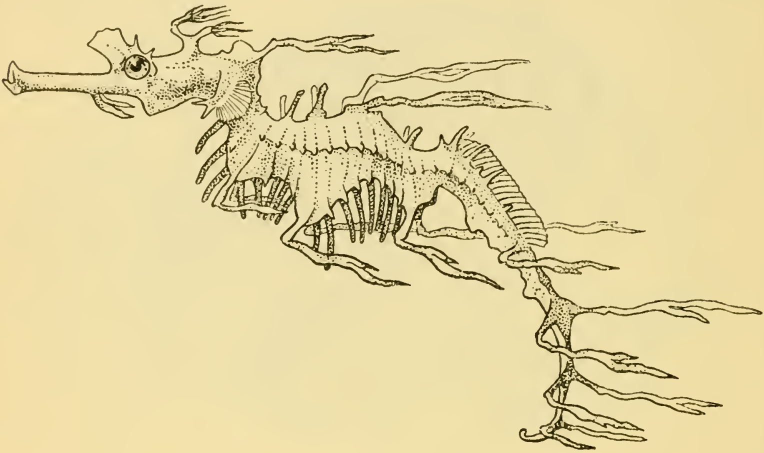


Fig. 86.

Sea Dragon (*Phyllopteryx eques*), × ½.

Some of the Poison-fishes (*Synanceia*), when lying motionless on the bottom and partially buried in the sand, have the appearance of lumps of rock or lava; the Gar Pike (*Lepidosteus*), when cautiously drifting towards its prey, bears a strong likeness to a piece of driftwood or a moss-covered log. Some small fishes found in the mangrove swamps of the islands in the Pacific look exactly like the old leaves of the mangrove trees among which they swim. Another fish (*Monocirrhus*), even more like a dead leaf, has been observed in the Amazon River, and here, not only the colour, but also the shape of the fish imitates the leaf, even to the extent of simulating a short stalk at one end (Fig. 87). In the Bay of Panama little fishes have been seen swimming about among pieces of driftwood, and so close was the resemblance that it was almost impossible to pick out the living fishes from the fragments of wood. Young Half-beaks (*Hemirhamphus*) appear very like pieces of seaweed when observed at the surface of the water, and it is said that when a net is passed over the water in their vicinity, or when they are otherwise alarmed, they at once become quite rigid, floating about in any position and apparently in a helpless, inanimate condition. Similar cases of mimicry might be multiplied indefinitely, but one more must suffice. Dr. Beebe has described some Slender File-fishes (*Monacanthus*) feeding among clumps of eel-grass,

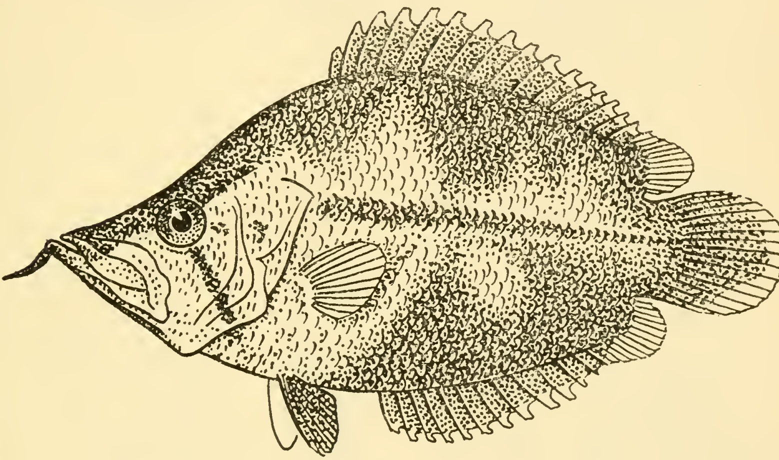


Fig. 87.

Monocirrhus polyacanthus, × 1.

and notes that when poised head downwards with the fins gently waving in the water, the general tapering form of the body, together with the undulating fins and mottled green colour, gives them a remarkable resemblance to a frond of seaweed or blade of the grass (Fig. 88).

The variation in colour found among individuals of the same species has already been mentioned, and in such a form as the common Brown Trout (*Salmo trutta*) of our own rivers and streams, the connection between a particular type of coloration and the nature of the surroundings is often striking. Dr. Günther has observed that "Trout with intense ocellated spots are generally found in clear rapid rivers and in small open Alpine pools; in the large lakes with pebbly bottom the fish are bright silvery, and the ocellated spots are mixed with or replaced by X-shaped black spots; in pools or parts of lakes with muddy or peaty bottom the Trout are of a darker colour generally, and when enclosed in caves or holes they may assume an almost uniform blackish coloration." In some Irish lakes the Trout on the boggy side have been observed to be dark and

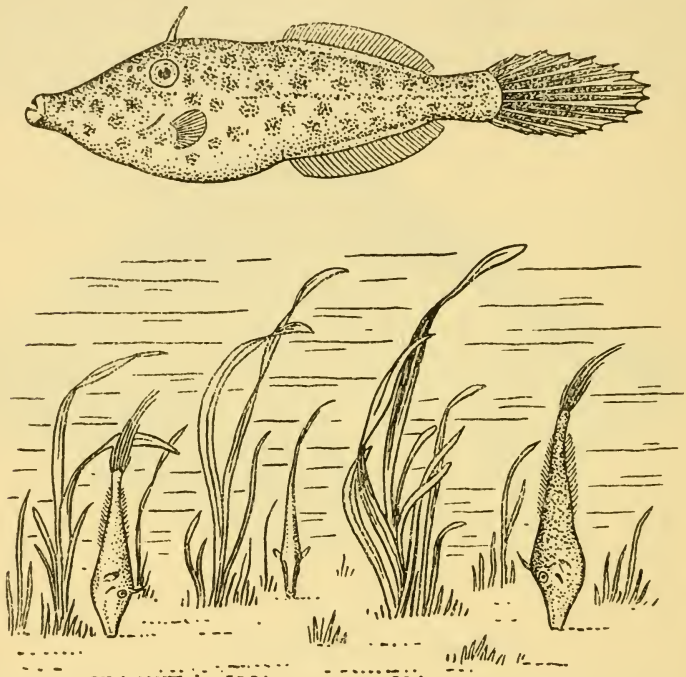


Fig. 88.

Slender File-fish (*Monacanthus scriptus*) among Eel-grass. (After Beebe.)

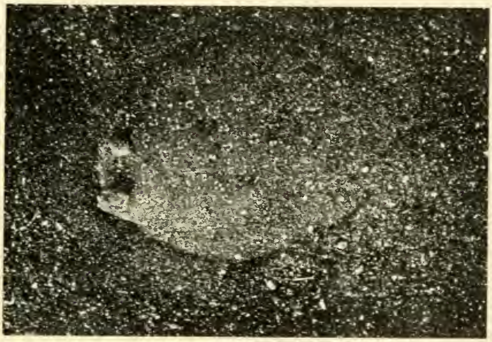
comparatively shapeless, whereas, on the gravelly side they are of the beautiful and sprightly form generally to be found in rapid gravelly or sandy streams. Two or three Trout from the Thames sent to the British Museum during recent years exhibited all the characteristic silvery and black-spotted appearance of typical Sea Trout, but proved to be merely Brown Trout that had been living in shallow reaches with light gravelly bottom. In a stream near Ivy Bridge the Trout were observed to have become much lighter in colour after the water had been polluted with white china clay. Dr. Day has described two lochs in Inverness-shire which were both stocked at the same time with Trout from Loch Morar. The larger of the two, with a sandy and weedy bottom, had the effect after a few years of changing the fish into forms with golden sides and covered with numerous red spots, and with white flesh. In the smaller, where the water was dark coloured and the bottom rocky, the fish developed nearly black heads, yellowish-olive sides, comparatively few black and red spots on each side, and the flesh became pink. Numerous other cases of a similar nature might be described, but the above should suffice to show that the coloration may undergo a definite change in order to harmonise with the surroundings, and that these changes are connected particularly with the amount of light available and the nature of the bottom. Further, there is evidence to suggest that, in some cases at least, the nature of the food may have its effect on the colour of the fish.

Similar changes have been produced under artificial conditions, and Sticklebacks kept in glass dishes with a background of black and white tiles have shown considerable variation in colour, those on the white tiles tending to become partially bleached, while those on the black more or less retained their normal coloration. If only exposed to the white tiles for a few days they tend to regain the original colour when put back on the black, but prolonged exposure extending over a period of weeks seems to make the pale colour more or less permanent. Minnows (*Phoxinus*) kept for experimental purposes in a white porcelain sink will also assume a bleached condition which matches the background, and anglers will sometimes paint the interior of their minnow-can white, so that the bait will assume a lighter colour and thus be more conspicuous to Pike and Perch in deeper and dark water.

The colour changes in Trout just described are generally slow, but in some fishes they may be practically instantaneous. Most of the tropical Sea Perches (*Epinephelus*), for example, are capable of changing in a moment from black to white, yellow to scarlet, red to dull green or dark brown, and can equally readily switch on, as it were, a series of spots, blotches, bars or stripes. The ability of these and other fishes to assume half a dozen different liveries within the space of a few moments is amazing, and the Sea Perches and other forms from Bermuda exhibited in the tanks of the aquarium at New York are a source of constant interest to visitors on account of their chameleon-like activities. The director, Dr. Townsend, has made a detailed study of the colour changes undergone by the fishes under his charge, and he has found that fishes from the coral reefs might have anything from two to seven distinct normal colour phases, according to the species. These varied greatly in the different forms, being most marked in the Sea Perches or Groupers (*Epinephelus*), but nearly always included one very pale or even white phase, and another which was exceptionally dark. To describe even a few of these colour phases would be impossible, but Dr. Townsend's description of a species of Sea Perch known as the Nassau Grouper will serve as a typical example. "Eight phases of coloration are sometimes observed in a tank containing specimens of the Nassau Grouper (*Epinephelus striatus*). In one the fish is uniformly dark; in another creamy white. In a third it is dark above with white under parts. In a fourth the upper part is sharply banded, the lower pure white. A fifth phase shows dark bands, the whole fish taking on a light brown coloration. While in a sixth the fish is pale, with all dark markings tending to disappear. The seventh phase shows a light-coloured fish with the whole body sharply banded and mottled with black. This is instantly assumed by all specimens when they are frightened and seek hiding-places among the rock-work. The banded phase shown here is no more the normal appearance of the fish than the uniformly dark, the uniformly white, or any other phase. Singularly enough, no two photographs of this banded phase are quite alike, the extent of the markings being dependent apparently upon the degree of disturbance to which the fish has been subjected." Another observer has described a fish of a shining blue colour with three broad vertical bands of brown, which swam into a clump of coral, emerging a few minutes later "clad in brilliant yellow, thickly covered with black polka-dots."

It is, however, in the Flat-fishes (*Heterosomata*) that the capacity for changing the coloration in harmony with the surroundings reaches its height. In the Flounder (*Flesus*), for example, the colour is generally greyish-olive, often more or less marbled with brown, but this may vary from yellow to almost black, and so perfect is the resemblance to the mud, sand or gravel on which the fish happens to be resting, that unless it moves it is wellnigh invisible. The bright orange-red spots of the Plaice (*Pleuronectes*) will be familiar to all, but few are aware that when the fish moves on to a piece of ground

a. On Gravel.



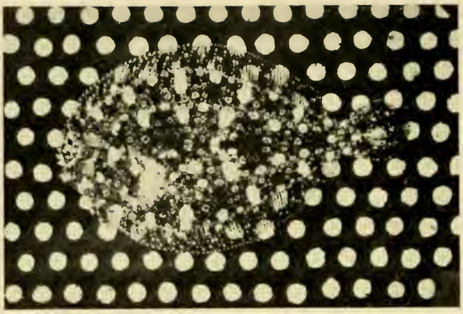
b. On Coarse Sand.

c. On Shingle.

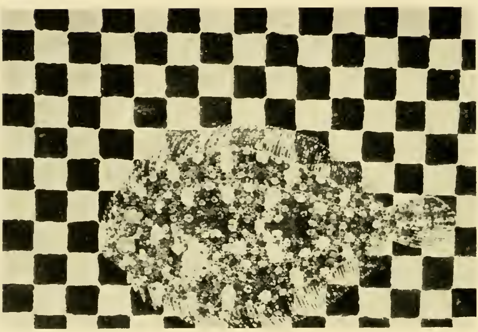
Plate IIA.

Colour changes in a Mediterranean Flat-fish (*Bothus podas*).

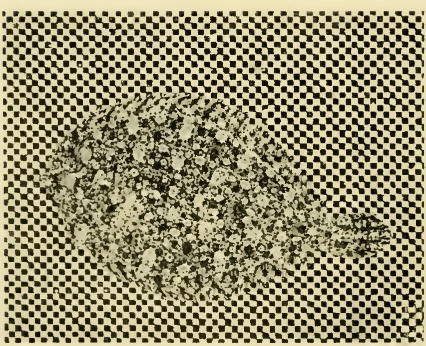
By permission of Professor F. B. Sumner.



a.



b.



c.

Plate IIb.

Colour changes in a Mediterranean Flat-fish (*Bothus podas*). On three different artificial backgrounds.

By permission of Professor F. B. Sumner.

covered with little white pebbles the red spots are said to become white to match the altered surroundings. The Turbot (*Rhombus*) living on dirty mud or sand on the sea bottom is a dull-greyish fish, but in an aquarium tank with sanded floor it is of a pale yellowish hue, and if placed on a background of coarse gravel, yellowish spots are developed over the head and body, separated from one another by a dark network.

Some experiments conducted at the aquarium at Naples on a Mediterranean Flounder (*Bothus*) are of interest (Pl. IIA, B). The same individual was successively placed in glass dishes on the bottom of which were painted chessboard backgrounds of black and white squares, black and white circles, and so on, and was induced to imitate the pattern, but as the background was an unaccustomed one, the colour change took about half an hour instead of the usual second or so. It was found, however, that with practice a fish was soon able to harmonise with the background more rapidly than at first, but its capacity for colour change was limited to the black, brown, grey and white of its ordinary surroundings. An American investigator, experimenting on Flounders (*Paralichthys*, etc.), carried the matter further, and found that when placed on backgrounds of white, black, grey, brown, blue, green, pink, and yellow, they made very good attempts to produce a coloration similar to that on which they were lying. They copied red backgrounds with less accuracy than those of other shades, and whereas yellows and browns were simulated with rapidity, greens and blues took a greater time, and a considerable interval sometimes elapsed before the full effect was obtained.

Although an impulse to conform to the environment is undoubtedly the principal motive for the colour changes of fishes, there are cases in which other factors are involved. Just as we ourselves may undergo a sudden flushing or pallor, certain colour changes of fishes seem to be definitely emotional, and such expressions as "white with fear" and "crimson with rage" assume a literal meaning when applied to some of the "chameleons of the sea." It has been observed that in captivity, under the stress of excitement due to food being thrown into a tank or the artificial light being suddenly turned on, fishes tend to exhibit definite colour phases and markings, and that other "distress phases" are shown by injured or sick individuals, or when the stoppage of the normal flow of water causes actual discomfort to the inhabitants. The very marked colour changes seen in the Bullhead (*Cottus*) of our own streams and rivers have been shown to be associated with such emotions as greed, anger, or fear. Although in ourselves a feeling of extreme fear is followed by pallor, in fishes the experience of this emotion is generally followed by the assumption of a dark coloration.

Very remarkable colour changes often occur after death, and the hues of many fishes a few hours after capture are quite different to those exhibited in life. In Mackerels (*Scomber*), Mullets (*Mullidae*) and other brightly iridescent forms, the colours appear to be brightest at the time intervening between the capture of the fishes and their death, and in Roman times Red Mullet were not infrequently brought alive to the banqueting table, swimming round and round in a glass vessel, so that the guests might gaze on the brilliant display of colour changes afforded in their death struggles. So esteemed were these fishes for their vivid hues and exquisite flavour that at the height of the Roman Empire fabulous sums were paid for particularly fine specimens. Suetonius mentions three fish for which, roughly, £240 was paid, and a single individual in the reign of Claudius is said to have fetched more than £50.

There are, of course, other functions of coloration besides concealment. The question of recognition marks has already been touched upon (*cf.* p. 154), and it is difficult to find any other explanation of the sudden switching on, for example, of a row of black or white spots along the side of the body. Many species exhibit peculiar markings which are remarkably constant in all the individuals—a spot below or behind the eye, a stripe from eye to mouth or at the angle of the mouth, a blotch on the gill-cover, a bright red fin, a brilliant margin to dorsal, anal, or caudal fins, a purple or emerald spot in the axil of the pectoral or pelvic, or a brilliant eye-like spot often ringed with white or yellow on a particular part of the body or fins. Any explanation of these as recognition marks is naturally hypothetical, but the theory that such marks are intended to aid the individuals of a species to recognise one another is quite as plausible as that which assigns this purpose to certain patches of coloured feathers in birds or similar specific markings in mammals.

The young of some species are conspicuously differently coloured to the adults, and although in some cases this may be shown to go hand in hand with a corresponding difference in habits or environment, and is undoubtedly protective, in others no such connection seems to exist. The characteristic "parr-marks" of a young Salmon or Trout, which disappear altogether as the fish grows up, may be regarded perhaps as vestiges of a coloration which was characteristic of the ancestors of these fishes and which is repeated as a passing phase during early life. In many fishes, again, the two sexes exhibit differences in coloration, particularly in those forms which pair at the breeding season and indulge in some sort of courtship (*cf.* p. 299). The difference in colour may be noticeable at all seasons, or may be developed in the male only and make its appearance as the time for breeding approaches, the colours afterwards vanishing and leaving the two sexes once more alike. It is of interest to note that, although species with dimorphic coloration

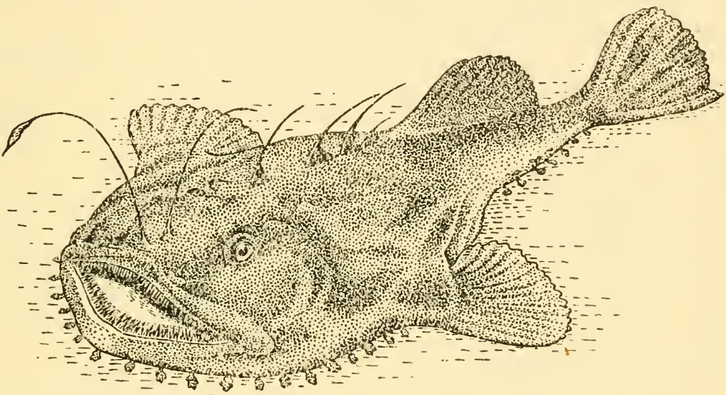


Fig. 89.

Angler (*Lophius piscatorius*), $\times \frac{1}{8}$.

are as common among marine fishes as in fresh-water forms, nuptial colours rarely occur in marine species.

Finally, some types of coloration seem to be of the nature of "warning colours," a signal to would-be enemies that their possessors are dangerous, either by virtue of their poisonous flesh or on account of the possession of venomous spines and the like. The brilliant hues of such poisonous tropical forms as the Trigger-fishes (*Balistidae*), Trunk-fishes (*Ostraciontidae*), and Globe-fishes (*Tetrodontidae*), probably partake of this nature, and act as danger signals to predaceous fishes that have learnt to associate a particular type of coloration with unpalatable qualities, thus operating to the mutual advantage of both parties. One or two species of Serpent Eels (*Ophichthyidae*) of the South Seas have a banded coloration similar to that of the venomous Sea-snakes, for which it would be to their advantage to be mistaken. The Weever-fish (*Trachinus*) provides another example of warning coloration, the dorsal fin, which is the only part of the fish visible when it is buried in the sand, being intense black in colour, and in contrast with the pale yellow and brown tints of the rest of the fish, and of the surrounding sand, is clearly visible from a considerable distance (Fig. 58A). Upon provocation this fin is erected and spread out in a conspicuous manner, and it is suggested that this acts as a danger signal to warn predatory fish of the Weever's whereabouts, fish which might otherwise mistake it for a harmless species of similar size and habits. It is significant that the Dragonet (*Callionymus*), a fish very like the Weever in many respects, and with the same burying habits, is frequently taken from the stomachs of Gurnards, but rarely, if ever, the Weever itself. The Common Sole (*Solea*) has a deep black patch on the pectoral fin of the upper side, and, when alarmed, is in the habit of burying itself in the sand, and raising this fin vertically like a small flag. It has been suggested that the pectoral fin of the Sole mimics the dorsal fin of the Weever, and the fish is thus left severely alone. In the Star-gazers (*Uranoscopidae*) and Flat-heads (*Platycephalidae*), likewise armed with poisonous spines, the dorsal fin is generally black and is the only part visible when the fish is buried in the sand.

The colours of a fish are mainly due to the presence in the dermal layer of the skin, either above or below the scales, of numerous pigment-containing cells known as chromatophores (Fig. 90). Each of these has the form of a small sac with thin and highly elastic walls, supplied with fine strands of muscle fibres associated with delicate nerve-endings. By the expansion or contraction of these fibres the sac may be drawn up into a minute globe, or flattened out to form a relatively large disc. The granules of pigment deposited in each of the chromatophores may be either red, orange, yellow, or black, and other shades are produced by the combination or blending of two or more of these primary colours. The exquisite green colour on the back of the Mackerel (*Scomber*) is due, not to a green pigment, but to a mixing of black and yellow chromatophores in suitable proportions: in the same way, a blending of yellow and black, or of red and black, may give a brownish coloration, and by the appropriate mixing of chromatophores of different colours almost any shade is produced. A black spot or stripe may be due either to the concentration of the black chromatophores in certain regions and their comparative absence elsewhere, or to their expansion in particular areas as contrasted with their contraction in other parts of the body.

But the colours are not all due to pigment, and the presence of a peculiar reflecting tissue composed of structures known as iridocytes also plays an important part. These are made up of opaque crystals of a substance called guanin, owing its origin to a waste product given off from the blood, whose chief feature is the power of reflecting light. Both the chalky white

Fig. 90.

The coloration elements in the skin of the upper side of a freshly killed Flounder (*Flesus*), seen by transmitted light.

and the bright silvery appearance of fishes are due to the manner in which light is reflected from them, and by interference these same colour elements are also responsible for the prismatic hues and brilliant iridescence characteristic of so many fishes. The relative abundance of either type of colour agent varies greatly, not only in different species, but in different parts of the same individual, chromatophores being most abundant in the dark back region, whereas, in the pale belly the iridocytes play the chief part.

Thus, the relative abundance of chromatophores and the kind of pigment they contain, the manner in which they are blended, mixed and distributed in the skin, as well as the iridescence and the reflecting powers of the iridocytes, all play their part in determining the characteristic colour of a fish. The dark bluish-grey colour of the back of a Whiting (*Gadus merlangus*) is due largely to the abundance of black and yellow chromatophores in this region, but these are much less numerous on the sides and absent altogether on the pale belly. The iridescence and silvery appearance of the sides are due to the iridocytes lying above the scales, combined with the reflecting but non-iridescent layer of similar structures below the scales. The dead white of the abdominal region owes its appearance to the different reflecting power of another deep layer of iridocytes in this region known as the argenteum, and to the absence of chromatophores.

The colour changes described in the foregoing pages, whether slow, rapid, or instantaneous, are all due, therefore, to the action of the chromatophores. If these be expanded, the contained pigment is diffused and the particular shade of colour thereby intensified: when contracted, they may shrink to mere dots and thus diminish the vividness of the colour involved. This latter process may even change the colour, for yellow chromatophores become orange when contracted, and orange or red appear brown or black. At the same time, the prevailing hues of the body are altered, not only by the expansion or contraction of the chromatophores, but also by an increase or decrease in their numbers, or by an alteration in the manner of their distribution in the skin.

The initial stimulus to colour change is received through the eyes, as is clearly shown by the following facts. A blind Turbot (*Rhombus*), although living on a light sandy background, remained much darker and more conspicuous than its normal fellows, and dark-coloured Trout (*Salmo*), observed among light individuals in a chalky stream, likewise proved to be blind. Further, a Flounder (*Paralichthys*) placed with its head on a background of one colour and its body on another, always assumed the colour of that on which its head was resting. Even when the whole of the body as well as the posterior part of the head was resting on a white background, the entire fish remained dark so long as the front of the head and the eyes were on the black. Thus, the fish sees the surroundings before making any attempt to imitate them, and an appropriate sensory impulse goes from the eyes to the brain, from whence a motor impulse is transmitted to the muscle fibres controlling the chromatophores. The whole process is purely reflex, and occupies only the fraction of a second.

Some fishes exhibit a condition known as xanthochroism, sometimes occurring in the wild state, but generally brought about by the artificial conditions associated with domestication. In such individuals the black or brown pigment is entirely wanting and the whole body has a golden coloration, or, if the orange and red are also undeveloped, a uniformly silvery hue. The familiar Gold-fish (*Carassius auratus*) is a native of Eastern Asia, and in its natural habitat has the greenish and brownish colours of the other Cyprinids, only the domesticated varieties exhibiting the golden or silver liveries. Individuals that have escaped from artificial ponds and regained the rivers often revert to the original coloration. Golden Tench (*Tinca*), Golden Orfe (*Idus*), and Golden Trout (*Salmo*) are other well-known varieties produced by fish culturists, but Trout of this type are sometimes found in the wild state, and golden-coloured Eels (*Anguilla*) are by no means rare.

The relation between the incidence of light and the distribution of pigment in the skin has already been mentioned in connection with obliterative shading, and it is interesting to find that in the African Cat-fish (*Synodontis*), with the remarkable habit of swimming *with the belly upwards* (*cf.* p. 30), the normal coloration is reversed, the lower parts being dark-brown or black and the back a pale silvery grey (Fig. 11). It has been stated that the Shark-sucker or Remora (*Echeneis*) exhibits a similar reversal of coloration when attached to a shark by the sucker on top of its head, but this requires confirmation. It has been suggested that the absence of dark pigment on the lower surface of a fish has no relation to concealment, but is due to the fact that these parts are shaded from the light. There is certainly some evidence in support of the view that the action of light may be directly related to the production of pigment, and fishes living in caves and wells, where light is absent, are almost invariably colourless (*cf.* p. 232), while bottom-living forms are generally unpigmented on the lower side. Professor Cunningham carried out a series of experiments in the laboratory at Plymouth, in which the lower sides of Flounders were illuminated by a special arrangement of mirrors at the bottom of the tank. He found that chromatophores were slowly developed on the lower surface, which is normally quite colourless, and in some individuals exposed to these conditions for one, two, or three years the lower side became nearly as completely pigmented as the upper.

All Flat-fishes (*Heterosomata*) are, of course, coloured on one side only, the right side in some species, the left in others. The Arabs have a curious legend to account for this, saying that Moses was once engaged in cooking a Flat-fish, and that when this had been broiled until it was brown on one side the oil gave out; this so annoyed him that he threw the fish into the sea, when, although half cooked, it promptly came to life again, and its descendants have preserved this curious arrangement of colour ever since. Mr. Radcliffe has described a Russian legend which states that the Virgin Mary heard the tidings of the Resurrection when engaged in eating a *Rhombus* (Turbot or Brill): "incredulous and as one of little faith she flung the uneaten half of the *Rhombus* into the water, bidding it, if the message be true, come back to life whole! And lo! this it instantly did!" It sometimes happens that a Flat-fish is captured with pigment on the lower side as well as on the upper. This colouring may take the form of scattered brown or black spots on a white ground, or the hinder part of the lower side may have a complete coloration similar to the upper surface. In the Plaice (*Pleuronectes*), for example, the pigmentation of the blind side may even include the red spots so characteristic of this species. Often the pigment extends over the whole body, only the under side of the head remaining white, and in rare cases even this is coloured. This phenomenon of ambicoloration is of particular interest, for it is known that Flat-fishes are descended from symmetrical fishes of the Sea Perch kind, and it has been observed that complete (or nearly complete) pigmentation of the blind side, in whatsoever species it occurs, is almost invariably accompanied by other variations towards this original symmetry. The skin and scales of the lower surface not only assume the colour of those of the upper side, but also resemble them in structure. In a normal Dab (*Limanda*), for example, the scales on the eyed side are spiny, those on the blind side smooth, but in ambicolorate examples they are spiny on both sides. In the Turbot (*Rhombus*) bony tubercles are present on the upper surface but not on the lower, but in ambicolorate individuals they are nearly equally developed on both sides.

Finally, the occurrence of albino fishes, in which no pigment is developed at all, may be mentioned. The body is white, often tinged with pink, but, as a rule, the albinism is not complete, the fish retaining patches or spots of black or brown, as in the black and silver varieties of the Gold-fish (*Carassius*). Completely albino Flat-fishes (*Heterosomata*) are caught from time to time, and it is probable that a number of such cases occur in a natural state; but the fish are at such a great disadvantage in the struggle for existence, being visible to their enemies against almost any background, that comparatively few of them survive to reach maturity.

CHAPTER XII

CONDITIONS OF LIFE

Deep-sea fishes. Cave-dwelling fishes: Kentucky Blind-fish, Cuban Blind-fishes. Evolution of cave faunas. Californian Blind Goby. Sponge-inhabiting Gobies. Hill-stream fishes and their modifications. Effects of temperature on fishes. Catastrophe of Tile-fish. Hibernation and aestivation. Association of Pilot-fish and Shark. Commensalism: Remora and Shark, Pomacentrid and anemone, Rudder-fish and jelly-fish, *Fierasfer* and echinoderm or oyster. Symbiosis. Parasitism: Candiru.

In describing the various organs of a fish's body, the relation between the environment or conditions of life and the structural modifications has been stressed throughout. Just as the struggle for existence in terrestrial regions has led to the colonisation of the air by the birds, and the return to the sea by the whales and other aquatic mammals, so, under the stress of competition, certain fishes have been compelled to penetrate into regions where it would seem impossible for them to survive, or to adopt some markedly unusual mode of life. In the present chapter some of the more interesting of these specialised forms may be considered, and their bodily peculiarities described.

The middle layers and abyssal depths of the oceans provide a number of special physical conditions which are clearly reflected in the structural modifications of the fishes inhabiting these regions. The great pressure under which many of them live, for example, has led to a marked reduction in the skeletal and muscular systems, these parts being but feebly developed as compared with the same structures in littoral forms. The bones are very thin, light, frequently quite flexible, and the ligaments connecting them are fragile and easily torn. The lateral muscles of the trunk and tail, although powerful enough, are often extremely thin, and the connective tissue binding them together loose and feeble. The skin may be little more than a fine membrane, and capable of great distension. Other characteristic modifications involving the light-producing organs, muciferous system, barbels, eyes, teeth, colour, and so on, have been adequately considered in earlier chapters.

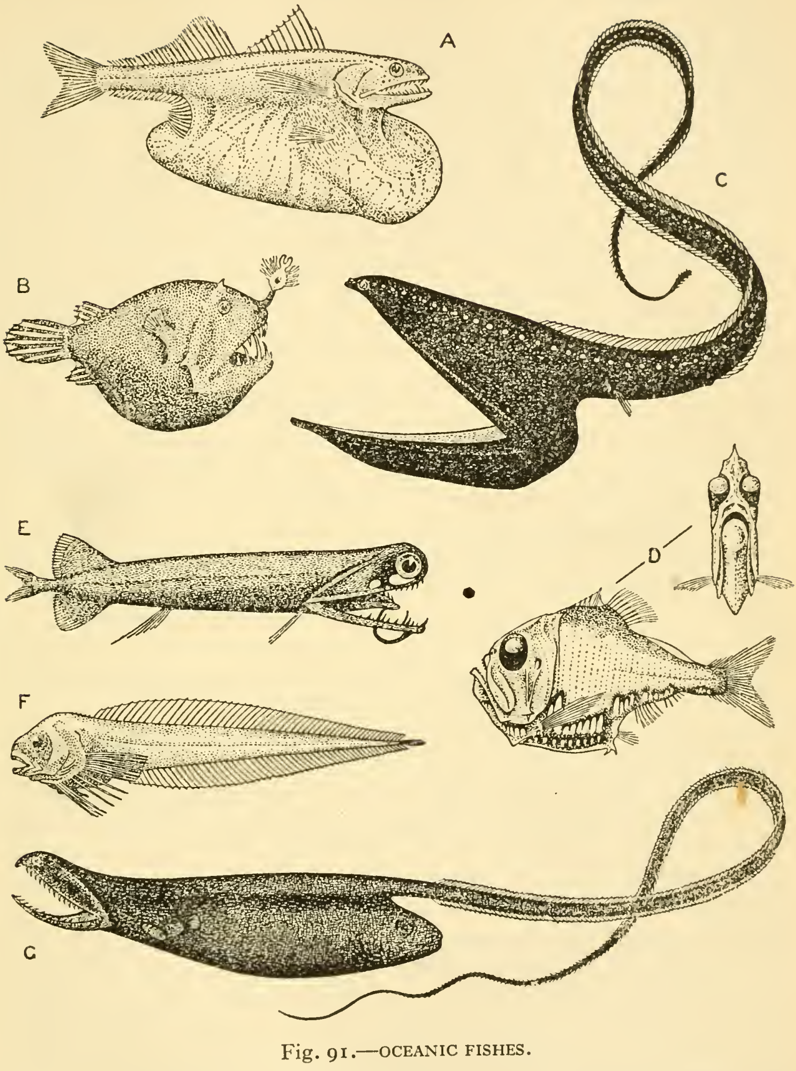


Fig. 91.—OCEANIC FISHES.

A. "Great Swallower" (*Chiasmodon niger*), $\times \frac{1}{2}$; B. *Borophryne apogon*, $\times \frac{1}{2}$; C. "Gulper" (*Eurypharynx pelecanoides*), $\times 1$; D. Hatchet-fish (*Argyropelecus sp.*), $\times \frac{1}{2}$; E. "Wide-mouth" (*Malacosteus indicus*), $\times \frac{1}{2}$; F. *Paraliparis sp.*, $\times \frac{1}{2}$; G. "Gulper" (*Saccopharynx ampullaceus*), $\times \frac{1}{4}$.

In some parts of the world the abundance of food in caves, wells, and other subterranean waters, coupled with the absence of larger predaceous fishes, has led certain species belonging to very different families to take up their existence in these regions of more or less total darkness. These include two or three Cyprinid fishes allied to the Barbels (*Barbus*), found in wells and subterranean lakes in Africa; Cat-fishes of four different tribes inhabiting caves and wells in Africa, the United States, Trinidad, and Brazil; the famous cave-dwelling Cyprinodonts of the United States; and the blind Brotulids of Cuba. As might be expected, where the cave-dwelling habit has been adopted comparatively recently the fishes are not especially modified, but in nearly every case the absence of light has led to the reduction or loss of the organs of vision, and a complete loss of pigment, sometimes accompanied by the special development of certain sense organs to compensate for the loss of sight (*cf.* p. 189). In the Cyprinid species the scales are either very thin and flabby or are absent altogether, and the sensory organs of the skin are highly developed.

The most interesting of the blind forms are the Killifishes or Cyprinodonts of the family *Amblyopsidae*, all small fishes under four or five inches in length, and all occurring in the United States of America. Eight species are included in this family, some of them cave-dwellers, some living in the open, but all agree in possessing degenerate eyes, and in having the vent placed remarkably far forward in the region of the throat. One (*Chologaster cornutus*) inhabits open streams and ditches, being particularly abundant in the ditches of the rice-fields of South Carolina. This fish is normally coloured, and the body is striped with longitudinal bands of black. Another very closely related form (*C. agassizii*) found in the subterranean streams of Tennessee and Kentucky is coloured pale brown and the sides are unstriped. Both these fishes have small but quite functional eyes, and no special development of sense organs is apparent. A third species (*C. papilliferus*), likewise related to the above, has the black stripes on the body, small eyes, and, in addition, ridges of sense organs developed on the head and body. The remaining members of the family (*Amblyopsis*, *Typhlichthys*), including the famous Kentucky Blind-fish (*Amblyopsis spelaeus*) first described in 1842 (Fig. 81B), all live permanently in the underground waters of limestone caves. They are translucent and colourless, the eyes are variously degenerated and generally represented in the adults by mere vestiges hidden under the skin, and elaborate ridges of sensitive papillae are present to a varying degree on the head and body.

In the underground streams of Cuba, and perhaps also in Jamaica, are found the well-known Cuban Blind-fishes (*Lucifuga*, *Stygicola*) or "Pez Ciego." The streams inhabited by these fishes first run above ground, then enter the ground, and finally emerge again near the coast. They are in no place far below the surface, and here and there the roofs of the channels are cracked and broken, forming the entrances to the so-called caves. The two forms represent the only fresh-water members of a large and varied family of fishes known as Brotulids (*Brotulidae*), the majority of which live at considerable depths in the oceans. They grow to a length of about five inches, and the coloration varies from dark blue to pinkish. They are

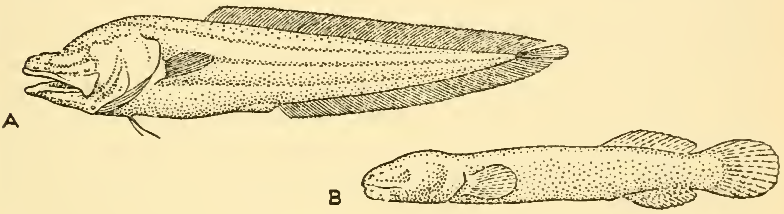


Fig. 92.—BLIND-FISHES.

A. Cuban Blind-fish (*Stygicola dentatus*), × about 1 ; B. Californian Blind Goby (*Typhlogobius californiensis*), × 1.

quite blind, the eyes, which are comparatively well formed in the young, degenerating in the adult and becoming covered with skin (Fig. 92A). The head, however, is provided with numerous minute sensitive barbels.

It seems clear that the adoption of cavernicolous habits inevitably leads to the loss of the body pigments and to the degeneration of the eyes; and further, if this mode of life is extended over a considerable period, the reduction of the visual sense is compensated for by the special development or improvement of some other organ or organs of sense. The ridges of papillae present on the head and body in the Cyprinodonts are regularly arranged, and, as might be expected, are only slightly developed (if at all) in those species which possess eyes, and reach their maximum development in the totally blind forms. Their function is almost certainly the same as that of the lateral line (*cf.* p. 202), enabling the fish to perceive movements in the water, and thus to avoid obstacles or to detect the presence of their prey. It is of some interest to note that even the species with comparatively well-formed and functional eyes depend very little on the sense of sight to obtain food, and it has been found that if the eyes are removed from some individuals they are able to detect the presence of the prey just as quickly as the normal ones. Further experiments have shown that the senses of smell, taste, and hearing of these fishes are, on the whole, much the same as those of other fishes, and that it is the intensification of the "lateral line sense" which serves as compensation for the loss of sight.

The suggestion that Blind-fishes were originally carried into the caves by accident, or that individuals without eyes or with relatively feeble eyes arose in the open as mutations or "sports," and by finding their way into caves were enable to survive, may be dismissed as highly improbable. In the case of the Cuban forms it seems likely that they developed along with the caves. Their ancestors, no doubt, lived in the sea among the coral reefs, and may have been left behind in their original habitat, when these reefs were eventually elevated and carried away from the sea, gradually accustoming themselves to a life in fresh water. In all the other Blind-fishes the penetration of the caves must have been a voluntary matter, and in this connection it must be remembered that nearly all are species of a type which might be described as peculiarly fitted to be blind! The Cat-fishes, for example, live mostly in muddy rivers and streams, and depend more on the sensitive barbels than on the eyes in obtaining food. The blind Cyprinodonts must have been descended from the eyed forms belonging to the same family, or at least from some very similar forms now extinct, and these eyed forms already inhabit situations in which the eyes are of little use and are much reduced in size. Further, one of these species is habitually found under stones in small rivulets, and another, which has reached the underground streams, has developed ridges of sensory papillae.

On the whole, therefore, it seems probable that fishes which have elsewhere become accustomed to do without light, and have adapted themselves to such conditions, have voluntarily penetrated into caves, colonising them gradually step by step, becoming more and more specialised for a life in darkness as each successive generation penetrated deeper and deeper into the recesses. All kinds of fishes abound in the so-called twilight regions near the entrances to caves, and some of these might well be tempted to enter the caves themselves, drawn thither by the abundance of food, and the stress of competition in the outside world. It is well known that fishes living in holes in river banks or under stones tend to have reduced eyes, and it is possible that the ancestors of the existing Blind-fishes spent their lives in such a manner.

The peculiar Blind Goby (*Typhlogobius*) is found on the reefs of the shores of southern California, fastened to the underside of rocks or crawling about in the crevices or in the burrows made by crustaceans. It is about two inches in length, pale pink in colour, with a smooth, naked skin. The eyes are small but functional in the young, but are mere vestiges hidden under the skin in the adult fish. The head is well supplied with dermal sensory organs (Fig. 92B). The channels excavated by a species of burrowing shrimp are used by at least two other kinds of Goby as well as by the blind form, but these normally live outside the holes and only retire into them when danger threatens, whereas the Blind Goby never leaves the shelter of the burrows. Further, the normal Gobies are found all over the shore in this region, but the blind form is restricted in its distribution to a particular part. There can be little doubt that the Blind Goby is descended from a species which habitually sought the crevices and holes in the rocks, and in which the eyes were already reduced and the sensory papillae more extensively developed than in most members of this tribe.

Certain other Gobies (*Evermannichthys*, etc.) habitually live inside sponges, the bodies of the little fishes being of an even diameter which allows them to slip in and out of the larger orifices of the sponge's surface. The scales of these forms are mostly either absent or very feebly developed, but along the lower posterior line of the sides there are two series of large, well-separated scales, the edges of which are produced into long spines, while a series of four more is situated in the middle line behind the anal fin. It is suggested that these specialised structures are used for climbing up the inner surfaces of the sponge cavities.

Another unusual environment to which many fishes have successfully adapted themselves is provided by the torrential streams of hills and mountain ranges. Here again the fishes probably colonised the streams very gradually, being driven from the more sluggish waters of the lowlands by the need for further food supplies and the prevalence of enemies of all kinds. Among the more interesting of the hill-stream forms are the naked and degenerate members of the family of Mailed Cat-fishes (*Cyclopium*), found only in the torrential creeks and rivers of the Andes, most of them merely a succession of falls, cascades, pot-holes and short "riffles"; and the Cyprinids, Loaches, Suckers and Cat-fishes of the hills of Asia, India, and the Malay Archipelago.

Some idea of the difficulties encountered by fishes taking up their abode in hill-streams may be gained if it is borne in mind that huge volumes of water have to be carried away by a number of relatively tiny streams after heavy falls of rain. In the region of the Khasi Hills in India the average annual rainfall is no less than 458 inches, and so great is the rush of water at times that huge blocks of rock measuring four feet across have been described as rolling along almost as easily as pebbles in an ordinary stream, while the torrent of water is said to be actually turbid with pebbles of some inches in size, suspended in the water like mud. Describing the creeks and rivers of the Andes, Mr. Johnson remarks that "the heavy rainfall, at times amounting to four or five inches within a few hours, produces flood of immense volume. These go charging down the canyons with fearful fury, and at times it would appear that nothing could withstand their sweeping energy."

Thus, the strength of the current of water is the principal factor influencing the evolution of fishes in torrential streams, but food is also of primary importance, for, although quite abundant, this consists largely of fine weeds and slime covering the rocks and stones of the bed of the stream. No other type of vegetation is able to avoid being swept away by the force of the current, and although insect larvae are found in fair numbers in certain regions and form an important article of fish diet, the ultimate source of food is vegetable. Another adverse factor, but one of less importance, is the extraordinary clearness and shallowness of the water, which means that during the day the inhabitants have to endure an intense light. On the credit side of the account may be reckoned the rocky nature of the bottom, with its large boulders and pot-holes, forming ideal hiding-places for small fishes, and the abundance of air dissolved in the water, due to its rapid and constant motion.

The structural modifications resulting from these conditions are of special interest, and involve such diverse parts of the body as the skin, scales, mouth, fins, intestines, and air-bladder. Nearly all are connected with the need for providing against the danger of being swept away by the force of the current, but others have been brought about by one or more of the other factors just mentioned.

All hill-stream fishes are necessarily bottom-living forms, and their bodies are generally much flattened from above downwards, sometimes being almost leaf-like (Fig. 35c). The Loaches (*Cobitidae*) form an exception, but their small size and narrow cylindrical form are admirably adapted for creeping into holes and crevices beneath stones. The lower surface of the body in other forms is almost invariably flat, and in order to allow of the adhesion of this surface to that of rocks or stones, the scaly covering is much reduced below, especially in the region of the chest and belly. At the same time, the absence of larger predaceous fishes has obviated the necessity for armour above, and thick scales, scutes, and spines are normally absent. In the Loricariids, for example, the bony scutes with which the whole head and body are covered in the numerous lowland species are entirely wanting in those of the streams of the Andes. Where the current is rapid, a smooth flat lower surface may not be sufficient to obtain a hold during periods of heavy rains, and many fishes have developed a more elaborate adhesive apparatus. In some Asiatic Cat-fishes (*Glyptosternum*, *Pseudecheneis*) the skin of the lower surface is puckered up into grooves and ridges, these being generally most prominent on the thorax or on the under side of the outer ray or rays of the pectoral or pelvic fins. These ridges seem to act as a mechanical friction device, designed simply to prevent the fish from slipping, but where the skin is produced into loose folds a more or less effective vacuum may be created by raising or depressing the folds, the apparatus functioning in much the same way as the sucker of a Remora (*cf.* p. 70). In some Cyprinids the skin covering the lower surface of a few of the outer rays of the paired fins is greatly thickened, in places forming cushion-like pads which enable the fish to cling to the surface of a rock. In others, some sort of adhesive disc working on the vacuum principle is developed, generally taking the form of a rounded or oval structure composed of a pad-like central portion surrounded by a membranous flap. As a rule this lies close behind the mouth, the surrounding membrane being formed by the modification of the lips. In the Loaches (*Cobitidae*) and Suckers (*Gastromyzonidae*) it is the mouth itself that forms the disc, the lips being greatly swollen and divided in the middle, so that when pulled outwards away from the mouth they provide a ring-like sucker. Some of the Asiatic Cat-fishes (*Glyptosternum*, *Exostoma*, etc.) have the lips reflected even more outwards and backwards, these structures being provided with folds, ridges, or papillae on their inner surfaces, and spread continuously round the mouth in the form of a broad, flat sucking disc. The

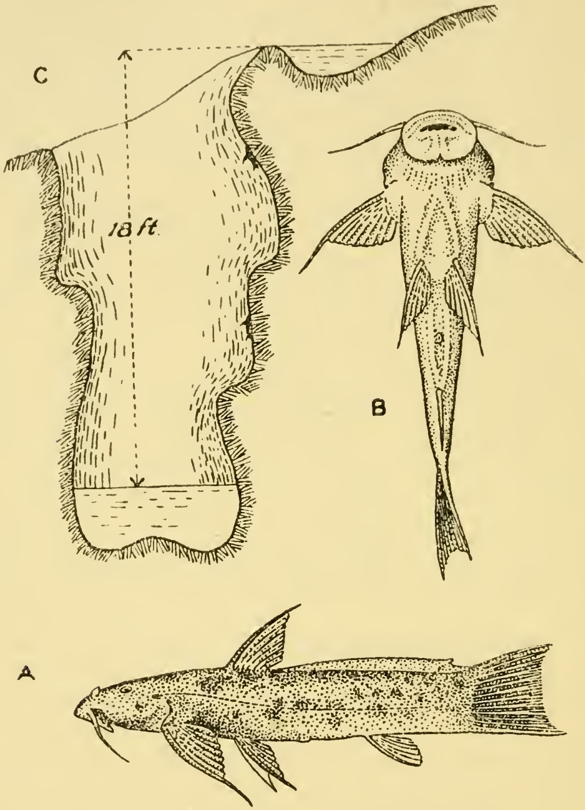


Fig. 93.

A, B. " Capitane " (*Cyclopium marmorata*), × about $\frac{1}{2}$; C. Section of a pot-hole 22 feet deep in Santa Rita Creek, Colombia, showing the fishes ascending the rocky walls. (After Johnson.)

Loricariids of the Andes (*Cyclopium*) have a similar sucker-like mouth, which, in conjunction with an apparatus formed by the lower surfaces of the pelvic fins, also serves as an organ of locomotion (Fig. 93A, B). By means of the alternate action of the mouth and of this apparatus the fish is able to creep slowly forward against even a rapid current, and has been observed to ascend the vertical walls of the large pot-holes in the bed of the stream (Fig. 93C). In other hill-stream fishes the paired fins also take part in the formation of an adhesive disc, generally being placed more or less horizontally at the sides of the body, as in the Bornean Sucker (*Gastromyzon*), in which there are as many as twenty-six to twenty-eight rays in each pectoral fin, and twenty or twenty-one in each pelvic (Fig. 35C).

Other modifications of the mouth and associated structures are connected with the food and methods of feeding in these waters, and may be directly traced to the habit of stripping vegetable slime or weeds from the surfaces of rocks and stones. The snout is nearly always broad and flat, and the mouth, generally crescentic in outline, lies on the under side of the head. In rapidly flowing water barbels would be a hindrance, and these are reduced to minute proportions or absent altogether. In the toothless Cyprinids the jaws may be sharp and cutting at their edges, and in some species they are covered with a strong horny sheath. In the Cat-fishes of the family *Sisoridae* the jaws are often armed with broad bands or patches of minute teeth of various shapes, which act after the manner of miniature rasps. A remarkable Cyprinid (*Gyrinocheilus*), found only in the mountain streams of the Malay Peninsula and Archipelago, has taken to feeding solely on mud, and the pharyngeal teeth, so characteristic of other members of this tribe, have entirely disappeared, the pharyngeal bones themselves being vestigial, and the horny pad at the base of the skull absent. The lips surround the mouth and form a funnel-like sucker, serving not only to scoop up the mud, but also to enable the fish to cling to stones and other objects. The diet has also led to changes in the internal organs, and, since the proportion of nutritive matter in mud is very small, large quantities must be swallowed at a time, and so the intestine has become very much elongated, being about fourteen times the length of the fish itself.

When attached by the mouth to stones in the stream bed, or engaged in feeding, it is obvious that these fishes are often unable to take in water through the mouth for breathing purposes in the usual manner. In the Malay Cyprinid just mentioned, this difficulty is overcome by having the external gill-opening on each side divided in such a way that the water flows in through the upper part and out through the lower, and a similar arrangement is adopted by some of the Cat-fishes. In other hill-stream forms, however, the method of breathing seems to be normal, but they are capable of suspending their respiratory movements for considerable periods. The external gill-openings are generally much reduced in size, and this modification enables the fish to retain a certain amount of water in the gill-chambers during these periods of inactivity. The relatively high amount of air dissolved in the water of hill-streams, coupled with the low temperature of the water, enabling the fish to exist with a small consumption of oxygen, are other factors which help to make this temporary cessation of breathing possible. In certain fishes the inner rays of the pectoral fins are kept in constant motion, and are believed to assist respiration by forcing water out of the gill-openings, or, by driving away any excess of fluid, to assist adhesion.

The modifications undergone by the eyes, air-bladder, etc., must be briefly dismissed. With the flattening of the fish the eyes tend to be pushed more and more towards the upper surface, and in many species they lie close together on the upper side of the head. They are generally reduced in size, probably on account of the intense light encountered in clear shallow water. In fishes living mainly on the bottom, upward and downward movements are comparatively few, and in rapidly flowing water solidity rather than buoyancy are required. For this reason, the air-bladder is always much reduced, and may be encased in a solid bony capsule. Finally, it may be noticed that in hill-stream forms the tail is especially muscular and capable of whip-like movements, by means of which the fish is able to dart rapidly from one stone to another.

The general effects of temperature on the life of a fish may conveniently be considered here, for although extremes of heat and cold do not appear to have led to marked structural modifications, they play an important part in limiting the wanderings of certain species. The range of temperature under which different fishes live is very great, the frozen streams of Alaska and Siberia and the hot springs and warm stagnant pools of equatorial swamps all being inhabited by some forms of fish life.

As far as the fresh-waters are concerned, certain species have pushed very far northwards, being held up only when the water becomes actually frozen. Some, indeed, are able to survive in regions where the water is only liquid for a few months in the year. The little Black-fish (*Dallia*) of Alaska and Siberia (Fig. 32H), a relative of the Pike (*Esox*), is renowned for its extraordinary vitality, remaining frozen in solid ice for weeks on end and thawing out again as the spring approaches in an active condition. It is recorded that one of these fishes was swallowed frozen by a dog, thawed out in the stomach, and vomited up alive. Dr. Gill describes how he kept some little Mud Minnows (*Umbra*) in a large glass jar of water, which froze solid during an exceptionally severe spell of weather, the jar being broken. The lump of ice was allowed to melt gradually, and every one of the fishes revived and swam about in a new receptacle in a perfectly normal manner. Marine fishes have also succeeded in adapting themselves to low temperatures, and quite a fair number of species are found in Arctic seas, although a mere handful as compared with the number found in tropical and temperate regions. In the Antarctic there is a fairly rich fish fauna, even within the limits of the pack-ice. At certain seasons of the year some of these circumpolar fishes live in water that is at or very near to freezing-point. Many oceanic fishes must also endure very low temperatures, the deeper layers of the oceans being at the most three or four degrees Fahrenheit above freezing.

Few, if any, marine fishes are able to endure water of any great heat, but some fresh-water forms, and particularly the inhabitants of tropical swamps, are able to live in water which, during certain seasons, becomes considerably heated. The hot-springs of Arabia, many of them containing water which feels hot to the hand, all serve as dwelling-places for swarms of tiny Cyprinodont fishes (*Cyprinodon*), apparently unharmed by the high temperature. A small Cichlid (*Tilapia*) found in large numbers in Lake Magadi, in the bottom of the Rift Valley, Kenya Colony, is especially interesting. This lake is completely isolated, and the fishes occur in the thermal springs of soda liquor on its eastern shore. The temperature varies in the different springs, but the fish seem to thrive equally well in water, or rather soda, ranging from 80° F. to 120° F.

Although certain kinds of fishes are able to survive in waters of extreme temperature without apparent hurt, it must not be supposed that this is always the case, and actually the range of temperature in which the average fish can live in comfort is comparatively limited, about 12° to 15° for most species. Some experiments conducted by two French scientists on such well-known forms as the Roach (*Rutilus*), Tench (*Tinca*), Gudgeon (*Gobio*), Bleak (*Alburnus*), and Eel (*Anguilla*) are of interest. They subjected individuals kept in aquaria to varying temperatures, carefully noting their behaviour in every case, and found that, as a general rule, few were able to endure water that was hotter than about 99° F., and that cold was resisted much more easily than heat. The fishes were found to behave in a perfectly normal manner in water heated up to 73° to 75° F., their breathing was affected at 93°, a loss of equilibrium occurred at 99°, coma and convulsions at 106° to 109°, and death supervened when the temperature reached 113° to 116°. In the reverse experiment, the fish were normal until the water reached 64°, breathing movements were exaggerated at 60° to 57°, much affected at 53.5° to 50°, equilibrium was upset at 43° to 39°, convulsions occurred at 37.5° to 35.5°, followed by death before freezing-point was reached. The power of resistance to heat or cold varies considerably in different fishes, but it is a little difficult to explain why some species should be so much more easily affected than others. It is clear that those fishes which are less sensitive to change of temperature are most easily acclimatised in new countries, and for this reason the Carp (*Cyprinus*) and some of its allies, such as the ubiquitous Gold-fish (*Carassius*) thrive equally well in tropical and temperate countries. This is not to say that they can stand a sudden and violent change in the temperature of the water, and ignorance of this fact has led to the death of many a pet Gold-fish, which has met its end through being plunged suddenly into fresh *cold* water from the tap during the process of cleaning the bowl or aquarium. Salmon and Trout (*Salmo*) bear transplantation fairly well so long as the water is clear and rather cold, but the closely related Grayling (*Thymallus*) is highly sensitive to the slightest change in its conditions.

A curious and interesting example of a marine catastrophe, believed to be due to such a climatic cause as a sudden influx of cold water, was provided in 1882 by the Tile-fish (*Lopholatilus*), an inhabitant of the deep water below the Gulf Stream in the Atlantic (Fig. 94B). This species was unknown in 1879, but in the following year was found to be extremely abundant everywhere off the coast of southern New England at a depth of from seventy-five to two hundred and fifty fathoms below the surface. Numerous specimens, varying from ten to fifty pounds in weight were captured, and as the flesh was well flavoured, the Tile-fish became the object of an extensive American fishery with long lines. In March 1882, however, following heavy gales, millions of these fishes were to be seen floating dead at the surface of the water, covering an area of no less than fifteen thousand square miles of the sea. For many years afterwards not a single fish was caught, and the species was believed to be extinct, but in recent years it has reappeared in its old haunts. The Scabbard-fish (*Lepidopus*), an oceanic member of the tribe of Trichiuroids or Hair-tails (Fig. 94A), is another species that is remarkably sensitive to cold weather. It is found in all warm seas, and in New Zealand it is known as "Frost-fish," a name which refers to its habit of swimming ashore in thousands on cold nights, apparently in a state of temporary insanity. The related Cutlass-fish (*Trichiurus*) has been observed in a benumbed condition off the coast of Florida while the temperature was still above freezing-point.

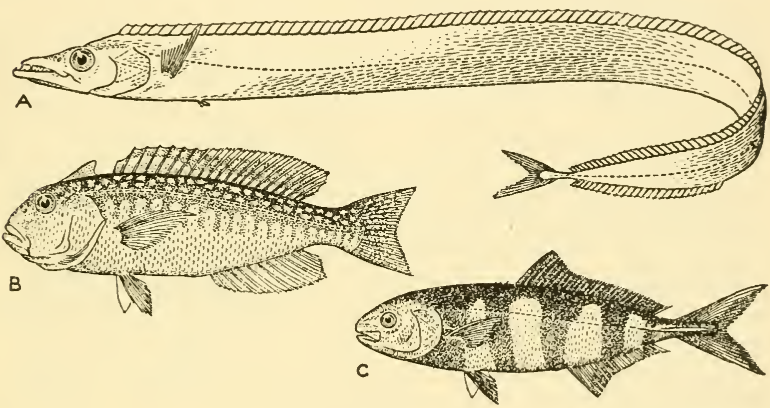


Fig. 94.

A. Frost-fish (*Lepidopus caudatus*), × about $\frac{1}{20}$; B. Tile-fish (*Lopholatilus chamaeleonticeps*), × about $\frac{1}{20}$; C. Pilot-fish (*Naucrates ductor*), × about $\frac{1}{25}$.

A few fishes solve the problem of severe weather by going into a winter sleep or hibernation, which is gradually induced by the fall in temperature as winter approaches, and is sustained until the mercury once again rises in the spring. They do not seem to fall into a complete unconsciousness like the reptiles or such mammals as the dormouse, but simply cease to feed, seek shelter among weeds or stones, and become more or less torpid. The Carp (*Cyprinus*), for example, always moves into deeper water, and this species spends the winter in groups, some of which may contain fifty to a hundred individuals. They make a cavity in the ground and pass the time until spring huddled together in circles with their heads together. Respiration is so much slowed down that the movements of the gill-covers are scarcely apparent. The Tench (*Tinca*) spends the winter actually buried in the mud, and individuals which were dug up and placed on the bank of a river showed no sign of life until struck smartly with a stick. Fresh-water Eels (*Anguilla*) generally seek deep water and lie buried in the mud in a torpid condition. Mr. Thompson records that in 1841 large numbers of these fishes were killed in parts of Ireland owing to the protracted hard frosts with severe easterly winds, and he describes how their bodies floated down the Lagan to Belfast. Among marine fishes hibernation is practically unknown, but there is reason to believe that young Plaice (*Pleuronectes*) remain in shallow water, and pass the cold period in a quiescent state buried in the sand.

Aestivation or summer-sleep does not occur among the inhabitants of the sea, but among fresh-water fishes, and particularly among those that inhabit equatorial swamps which are liable to dry up for weeks or months at a time, this is by no means uncommon. Many of the Labyrinthic fishes such as the Climbing Perch (*Anabas*), Gouramis (*Osphronemus*), and Snake-heads (*Ophiocephalus*), as well as other forms provided with accessory breathing organs, pass the dry season in a torpid condition buried in the mud, emerging again when the rains once more fill their ponds and streams. The natives of some parts of India obtain a regular supply of fresh fish by digging up the Climbing Perch with a shovel.

Among the Lung-fishes (*Dipneusti*) more elaborate preparations are taken for avoiding death during the dry weather. The Mud-fishes or African Lung-fishes (*Protopterus*) live in streams and small rivers which may be absolutely drained for lengthy periods, and their mud beds baked hard by the tropical sun. As the dry season approaches, each fish burrows down into the mud, and the copious slime secreted by its skin mixes with the mud and forms a hard cocoon in which the fish lies dormant until the next rain. A small passage leading from the inside of the prison to the exterior enables it to breathe air during the period of incarceration. From time to time some of these cocoons have been dug up and sent to Europe, and, even after a period of six months, when one of these was placed in tepid water the coating of mud dissolved away and in a few minutes the captive fish was swimming about freely in the water. The South American Lung-fish (*Lepidosiren*) constructs a somewhat similar burrow in the mud, but leaves an opening to the exterior, which is closed by a porous lid of clay.

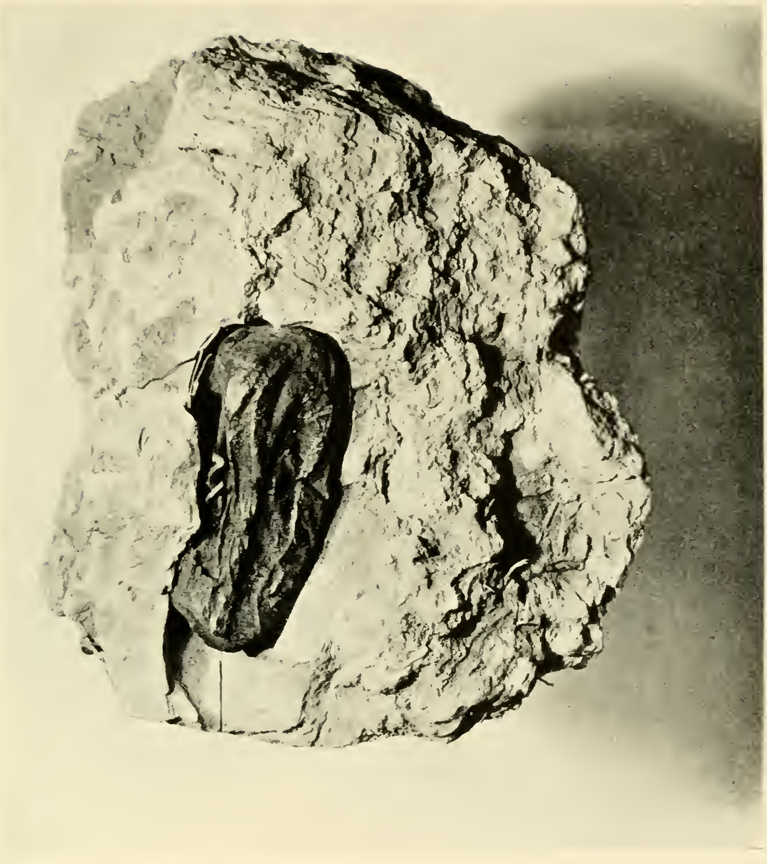


Plate III.

Cocoon of African Lung-fish or Mud-fish (*Protopterus annectens*) embedded in mud. From a specimen in the British Museum (Natural History).

Photograph by Mr W. H. T. Tams.

To eat and to avoid being eaten by others are the most important factors in the daily life of a fish, and certain species, in order to further these ends, have taken to associating with other fishes, or have entered into partnership, as it were, with other animals. Such associations are generally to the advantage of the fish, but frequently for the mutual benefit of both parties. The little Pilot-fish (*Naucrates*) provides an example of one type of association, and has derived its name from the habit of accompanying ships and large fishes, particularly Sharks. It is a small oceanic species, rarely exceeding fifteen inches in length, and is found in practically all warm seas (Fig. 94C). Its general coloration is bluish above and lighter below, and the body is crossed by broad dark bands. It is common in the Mediterranean, and was well known to the ancients under the name of *Pompilus*. Most of the accounts of this fish given by Greek or Roman writers refer to an association with whales and dolphins rather than with sharks, and Aristotle refers to it as the "Dolphin's louse." It was credited with the power of guiding sailors lost upon the ocean, and of announcing the vicinity of land by its sudden disappearance.

For many years it has been accepted that the Pilot-fish is in the habit of guiding Sharks to their food, enjoying in return a degree of protection from its enemies by the proximity of its formidable companions, but it seems clear that many observers have been led astray by sentiment, as well as by the tendency of some people to ascribe human emotions to all the lower animals. It is quite true that one or more of these fishes are usually to be found accompanying Sharks, and that they will also follow slow-moving ships for considerable distances, but it is more than likely that the fragments of the Sharks' meals or the food thrown overboard from the ships provide the attraction, and that their immunity from attack is due solely to their exceptional agility which enables them to avoid being caught by the Sharks. The Pilot-fish does not always leave a ship as land approaches, and in warm weather they have been known to follow vessels as far as the south coast of England, even accompanying them into harbour on occasions. The fact that some individuals have been caught with their stomachs full of small fishes suggests that they do at times pursue their prey on their own account.

In the case of the Shark-sucker or Remora (*Echeneis*) already described (*cf.* p. 70) the association between the two fishes is more intimate, and is of a type known as commensalism.

When the host is feeding on some other animal the Remora obtains some of the fragments floating in the water, but on some occasions the Shark is used merely as a vehicle to carry the Remora to fresh feeding-grounds, where it detaches itself and becomes an independent hunter. Often, however, the Remora enters the mouths or gill-cavities of large Bony Fishes such as the Sword-fish (*Xiphias*), Sail-fish (*Istiophorus*), and Sun-fish (*Mola*); it appears to be tolerated by its host, and gains not only protection from enemies, but also scraps of food.

Interesting examples of commensalism occur among the Pomacentrids or Damsel-fishes (*Pomacentridae*) of tropical coral reefs, some of which are in the habit of entering into partnership with sea anemones. In many cases the fish seems to be an uninvited guest, conferring no benefit on the tolerant host, but Mr. Saville Kent has described an association of this nature in which it is claimed that both parties to the partnership derive a benefit. Among the coral reefs of Thursday Island in the Torres Straits between New Guinea and Australia, he found a brilliantly coloured Pomacentrid (*Amphiprion*), bright vermilion red with three white cross-bands, which habitually lives in the interior of an anemone measuring no less than two feet in diameter when fully expanded. The fish seems to be quite unharmed by the veritable battery of paralysing stinging-cells with which the tentacles of the anemone are armed, or by its digestive juices. In the ordinary way the slightest touch of any animal is sufficient to cause the anemone to contract and to seize the intruder in its tentacles, and it is open to question whether it really tolerates the presence of the fish or whether the latter is active or skilful enough to avoid contact with the tentacles or with the walls of the gastric cavity. Mr. Kent is convinced that the brilliantly coloured fish serves the anemone as a decoy to the mutual benefit of itself and of its host. Issuing forth, it attracts the attention of some watchful predaceous fish, and when chased plunges back into the interior of the anemone: this brings the pursuer within reach of the tentacles with their deadly stinging-cells; it is promptly paralysed and engulfed, and anemone and its assistant share the spoils!

Among the members of the tribe of Rudder-fishes (*Stromateidae*) the young individuals often shelter under jelly-fishes, apparently without fear of the long tentacles with their myriads of poison-cells. One of these fishes is called the Portuguese Man-of-war-fish (*Nomeus*) on account of its constant association with the large and curiously shaped jelly-fishes known as Portuguese Men-of-war. Here we have a type of partnership in which the fish definitely enjoys protection from its enemies, but confers no benefit on its host. It was formerly believed that, in spite of the fact that jelly-fishes seized and devoured other small fishes, they did no harm to those that normally sought shelter beneath them; but it is more than probable that these fishes sometimes fall victims to the paralysing stinging-cells, and that they owe their comparative immunity to their agility in avoiding the tentacles when entering or leaving the sanctuary. Dr. Beebe gives a graphic description of a shoal of jelly-fishes or "Quads," of which roughly one in every four had one or more little Carangid fishes or Bumpers as passengers: small quads with half-inch fish, and large ones, perhaps four inches across, with several two-inch fish or about a dozen of the smaller size. He watched the little fishes manœuvring for several moments before darting between the tentacles, and noticed that they were not infrequently killed while entering their retreat. "The Quad," he writes, "probably does not even know of the fishes' presence until one of them ineptly bumps against the hair-trigger of its nettle batteries, and affords it a hearty meal. . . . When from a Quad measuring two by four inches, there pours forth no fewer than a dozen healthy little fish, these must have been packed together like sardines in a tin."

The Rudder-fish (*Lirus*) of the North Atlantic, another member of the same tribe, has the curious habit of accompanying floating logs or planks, or of taking up its abode within floating barrels or broken boxes, a habit which has earned for the species the name of "wreck-fish." A story is related of a shoal of these fishes that accompanied a floating log which was finally washed ashore at the Aran Islands off the west coast of Ireland, to the great consternation of the inhabitants, who were convinced that these fishes, with which they were quite unfamiliar, were sheogues or fairies. They ran away thoroughly frightened, and one old man, who was bold enough to carry some of the fishes home with him, was not permitted to take them into his house. The attraction to the fishes is the barnacles and other minute and succulent forms of animal life with which derelict timber is almost invariably covered.

In the association between fishes and jelly-fishes described above the benefit is all on the side of the former, and a number of other examples of such a one-sided partnership are known.

A little eel-shaped fish, related to the Blennies, without pelvic fins and with the anal fin extending forward nearly to the head, is in the habit of sheltering within the bodies of marine animals known as Holothurians or Sea Cucumbers, allies of the Star-fishes and Sea Urchins. This fish is known as *Fierasfer*, a name derived from a Greek word meaning sleek and shiny, and has a transparent body with a number of scattered dots of pigment in the skin. When desirous of entering a holothurian the fish searches for the anus with its head, and then bends the tail round, inserts it into the opening, and straightening its body, wriggles backwards until completely housed within the body of its host (Fig. 95). More than one fish can occupy the same "dwelling," and no fewer than seven have been observed to enter a sea cucumber, one after another. By this habit the *Fierasfer* obtains shelter during the day, and at night sallies forth in search of the small crustaceans on which it feeds. The unfortunate holothurian gets no return for its services, and its internal organs may even suffer damage through the presence of its uninvited guest. It is of interest to note that the holothurians living more or less close to the shore are always free from the fishes, whereas those from deeper water generally contain one or more tenants.

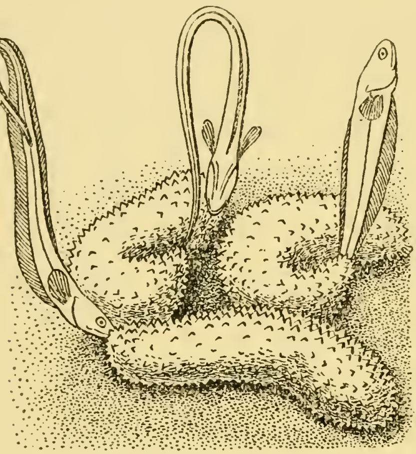


Fig. 95.

Fierasfer acus and Holothurians, × about $\frac{3}{10}$. (After Emery.)

A Japanese species of *Fierasfer* has been found inside a Star-fish, and on the coast of North America it is not uncommon to find these fishes living inside the Pearl Oysters. This association may be fatal to the fish, however, for it is sometimes imprisoned by the oyster and its body sealed up in a layer of mother-of-pearl. Quite recently a little Cardinal-fish (*Apogonichthys*) has been discovered on the coast of Florida, which habitually shelters within the mantle cavity of a large Sea Snail or Conch, leaving its host at intervals to search for food. Other related species are equally at home within the cavities of sponges (*cf.* p. 235). A little Goby (*Gobius*) has been found living inside the gill-chamber of a Shad (*Alosa*), lying curled up quite comfortably beneath the operculum of its host, and a similar association between small Eels and Devil-fishes (*Mobulidae*) has also been described. Small Eels are said occasionally to find their way into the body cavities of larger fishes, generally with fatal results as far as the Eel is concerned.

Yet another type of association is known as symbiosis, where two animals live together in such a fashion that *both* receive

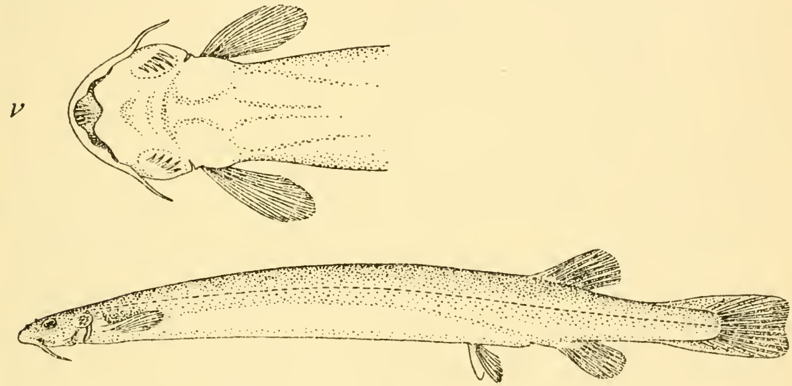


Fig. 96.

Candiru (*Vandellia cirrhosa*), × 1½ ; v. Lower view of head, × 3.

some sort of benefit from the other. In the seas of India, for example, there is a little Scorpion-fish (*Minous*), and practically all the individuals of this species are more or less covered with a thick fleshy colony of hydroid polyps (plant-like animals sometimes spoken of as Zoophytes). Many examples of this fish have been captured, but very few indeed are without the polyps, and the hydroid itself has never been found living apart from the fish. The benefits derived from this association are mutual, the encrusting polyp growth concealing the fish from watchful enemies by giving it the appearance of a weed-covered stone, while the hydroid colony is carried about constantly by the fish and thus obtains fresh feeding-grounds without effort.

Finally, there is the type of association known as parasitism, where one animal dwells on or inside another, nourishing itself at the expense of the living tissues of its host. In man, the louse provides a good example of an ectoparasite, while the tape-worm is a well-known endoparasite. As might be expected, such a mode of life is nearly always accompanied by some degree of degeneration on the part of the tenant, and throughout the whole of the animal kingdom internal parasites are, with few exceptions, degenerate creatures, and in extreme cases only the reproductive organs retain any semblance of their original perfection. Cases of true parasitism among fishes are very rare, although the Lampreys (*Petromyzonidae*) and Hag-fishes (*Myxinidae*) may be regarded as ectoparasitic. Certain members of a family of South American Cat-fishes (*Pygidiidae*) are in the habit of attaching themselves to any kind of fish or animal, piercing the skin and gorging themselves on the blood of the living victim. Others, known to the natives as "Candiru" or "Carnero" (*Vandellia*), habitually live within the gill-cavities of large Cat-fishes (*Sorubim*, *Platystoma*, etc.), and other fresh-water fishes, their slender form enabling them to penetrate between the gills, the sharp teeth and opercular spines being used to start a flow of blood from the host, which is sucked up by the mouth (Fig. 96v). The patches of spines on the gill-covers also serve to assist the fish to wriggle between the gill-lamellae, and to retain their hold when once established. In some parts of Brazil the Candiru are very much dreaded by the natives, owing to their unpleasant habit of entering the urethra of persons bathing in the rivers, and both men and women are in the habit of wearing special sheaths made of palm fibres to protect the external genitalia, when obliged to enter the water. The little fish appears to penetrate into the urethra especially, if not always, during micturition, and it has been suggested that it is definitely attracted by urine. It seems more probable, however, that the flow of urine is merely mistaken by the fish for the respiratory current coming from the gill-opening of a fish. An accident of this nature may have serious consequences, for once the fish has entered it cannot always be pulled out on account of the erectile opercular spines, and a prompt surgical operation is necessary to prevent it from reaching the bladder and causing death from inflammation. Dr. Bach, who has travelled extensively in the Jurua district of the Amazon system, records that he examined natives—a man and three boys—in which the penis had been amputated as a result of this dreadful accident.

The only other case of parasitism occurs among the oceanic

Angler-fishes (*Ceratioidea*), and will be considered in detail in a subsequent chapter (*cf.* p. 315). Here the dwarf male is a parasite on the female, spending the greater part of his life as a mere appendage attached to the body of his mate, and deriving nourishment from her blood.

CHAPTER XIII

DISTRIBUTION AND MIGRATIONS

Science of Zoogeography. Marine and fresh-water fishes. Oceanic fishes. Coastal fishes. Zones of distribution. Tropical Zone: Panama and Suez Canals. South Temperate and Antarctic Zones. North Temperate and Arctic Zones. Migrations of marine fishes: Tunny, Mackerel, Pilchard, Herring, etc. Races of Herring. Origin of fresh-water fishes. Catadromous and anadromous fishes. Distribution of Salmonidæ. Distribution of Ostariophysi. Zoogeographical regions. Australian region: Wallace's Line. Madagascar. Neotropical region. Fishes of South America and Africa compared. Ethiopian and Indian regions. Palaearctic region. British fresh-water fishes. Nearctic region.

THE science of zoogeography or the geographical distribution of animals presents many fascinating problems to the biologist, who has to consider a variety of factors in order to understand the almost cosmopolitan range of some species and the extremely restricted habitat of others. In the case of terrestrial vertebrates, the presence of such physical barriers as mountain ranges, arid deserts, large stretches of water, and dense forests is generally sufficient to explain the localisation of faunas into their own particular regions. Similar physical factors probably serve to limit the wanderings of many fresh-water fishes, but with all the great oceans connected with one another, the dispersal of marine fishes must be restricted by barriers of another kind. The understanding of these involves the study of such diverse factors as the temperature and salinity of the water, its chemical properties, the nature and strength of the ocean currents, the configuration of the coast-line, the presence of submarine ridges and deeps, as well as the all-important subject of the available food supply and its distribution. Nor is it sufficient to consider only the barriers existing to-day, for the present geographical range of many species has resulted from conditions which exerted their influence in the more or less remote past, when the disposition of the great land masses was quite different (Fig. 97). A number of cases of apparently meaningless and anomalous distribution became clear when considered in relation to past history as unfolded by the geologist.

The first and most obvious distinction which suggests itself is between the seas on the one hand and the fresh-waters on the other, the conditions in the two regions being, for the most part, of a very different nature. Certain fishes, like some of the Sharks (*Carcharinus*), Saw-fishes (*Pristidae*), and Sting Rays (*Trygonidae*), ascend rivers for considerable distances, and others like the Flounder (*Flesus*) and Stickleback (*Gasterosteus*) are equally at home in either salt or fresh water. They are unable to survive a sudden change from fresh to saline water, but can pass quite rapidly from the sea to the brackish estuary, and from thence to the fresh water proper, and *vice versa*, without seeming to notice the difference. Others, such as the Salmon (*Salmo*) and Shad (*Alosa*) migrate annually from the sea

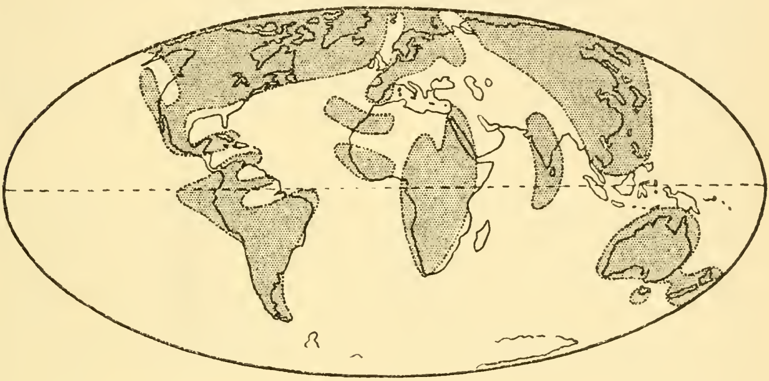


Fig. 97.

Land distribution in Eocene times. (After Gregory.)

to the rivers for spawning purposes, and others, again, like the Common Eel (*Anguilla*) leave the fresh water for the sea as the breeding time approaches.

Two main categories of marine fishes may be conveniently distinguished: oceanic and coastal or littoral. In the open oceans, from the surface down to about one hundred and fifty metres, large, swift, predaceous fishes such as the Tunny (*Thunnus*) and Sword-fish (*Xiphias*) are found, together with swarms of smaller forms such as the Lantern-fishes (*Myctophidae*); the region from one hundred and fifty to five hundred metres is mostly occupied by small silvery fishes of various kinds, the majority with large eyes. Below this the bathypelagic fishes occur—Wide-mouths (*Stomiatidae*), Ceratioid Angler-fishes, and so on—mostly blackish in colour with comparatively small eyes;

and finally, there are the abyssal fishes such as the Grenadiers (*Macruridae*) which spend their lives in the ocean depths and live on or near to the sea bottom. The pelagic fishes, and those dwelling in the upper layers of the ocean, are mostly found in the warm tropical and temperate regions, few penetrating into the colder waters of the Arctic and Antarctic. As far as the bathypelagic and abyssal forms are concerned, knowledge of their distribution is still incomplete, but there can be little doubt that many of them have an almost world-wide range, being little affected by the physical barriers that limit the wanderings of pelagic and coastal forms. Many seem to have a wide vertical range, spending part of their time comparatively close to the surface and part in the deeper layers of water. The contour of the ocean bed may play an important part in restricting the range of abyssal forms, and the submarine ridge, less than one thousand metres in depth, extending from Scotland to Iceland and Greenland, represents the northern limit of the Grenadiers (*Macruridae*).

Coastal fishes may be described as those forms that live comparatively near to the shore, dwelling either at or near the surface like the Herring (*Clupea*) and Mackerel (*Scomber*), or close to the sea-floor like the Gurnard (*Trigla*) or Plaice (*Pleuronectes*), the latter being found both in the shallow inshore waters and on the Continental Shelf. This plateau or shelf, varying greatly in width in the different regions, surrounds all the great land masses or continents, and is formed either by the erosion of the land by the waves or by the extension into the sea of deposits of mud or silt carried down from the land by rivers. This Continental Shelf slopes gradually downwards, its outer edge being about two hundred metres below the surface of the sea. Beyond this edge is the Continental Slope, with a much steeper declivity, extending to a depth of nearly two thousand metres, and below this is the true abyssal region. The coastal fishes generally present a far greater abundance and diversity in the shallower waters of the shelf, and as the abyssal depths are approached, the number of species and of individuals becomes progressively less and less. This relative abundance of fishes on the Continental Shelf and upper part of the Continental Slope is an important factor in the development of the sea fisheries, the prominence of the Atlantic and North Sea industries being due to the presence of large areas of sea-floor at a depth of five hundred metres or less in these regions.

By far the most important factor limiting the geographical range of coastal fishes is the temperature of the sea. This naturally shows some variation in different regions, as well as at different seasons of the year, but it is possible to construct a map to show the average annual temperature in various parts of the world. Such a temperature chart of the oceans is crossed by a series of wavy and irregular lines, running from east to west, and known as isotherms, or to give them their full title, mean annual surface isotherms, lines drawn through points of equal temperature (Fig. 98). In other words, the isotherm of 6° C. is a line connecting all the localities in which the average annual surface temperature of the sea is 6° C.

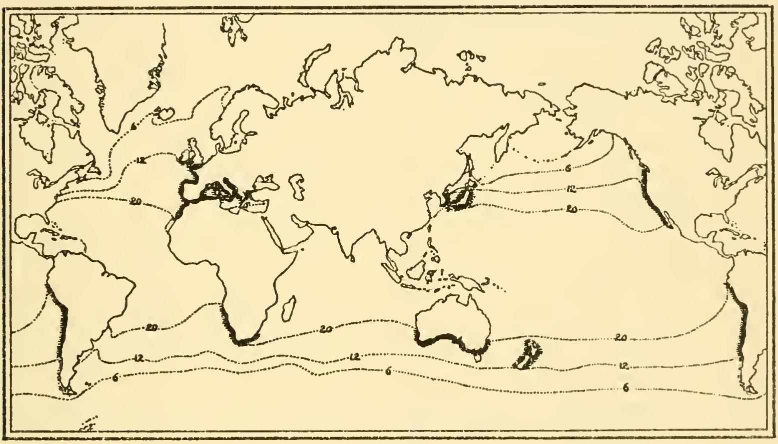


Fig. 98.

Distribution of the genus *Sardina*.
The mean annual surface isotherms of 6°, 12°, and 20° C. are shown.

The distribution of many pelagic and coastal fishes corresponds remarkably closely with the temperature of the water, and it is possible to divide the world into a number of zones of distribution, encircling the globe like a series of horizontal bands, each lying between two of these isotherms. In the centre is the broad Tropical Zone, limited by the isotherm of 20° C.; above and below are North and South Temperate Zones, extending to the isotherms of 6° C. in the north and south, each of which may be further subdivided by the isotherm of 12° C. into subtropical and subarctic and subantarctic zones; and finally, beyond the isotherms of 6° C. are the Arctic and Antarctic Zones, encircling the North and South Poles of the earth (Fig. 98).

The Tropical Zone contains by far the greatest number and diversity of genera and species, although as far as actual numbers of individuals are concerned some of the more northerly species like the Cod (*Gadus*) and the Herring (*Clupea*) probably surpass any of those in tropical climes. Among the characteristic oceanic forms inhabiting this region are the Tunnies, Bonitoes, and Albacores (*Scombridae*), "Sword-fishes" (*Xiphiidae*, *Istiophoridae*), Flying-fishes (*Exocoetidae*), and so on, and as all the coral reefs of the world are included within its limits, such typical reef-dwelling forms as the Butterfly-fishes (*Chaetodontidae*), Pomacentrids (*Pomacentridae*), Wrasses (*Labridae*), Parrot-fishes (*Scaridae*), File-fishes (*Monacanthidae*), Trunk-fishes (*Ostraciontidae*), etc., are largely confined to this zone. The vast majority of the marine Perch-like fishes (*Perciformes*)—Groupers, Grunts, Drums, Carangids, and the like—are inhabitants of the Tropical Zone, which also includes many diverse members of the Herring family (*Clupeidae*) as well as numerous kinds of Flat-fishes (*Heterosomata*).

As far as the coastal fishes are concerned, two main divisions or regions of the Tropical Zone may be recognised: Indo-Pacific and Atlantic. The same genera may occur in both regions, but are nearly always represented by distinct species. A careful examination of the fishes living on either side of the continent of America, and particularly of those in the neighbourhood of the narrow isthmus connecting North and South America, reveals the fact that those of the Atlantic bear a marked resemblance to those of the Pacific. Indeed, in the Panama region many of the species can be arranged in pairs, one being found on the Atlantic side and its nearest relative on the Pacific, the two being frequently so alike that they can only be distinguished with difficulty. How has this similarity of the two faunas been brought about? The artificially constructed Panama Canal, with its series of locks, may be dismissed as a connecting passage, and it is equally impossible for any mixing to have taken place *via* the cold waters of the Arctic and Antarctic Oceans. It is well known, however, that in the geological period known as the Eocene the present isthmus of Panama was submerged beneath the sea and the Atlantic and Pacific Oceans were continuous (Fig. 97). The same types of fishes were then found on both sides of the continent, but the subsequent formation of the isthmus provided a definite physical barrier, and the effects of isolation continued over a long period of time has led to the evolution of distinct species in the two oceans.

The vast Indo-Pacific region extends from the Red Sea and the east coast of Africa eastwards through the Indian Ocean and Archipelago to Northern Australia and the islands of Polynesia. It includes a far greater number of genera and species than the American region. The long and almost unbroken coast-line provided by the huge continent of Asia has enabled shore-dwelling forms to creep slowly and gradually, as it were, from rock to rock and from bay to bay, and as a result of this gradual extension of their geographical range some species now occur both in the Red Sea and in the islands of the South Seas. On the coast of West Africa the state of affairs is very different to that of the Indo-Pacific, and in place of the teeming and diverse fish-life of the latter region there is a comparatively poor fauna. A certain number of species are the same as those occurring on the Atlantic coast of America and must have been able to cross the ocean at some period of their history, others are identical with those found in the Mediterranean, while many others exhibit a definite affinity to those of the Indo-Pacific. As far as the pelagic and deep-sea fishes are concerned, the Cape of Good Hope offers no barrier to their dispersal, but since the isotherm of 20° C., the southern limit of the Tropical Zone, cuts off the south-western part of the African continent, the change of temperature provides an adequate barrier to the mixing of coastal species of the two faunas *via* the Cape (Fig. 98). Here, again, the configuration of the land masses in Eocene times explains to some extent the distribution of the existing forms, for during this period the Mediterranean extended much farther eastwards and opened into the Pacific (Fig. 97). Further, a study of the fossil fishes dug up in Southern Europe reveals the presence during this period of many typically Indo-Pacific genera and species, and there was nothing to prevent these from ranging in the other direction to West Africa. Later, the Indo-Pacific connection with the Pacific closed up, but the West African fauna remains as an indication of this former connection. At the present time the fish fauna of the Red Sea is totally different to that of the Mediterranean, but unlike the canal across the isthmus of Panama, the present Suez Canal, opened in the middle of the last century, probably provides a passage from one sea to the other for certain species. This is only about one hundred miles in length, there are no locks on its course, and the only physical barrier to bar the progress of fishes is the high degree of salinity of the Bitter Lakes which lie in its southern half. These seem to be effective in preventing the dispersal of some species, but do not form an insuperable barrier to others, and a recent investigation of the canal fauna revealed that the Bitter Lakes themselves possessed quite a rich fish-fauna, and, curiously enough, some of the fishes were found to grow to a larger size than the individuals living outside the canal in the Red Sea or Mediterranean. The results obtained from this investigation showed that about forty species of fish live habitually in the canal itself, including species from the Mediterranean and Red Sea in almost exactly equal numbers. Of these, one or two forms from the Mediterranean have succeeded in reaching the Gulf of Suez at the north end of the Red Sea, but have not gone far beyond the neighbourhood of the canal entrance. On the other hand, no less than eight or nine Red Sea fishes have appeared at Port Said, of which several appear to have become thoroughly established in the Mediterranean. For example, a little Sand Smelt from the Indo-Pacific (*Hepsetia*) has been caught about two hundred miles to the west of Alexandria, as well as on the coast of Palestine, and a species of Siganid (*Siganus nebulosus*), a genus of fishes normally confined to the Indo-Pacific region, has appeared near the island of Cyprus. It may be concluded, therefore, that a very gradual and far from complete mixing of the two faunas is taking place through the Suez Canal, and that the journey from Red Sea to Mediterranean seems to present fewer difficulties than that in the reverse direction. This may be explained by the presence of rapid tidal currents in the lower part of the canal, which would tend to sweep floating fish-eggs and larvae into the Bitter Lakes, and by the fact that in the northern half of the canal there is a slow, constant streaming to the north for ten months in the year.

Turning to the Southern Hemisphere, it may be noticed that south of the Tropical Zone the currents are not deflected by the land masses to nearly the same extent as in the north, and the zones of distribution are easier to define and the isotherms more nearly parallel. As far as the subtropical region of the South Temperate Zone is concerned, it is not unusual to find genera common to this region and that of the North Temperate Zone, the Cape fauna having many points in common with that of the Mediterranean. In the accompanying map the dotted areas illustrate the distribution of the genus of Pilchards or Sardines (*Sardina*), and it will be observed how closely their geographical range corresponds to the subtropical regions of the Temperate Zones. The Common Pilchard (*S. pilchardus*) occurs in the seas of Western Europe and in the Mediterranean; a second species (*S. sagax*) is found on the coasts of Chile and Peru, on the Pacific coast of the United States and Lower California, as well as in South Africa and Japan; and a third species (*S. neopilchardus*) in the southern half of Australia and in New Zealand. The absence of Pilchards on the Atlantic coast of America is difficult to understand, but this may be due to the sudden transition from subarctic to almost tropical conditions in the western North Atlantic, where the cold Labrador Current meets the warm Gulf Stream. It would be comparatively easy for a South Amercian species to reach South Africa or New Zealand, since the eggs of these fishes are pelagic and the young have been observed swimming at the surface as far as fifty miles from the shore, but it would be quite another matter to cross the Tropical Zone. The Hakes (*Merluccius*) represent another genus largely confined to these subtropical regions, but also extending into subarctic and subantarctic waters.

A remarkable illustration of the part played by temperature and currents in determining the distribution of fishes is provided by certain forms found round the small islands of Tristan d'Acunha and St. Paul, both of which lie in the subtropical region of the South Temperate Zone. Although about four thousand miles apart, the two islands lie roughly on the same isotherm, and the current known as the Antarctic Drift runs direct from one to the other. As a result of these physical factors, there are species of fish common to both islands, but found nowhere else in the world. A similar case of wide geographical range occurs in the subantarctic half of the same zone, three species being common to southern New Zealand and the Magellan-Falkland Islands area, but found nowhere else.

In the true Antarctic Zone, bounded on the north by the isotherm of 6° C., there is a peculiar and diverse fauna which must have taken a considerable period of time to evolve. The importance of temperature as a factor in distribution is again illustrated by the great similarity between the fishes of South Georgia and Graham Land, which are, however, quite unlike those of the Magellan-Falkland plateau. The great bulk of the Antarctic fauna is made up of fishes known as Nototheniids (*Nototheniidae*, etc.): some of these forms occur in the subantarctic region, but nearly always belong to distinct species. The Antarctic Zone may be conveniently divided into a glacial region, including the Antarctic continent and South Georgia, and a periglacial region, outside the limits of the pack-ice, including Kerguelen and Macquarie Islands.

In the Northern Hemisphere the seasonal variations in the temperature of the sea are very much greater, and the zones of distribution are not so easy to define, although on the whole the same isotherms may be regarded as giving fairly satisfactory boundaries. Whereas, in the south the isotherms are roughly parallel with each other, in the northern seas the spreading of the great ocean currents produces an effect that they are crowded together in the west, but widely separated in the east. This is particularly marked in the North Atlantic, and on the coast of North America the meeting of the cold Labrador Current with the warm water of the Gulf Stream produces a very abrupt change from ice-cold to almost tropical conditions, with a corresponding change in the characteristic fishes. The isotherm of 6° C. runs for a space almost directly north and south off the coasts of Labrador and Newfoundland, then turns in a north-easterly direction towards Iceland, curves to the south of that island, runs still further north-eastwards, and finally bends southwards to meet the Norwegian coast: starting from about 45° N. latitude on the coast of America, this isotherm ends at about 68° N. on the coast of Norway, a difference of latitude of more than one thousand two hundred sea miles (Fig. 98). The reasons for these irregularities of temperature cannot be detailed here, and it must suffice to point out that the principal factors involved are the Gulf Stream or North Atlantic Drift, which carries warm water to the shores of Western Europe, and the Labrador Current, which brings ice-cold water, with icebergs and pack-ice, southwards during the early part of the year.

A glance at the accompanying map (Fig. 98) shows that the isotherm of 12° C., marking the boundary between the subtropical and subarctic regions of the North Temperate Zone, runs roughly to the mouth of the English Channel, and it is in this region that the characteristic fish-fauna shows a definite change. It is, so to speak, the meeting ground of two great areas, and the Pilchard (*Sardina*), Anchovy (*Engraulis*), Red Mullet (*Mullus*), and other lovers of warm water, give place to the typically northern forms like the Herring (*Clupea*), Cod (*Gadus*), and Plaice (*Pleuronectes*). Many Mediterranean species have their northern limit at about this latitude, which also marks the southerly limit of the Salmon and Trout (*Salmo*) as marine fishes. The isotherm of 6° C., marking the northern boundary of the Temperate Zone, is not so satisfactory as a limit of distribution, but it is fairly close to the northern limit of many of our own fishes, and marks the southern limit of the typically Arctic Char (*Salvelinus*) as a sea fish.

In the North Pacific the isotherms, although less irregular than in the North Atlantic, have the same general arrangement, being close together in the west and farther apart in the east. Again, there seems to be a fairly close correspondence between the temperature and the range of the fishes, and such regions as the Bering Sea, Okhotsk Sea, and northern Japanese Sea, each have their characteristic faunas. Certain subarctic fishes are common to both Atlantic and Pacific, and in other cases the genera are the same, but there is one species in one ocean and a very closely related species in the other. The species common to both do not generally extend, however, along the northern coasts of Europe and Asia, but it is certain that they had such a continuous range in the Arctic Ocean in fairly remote times, when the climatic conditions are known to have been considerably milder than they are to-day. After the Eocene period there was a land connection between Alaska and Siberia, but in order to explain the similarity between the fish-faunas of the Atlantic and Pacific it is necessary to assume that this was subsequently broken, and there is evidence to suggest that this happened more than once. The Pacific Herring (*Clupea pallasii*) provides an interesting example of what is known as discontinuous distribution. This fish is related to our own Herring (*C. harengus*), and both species extend into the Arctic Zone. The Pacific species has an isolated colony in the White Sea, but outside on the coasts of Northern Europe and Asia, both to the east and to the west, the Atlantic species occurs.

The last of the zones, the Arctic, has a very poor fish-fauna. A certain number of Bull-heads (*Cottidae*) are common here, and some of the Cods (*Gadidae*) and Flat-fishes (*Pleuronectidae*), a few of which seem to have a very wide range right round the North Pole, are found only within the limits of this zone. One family (*Zoarcidae*) found in this zone also occurs in the Antarctic, but is represented by quite distinct genera in the two regions, and there are no species of fish common to the North and South Polar seas as was formerly supposed.

So much for the general distribution of marine fishes. Although a given species has a definite geographical range in the sea, within the limits of this area individual shoals, or even individual fishes themselves, are more or less constantly on the move, and may undertake extensive journeys from one locality to another. Such movements, or migrations, are rarely sporadic, but generally occur with regularity at certain seasons of the year. They are nearly always undertaken for one of two purposes—reproduction or food—and are consequently known as spawning or feeding migrations respectively. In the case of the Tunny (*Thunnus*), for example, shoals of these gigantic fish may make their appearance in a given locality, and after a stay varying from a few weeks to several months, disappear for the remainder of the year. The migrations of this species are still imperfectly understood, but there is little doubt that they are dependent on the movements of the shoals of Mackerel, Pilchard, Herring, and other smaller fishes on which the Tunny habitually preys. They enter the Mediterranean in huge numbers in the earlier summer, and the fishermen, being conversant with this habit, set special nets, sometimes miles in length, that serve to intercept the fish and to guide them into a very strong net, where they are surrounded, speared or clubbed, loaded on to the boats, and finally landed to be cut up and tinned. Mackerel (*Scomber*), which are essentially warm water fish, keep to the open water during the winter, but in summer, when the inshore waters become warmer, they approach the coasts on both sides of the North Atlantic, and in our own waters travel up the Channel into the North Sea. During May and June they spawn close to the coast, and then move into the bays and estuaries, drawn thither by the presence of shoals of larval and young fishes. During this period the Mackerel can be caught by means of seine-nets drawn on to the beach, but from November to the following May none are to be found in the North Sea. The Anchovy (*Engraulis*) is another species passing up the Channel in the spring, but here the spawning takes place in the outer part of the Zuyder Zee and in the estuary of the River Schelde. The Pilchard (*Sardina*) approaches the coast of Cornwall, the northernmost limit of its range, from July to November or December, but always retires to warmer regions on the approach of winter. It is of interest to note that only the adults appear to travel so far north, and the young or Sardines are never found in any abundance on the Cornish coast. In this species the migration is entirely connected with the movements of the food supply, for as has been already mentioned, spawning takes place in the open sea, well away from land. The Scad or Horse Mackerel (*Trachurus*) feeds almost entirely on the fry of Herring, Pilchard, and other fishes, and sometimes appears quite suddenly off our coasts in incredible numbers at certain seasons, and then equally suddenly disappears. Mr. Yarrell has described a shoal of these fishes seen on the coast of Glamorganshire in 1834, which passed the particular locality for a whole week in such vast numbers that the sea, looked on from above, appeared "one dark mass of fish." They were pursuing the fry of the Herring, and feeding-time was observed to be morning and evening.

On account of its great economic importance, and because of its sporadic occurrence, the migrations of the Herring (*Clupea*) are of special interest. The seasonal movements of the shoals have been studied extensively by the scientific men of several European countries, but although our knowledge of this intricate problem has been enormously increased, much has still to be learned. At some seasons Herrings may be found in huge numbers in a given locality, at others they will disappear almost entirely; in other places they may be caught all the year round, but the numbers captured on a given ground may exhibit an immense amount of variation from one season to another. These annual fluctuations in the yield of Herrings have attracted the attention of naturalists for many years, and amusing explanations were advanced by some of the earlier writers to account for them. That of Mr. Pennant, for example, smacks rather of extreme piety than of scientific reasoning. "Were we to consider this partial migration of the herring in a moral light," he writes, "we might reflect with veneration and awe on the mighty power which originally impressed on this most useful body of his creatures, the instinct that directs and points out the course, that blesses and enriches these islands, which causes them at certain and invariable times to quit the vast polar deeps, and offer themselves to our expecting fleets. That benevolent Being has never, from the earliest records, been once known to withdraw this blessing from the whole, though He often thinks proper to deny it to particulars; yet this partial failure (for which we see no natural reason) should fill us with the most exalted and grateful sense of His providence, for impressing so invariable and general instinct on these fish towards a southward migration, when the whole is to be benefited, and to withdraw it when only a minute part is to suffer." Some of the earlier accounts credited the Herring with very extensive wanderings, but this was due mainly to the confusion of the different races now known to exist. It has been discovered that the species may be divided into a large number of races, each with its own range of distribution and its own season of spawning. Thus, it is possible to recognise North Sea, Baltic, Norwegian, Icelandic Herring, and so on, and each of these may include forms spawning at various times of the year. Off the British coasts there is scarcely any month in which spawning is not taking place on one or other of the recognised grounds, and a broad distinction may be made between winter-spawning Herrings shedding their eggs close to the shore, and summer Herrings spawning in deeper water. The migrations undertaken by the different races, concerned either with reproduction or with food, vary greatly in extent, and the Norwegian Spring Herring may move from the south-west coasts of Norway as far north as the Barents Sea and back again, whereas some of the races spawning in the Cattegat and the Belt Sea do not leave these waters. The movements of the shoals between the spawning seasons are less understood, but there is reason to suppose that the fish do not move far away from the coast. It is clear that the times when they congregate in dense shoals are those when they may be most easily caught by the drift-nets of the fishermen, and, as a general rule, Herrings may be said to collect together at four periods of their life: as young fish, as mature fish just before spawning, as spawning fish, and as spent fish soon after spawning has occurred.

The sea was probably the original home of fishes, and the numerous and diverse forms found to-day in the rivers, streams, lakes, and ponds have been derived from marine ancestors who were driven to leave the sea through stress of competition, and who found in the fresh waters new food supplies, escape from many enemies, and quiet places in which to breed. Many of these pioneer visitors must have become permanent residents in the new habitat, and the changed conditions acting over many generations led to the formation of fresh-water races, and, as time went on, of species distinct from their marine relatives. In course of time these would tend to spread farther and farther inland, and to become more and more modified, until finally there would be whole families or even larger groups composed entirely of fresh-water fishes such as are found at the present time. To-day, almost every order of fishes includes a greater or lesser number of fresh-water representatives, and one

(*Ostariophysi*) has evolved entirely in fresh water, only a few of its members being secondarily marine.

Fresh-water fishes may be conveniently divided into two main categories: (1) those spending part of their life in the sea; (2) those living permanently in fresh water. Among the members of the first group are the Grey Mullets (*Mugilidae*), which inhabit the estuaries and may penetrate for considerable distances up the rivers, as well as fishes like the Flounder (*Flesus*) and Stickleback (*Gasterosteus*), equally at home in salt or fresh water. The Three-spined Stickleback (*G. aculeatus*) has a very wide range, being found on the coasts and in the rivers of the arctic and temperate regions of the Northern Hemisphere, extending as far north as Greenland, Alaska, and Kamchatka, and as far south as Japan, California, New Jersey and Spain. In northern regions it is essentially a marine fish; in the British Isles it is equally common on the coasts and in the rivers; and in Spain and Italy it is almost entirely confined to fresh water.

Also pertaining to the first category are the catadromous fishes, forms which feed and grow in fresh water, but return to the sea to breed. The Common Eel (*Anguilla anguilla*) is the best known of these fishes, and its distribution in Europe is of special interest when considered in relation to its life history, and particularly to its breeding habits. These will be described in a later chapter (*cf.* p. 288), but it may be noted here that the adult Eels cross the Atlantic to spawn in deep water to the south of Bermuda, the larvae subsequently making their way slowly in an easterly direction, reaching the coasts of Europe when about two and a half years of age. Here they become transformed into elvers, which are about three years old when they enter the rivers of the British Isles. A glance at the map (Fig. 106) shows that the distribution of the species in fresh water is a wide one, extending from Iceland and northern Norway to Morocco, and throughout the countries bordering the Mediterranean. Now these are just the coasts that the larvae reach at a time when they are ready to become elvers, or the further regions to which the elvers or young eels are subsequently able to make their way.

Among other catadromous forms mention may be made of a tribe of small fishes allied to our own Salmon and Trout that are found in the Southern Hemisphere. These Galaxiids (*Galaxiidae*) are for the most part confined to the rivers of the southern extremity of South America, the Falkland Islands, the Cape of Good Hope, Southern Australia and New Zealand, but one species from Patagonia, Australia, and New Zealand reverses the habit of its northern relatives and returns to its original home in the sea for purposes of reproduction.

Anadromous fishes are also to be included among those which spend a part of their life in the sea, for such fishes feed and grow in this habitat, merely ascending the rivers at more or less regular intervals to spawn. The best known examples of fishes of this type are the Sea Lamprey (*Petromyzon*), Sturgeon (*Acipenser*), Shad (*Alosa*), Salmon, Trout (*Salmo*), and Char (*Salvelinus*). The members of the Salmon family (*Salmonidae*) are primarily marine fishes of arctic and northern seas, but include a large number of species which have become permanently established in the fresh waters of Europe, Northern Asia, and North America. The various Salmon and Trout comprise a genus (*Salmo*) represented by about ten species in the North Atlantic and North Pacific: those from the Atlantic form a natural group distinct from those of the Pacific, the latter being placed by some authorities in a separate genus (*Oncorhynchus*). Our own Salmon and Trout are to be regarded as two very closely related species, each with roughly the same range in the sea, and each entering the rivers to breed. They are found in the sea from Iceland and the northern part of Norway southwards to the Bay of Biscay, but whereas the Salmon (*S. salar*) has succeeded in crossing the ocean and is found on the Atlantic coast of North America, the Trout (*S. trutta*), which normally does not go nearly so far out to sea, is absent from America. In some of the larger lakes and rivers of Quebec, New Brunswick, and Maine there are Salmon (*Sebago* and *Ouananiche*) which never go to the sea, having become permanent residents in fresh water. In Europe, where it occurs alongside the Trout, the Salmon does not generally form fresh-water colonies in this way, but Lake Wenern in Sweden, now completely isolated from the sea by inaccessible falls, possesses a stock of land-locked and non-migratory Salmon. The Trout forms fresh-water colonies in practically every suitable lake and river which it enters, and many of these permanent residents have become so much modified in the course of time that they present an extraordinary diversity of form, size, coloration, and so on, some of the fresh-water races being so different from their migratory ancestors that they have been regarded as distinct species. Indeed, it is difficult to believe that the lordly Trout of a deep lake, scaling as much as fifty pounds, and the small fishes of three or four ounces inhabiting the mountain streams of Wales, are one and the same species, as are the silvery Sea Trout and the non-migratory Brown Trout.

The presence of stocks of land-locked and non-migratory Salmon, and of fresh-water colonies of Trout is not very difficult to understand. It is clear that in former times all Salmon and Trout lived in the sea, entering rivers at times to spawn. Some of the young fish on their way back to the sea must have found a sufficiency of food, and perhaps a smaller number of enemies, in the lakes and rivers through which they passed, and, regarding these as good substitutes for the sea, they remained behind to found a fresh-water colony of an anadromous species, which would be reinforced from time to time by fresh additions from the sea. In other cases the change in habit may have been involuntary, some physical barrier preventing the young fish from descending to the sea in the normal manner. It has been already stated that the range of both species in the sea extends southwards only as far as the Bay of Biscay, and it is of interest to find that there are fresh-water colonies of Trout in the Atlas Mountains of North Africa, in the islands of Corsica and Sardinia, and in the countries north of the Mediterranean as far east as the Adriatic Sea. Further, in the rivers of Albania and Dalmatia is a small species (*S. microstoma*), never exceeding a length of fifteen inches, which is very closely related to the Salmon. There can be little doubt that the present marine distribution of the Salmon and Trout is limited mainly by temperature, and it is this factor which prevents them from entering the Mediterranean to-day. It may be assumed, however, that if the climatic conditions in Europe were colder, as they were known to be during the period known as the Ice Age, the limit of their range would be farther south. It is certain that during the glacial period both Salmon and Trout occurred in the Mediterranean and ran up suitable rivers to spawn, and that, when the migratory fish once more retreated northwards on the return of milder climatic conditions in Europe, fresh-water colonies were left behind in some of the rivers. The presence of a fluviatile race of Three-spined Sticklebacks (*Gasterosteus aculeatus*) in Algeria may be explained on the same hypothesis.

The fresh-water colonies or races of White-fish (*Coregonus*) and Char (*Salvelinus*) have originated in much the same way. The Char are primarily marine fishes, inhabiting the Arctic Ocean, and running up the rivers to spawn. They have at some time formed permanent fresh-water colonies in various lakes of Scandinavia, Switzerland, Scotland, Ireland, and the Lake District of England, but, as they only thrive in deep cold water, have not colonised the rivers like the Trout. In the same way the White-fish of our lakes, such as the Pollan (*Coregonus pollan*), Vendace (*C. vandesius*), Gwyniad (*C. pennantii*), etc., are descended from northern migratory species which were in the habit of ascending rivers to spawn, as do certain Arctic species to-day. There is little doubt that the Char and White-fish reached the lakes that they now inhabit from the sea during the glacial period, when the climate was considerably colder and the range of migratory Salmonids extended much farther south. When these again retreated northwards, isolated colonies remained behind in the lakes, and these have continued to evolve in various directions according to the nature of the local conditions, many being now so distinct from their migratory ancestors that they might well be regarded as separate species.

The fishes of the second category, spending their whole lives in fresh water, include fluviatile species of genera otherwise marine in habitat, or of genera normally anadromous, fresh-water genera of marine families, or families and even suborders which include only fresh-water fishes. The Bull-heads (*Cottus*), for example, represent a typically marine genus, but the little Miller's Thumb (*C. gobio*) of Europe, a species common in the rivers and streams of England and Wales, is entirely confined to fresh water. The Grayling (*Thymallus*) belongs to the family *Salmonidae*, but the genus is strictly fluviatile and contains no anadromous species. The family *Brotulidae* includes many diverse genera found at great depths in the oceans, and the Cuban Blind-fishes (*cf.* p. 233) are the only fresh-water members. The Cods and their allies (*Gadidae*) represent another big marine family, which includes a single fresh-water genus and species, the Burbot (*Lota lota*). The Atherines or Sand Smelts (*Atherinidae*) are little silvery fishes frequenting bays and estuaries, many of them entering the rivers. In countries where true fresh-water fishes are scarce or absent species of Sand Smelts have become permanently resident in fresh water, and there is a distinct tribe or sub-family of these little fishes in the rivers of Australia and New Guinea, while other forms occur in Madagascar. In the lakes of the Valley of Mexico there are about twenty species of Atherines, most of which grow to a fair size and are valued as food by the Mexicans, who know them as "*Pescados blancos.*" These must have entered the lakes (which lie at the southern end of the Mexican plateau) from the Pacific Ocean in remote times, before they had been cut off from the sea by inaccessible falls. The only other fishes in the lakes are a few Cyprinids which have found their way down from the rivers of North America.

The true fresh-water fishes, that is to say, the fishes which have evolved in the rivers and lakes, may form distinct families, such as the Sun-fishes (*Centrarchidae*) of North America and the Perches (*Percidae*) of the Old and New World, or even whole orders such as that which include the Pikes, Mud-fishes, and Black-fishes (*Haplomi*). To such fishes the sea may be looked upon as constituting a definite and generally impassable barrier, and their distribution is limited by factors which are rather different to those governing the geographical range of marine fishes. The distribution of the members of the order *Ostariophysi*, including the majority of the fresh-water fishes of the world, is full of interest, providing valuable evidence as to the past history of the continents, their former connections with one another, and the lines at which they were originally severed. There is good reason to believe that their evolution has taken place in fresh water, and that their dispersal, necessarily slow as compared with that of land animals, has been very gradually effected by hydrographical changes, among which the capture by one big river of the tributaries of another, the union of two or more rivers due to the elevation of the land, or the joining of two river-systems, the head-waters of which may be separated by only a few miles of swampy land, during abnormal floods, are probably the more important. It has been suggested that a species may have become established in a river system from which it was previously absent through the spawn being carried considerable distances by aquatic birds, through the agency of water-spouts, and by other accidental methods, but there is no direct evidence of such transferences having occurred. It seems more than probable that the present distribution of these fishes was accomplished mainly at the beginning of the geological epoch known as the Tertiary, and that the subsequent land connections and interchanges which had such important effects on the movements of the mammals and reptiles did little to influence the distribution of the fresh-water fishes.

In considering the distribution of the true fresh-water fishes, and particularly those of the order *Ostariophysi*, the land masses of the globe may be conveniently divided into a number of zoogeographical regions. These are: (1) an Australian region including Australia, New Guinea, and all the islands of the Indo-Australian Archipelago lying east of a line running between Borneo and Celebes and separating the islands of Bali and Lombok; (2) Madagascar; (3) a Neotropical region, including Central and South America; (4) an African or Ethiopian region; (5) an Indian region, including India, South-eastern Asia, and the islands of Java, Sumatra, and Borneo; (6) a Palaearctic region, including Europe and Asia as far south as the Himalayas and the River Yang-tse-Kiang; and (7) a Nearctic region, which includes Canada, the United States, and the greater part of Mexico.

The Australian region presents features of particular interest, and the hypothetical boundary known as Wallace's Line, running between Borneo and Celebes and Bali and Lombok, probably represents the original line of separation when Australia was severed from the Asiatic continent. This separation, which is known to have taken place at a very remote period, probably at or before the beginning of the Tertiary, has resulted in the almost complete absence of true fresh-water fishes in the Australian region, since the severance must have occurred before the *Ostariophysi* had even begun to evolve. In this region there are a number of fresh-water genera and species closely allied to marine forms, such as Gobies, Sea Perches, Herrings, Grey Mullets, Sand Smelts, etc., but there are no peculiar fluviatile families. The only true fresh-water species are two in number, and both belong to very archaic groups dating back at least as far as the Cretaceous period. The Australian Lung-fish (*Epiceratodus*) is found to-day only in portions of the Burnett and Mary Rivers of northern Queensland, and the other members of this ancient tribe occur in tropical Africa and South America (Fig. 99). The second is a species of Osteoglossid found in northern Australia and New Guinea, which belongs to a genus (*Scleropages*) containing one other species found in Sumatra and Borneo. The Osteoglossids are a very ancient family, of which the remaining existing members occur in Africa and South America (Fig. 100). The almost complete absence of fishes of the order *Ostariophysi* is remarkable, and a comparison of the fauna of Borneo on the one hand with the neighbouring island of Celebes on the other produces striking results: in the former there are hundreds of species of Cyprinids, Loaches, Suckers, Cat-fishes, Labyrinthic-fishes, etc., peculiar to the island or common to the Malay Peninsula and Archipelago as far as Wallace's Line, whereas, in Celebes, there is not a single indigenous true fresh-water fish. It is true that there are certain widely distributed Indian species in Celebes, as well as in Australia and New Guinea, but these are either estuarine fishes capable of crossing the sea, or

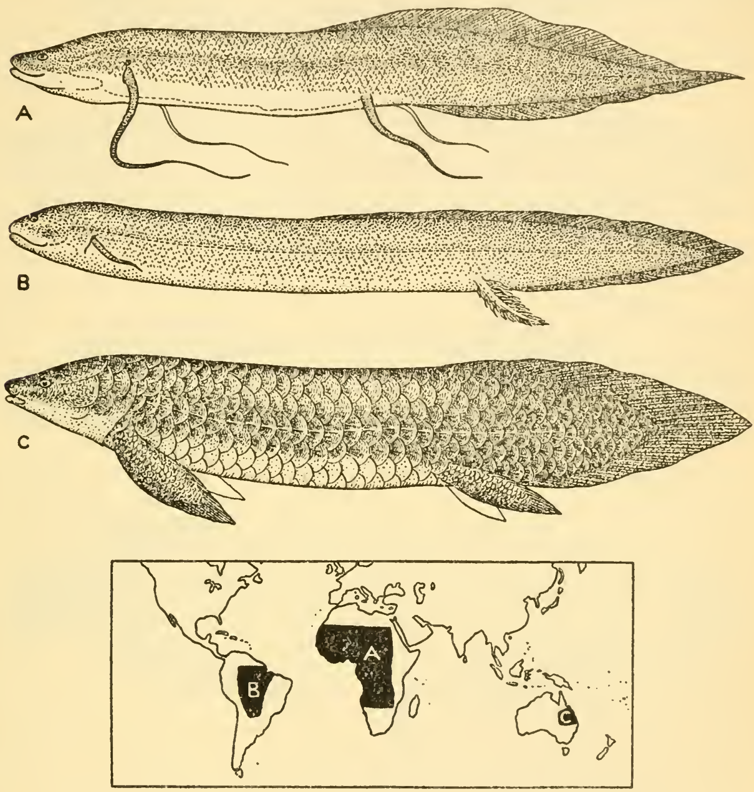


Fig. 99.—LUNG-FISHES (DIPNEUSTI) AND THEIR DISTRIBUTION.

A. African Mud-fish (*Protopterus aethiopicus*), × about $\frac{1}{8}$; B. South American Lung-fish (*Lepidosiren paradoxa*), × about $\frac{1}{8}$; C. Australian Lung-fish (*Epiceratodus forsteri*), × about $\frac{1}{10}$. In the map the black area marked A represents the distribution of the genus *Protopterus*, that marked B of *Lepidosiren*, and that marked C of *Epiceratodus*.

air-breathing forms which can be carried about alive in jars, and may well have been transported from one island to another by man. The only fishes of the order *Ostariophysi* in the Australian region are certain fresh-water genera and species of Cat-fishes, but these belong to two families (*Ariidae*, *Plotosidae*)

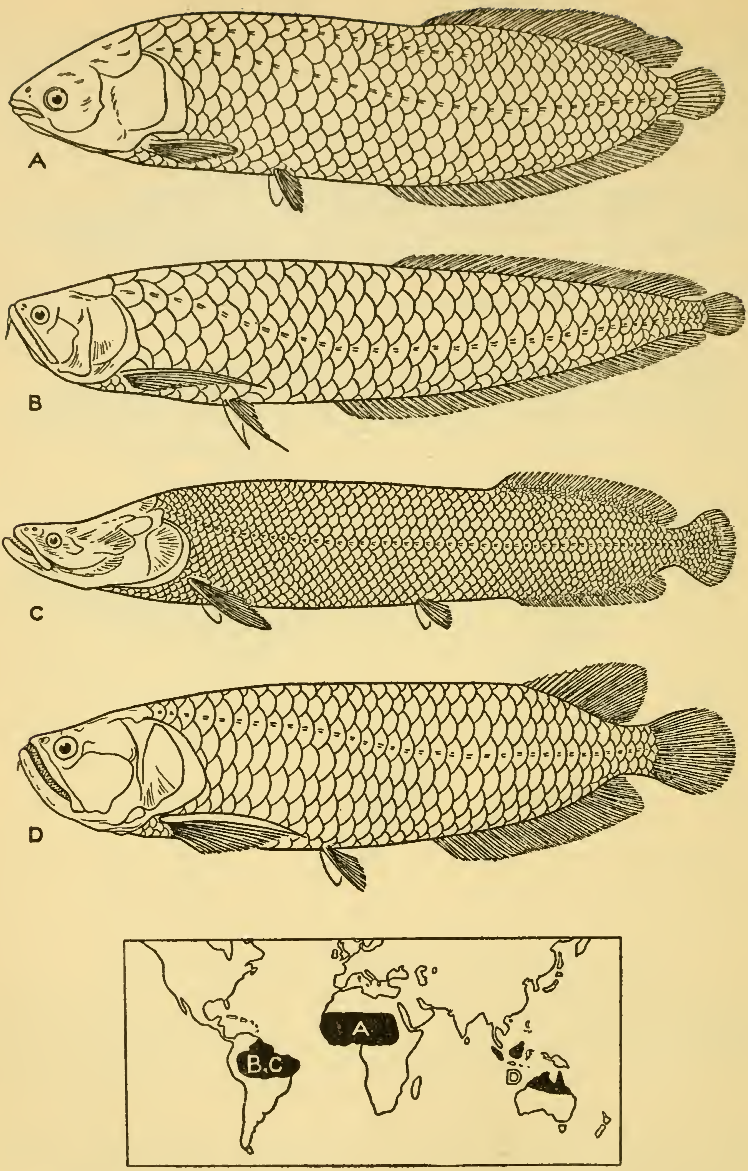


Fig. 100.—OSTEOGLOSSIDS (OSTEOGLOSSIDAE) AND THEIR DISTRIBUTION.

A. *Heterotis niloticus*, $\times \frac{1}{8}$; B. *Osteoglossum bicirrhosum*, $\times \frac{1}{4}$; C. *Arapaima gigas*, $\times \frac{1}{15}$; D. *Scleropages leichardti*, $\times \frac{1}{4}$. In the map the black area marked A represents the distribution of the genus *Heterotis*, that marked B, C of *Osteoglossum* and *Arapaima*, and that marked D of *Scleropages*.

which are known to have secondarily returned to a marine habitat, and certainly reached Australia by sea, and have there again formed fresh-water species.

In most respects Madagascar bears a marked resemblance to the Australian region, being characterised by the complete absence of *Ostariophysi*, with the sole exception of a species of a marine family of Cat-fishes (*Ariidae*). The characteristic African families of Carps (*Cyprinidae*), Characins (*Characidae*, *Citharinidae*), Cat-fishes (*Clariidae*, *Mochocidae*, *Amphiliidae*, etc.), and so on, are all absent, and only the Perch-like Cichlids (*Cichlidae*) are common to the two regions. But the Cichlids are not entirely confined to fresh water, certain species being known to thrive in brackish or even salt water, and all those found in Madagascar are of the estuarine type. It may be concluded, therefore, that the severance of Madagascar from Africa took place very long ago, probably at about the same time that Australia became detached from Asia, and that any fresh-water fishes found there to-day have reached the island subsequently from the sea.

In the Neotropical region the characteristic fishes might be expected to be somewhat similar to those of North America, but, in point of fact, the faunas of the two regions of the New World are of a totally different nature. South America may be said to be inhabited by two distinct fresh-water fish-faunas, different in composition and in origin. The Patagonian fauna, occupying the region south of a line drawn from Valparaiso to Bahia Blanca, is very poor in species, and consists mainly of immigrants from the sea which are more or less permanently established in the rivers, plus a few stragglers (Characins and Cat-fishes) from the north. The region from the La Plata River northwards to Central America is inhabited by a fauna extremely rich in genera and species, which bears a marked similarity to that of Africa. The tribe of Characins (*Characiformes*) is found in the African and Neotropical regions and nowhere else, and of the six families one (*Characidae*) is found in both continents (Fig. 101), four are exclusively South American, and one occurs only in Africa. The family common to the Old and New World presents a much greater diversity and number of genera and species in South America, and although there are no genera common to both, *Alestes* in Africa is very closely related to *Brycon* of South America. The peculiar Eel-like Gymnotids (*Gymnotiformes*) are confined to the Neotropical region, but there are no Carps, Loaches, Suckers, or

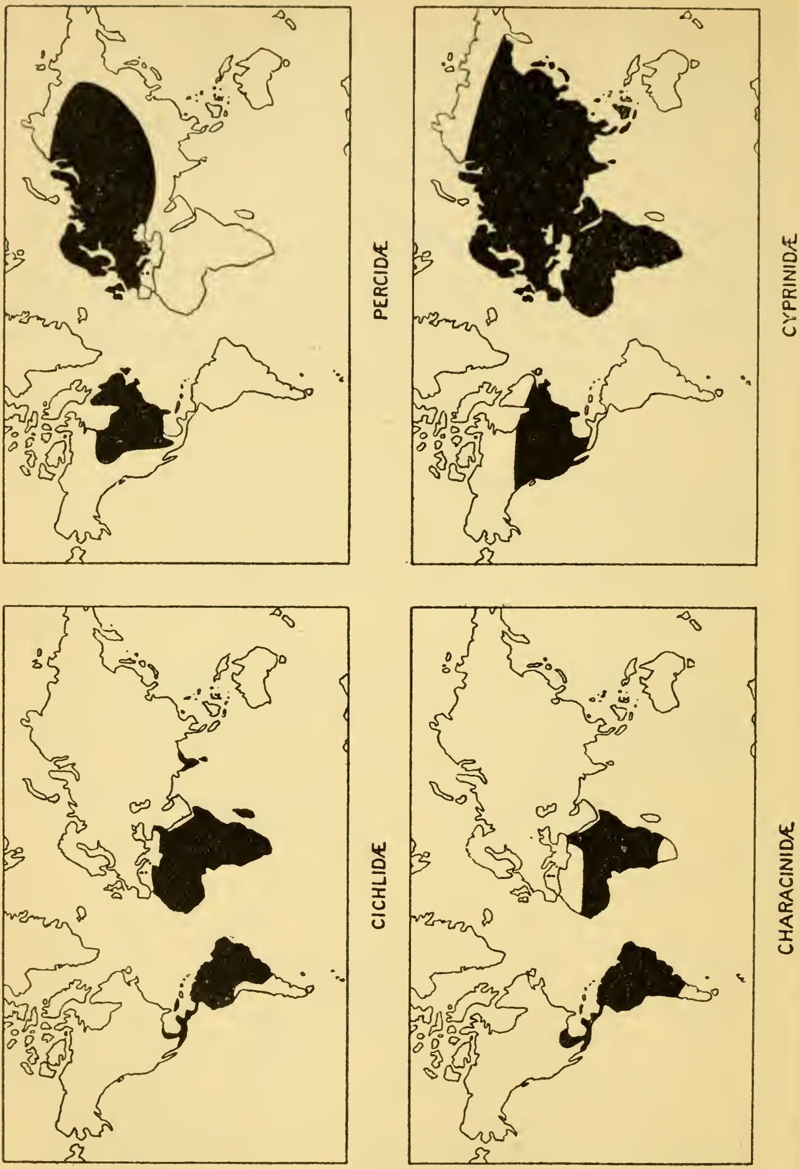


Fig. 101.

Sketch maps to show the distribution of four important families of fresh-water fishes. (After Regan.)

Labyrinthic fishes. Of the Cat-fishes there are nine families in the Neotropical region, all of them peculiar to this part of the world. The Cichlids (*Cichlidae*) are for the most part confined to Africa and Central and South America (Fig. 101), and certain genera of the Old and New World appear to be very nearly related. Cyprinodonts (*Cyprinodontidae*) are likewise found in both continents, but, like the Cichlids, they are fond of living in brackish-water lagoons, and cannot be regarded as strictly fresh-water fishes. Finally, the Lung-fishes are represented by one peculiar genus in each of the two continents.

How is this obvious similarity between the fish-faunas of Africa and South America to be explained? Some geological authorities hold that the great ocean beds are permanent features, and that the similarities are due to migrations from the north. Others believe that in past times the distribution of sea and dry land was very different from that seen to-day, and that the resemblance between the animals of the two countries may be explained by assuming the existence of a former land connection between them. It is impossible to discuss the mass of evidence for and against both of these conflicting theories, but it may be pointed out that that drawn from a study of the distribution of fresh-water fishes lends strong support to the latter view. It seems more than likely that in Cretaceous times the two land masses formed a single continent (with India), in which the *Ostariophysi* originated and underwent their evolution, and that at the end of this period Africa became permanently separated from South America. At this time South America was probably separate from North America, and the subsequent connection of the two by the formation of the Isthmus of Panama at the end of the Eocene period, which led to a great southward migration of mammals and reptiles, seems to have had very little effect on the fresh-water fishes. Certain typically Neotropical forms, such as some of the Characins and Cat-fishes, have pushed as far north as the southern part of Mexico, but none have succeeded in reaching the great Mexican plateau (Fig. 101). In the other direction a species of Gar Pike (*Lepidosteus tropicus*) has extended as far as Panama, but although a few other Nearctic fishes have reached Central America, none have penetrated to South America. It will be observed, therefore, that the very distinct Nearctic and Neotropical fish-faunas, separated by the volcanic chain of mountains which stretches across Mexico from Colima nearly to Vera Cruz, scarcely meet, much less overlap, a state of affairs which is very different when contrasted with the invasion of South America by northern mammals and reptiles.

The Ethiopian and Indian regions may conveniently be considered together, as the fish-faunas of the two areas have much in common. The relationship between the fishes of South America and Africa has been already considered in some detail, and it has been shown that in early Cretaceous times these two countries formed a single continent. Now, this continent must also have extended eastwards to India, but not, as has been sometimes suggested, through Madagascar. The order *Ostariophysi* must have originated and evolved in this great land mass, and when it broke up at the end of the Cretaceous period there were already primitive Cat-fishes and Characins in both South America and Africa, and Cat-fishes in India. The headquarters of the important family *Cyprinidae* lay in Southern Asia, a region in which occurs a great number and diversity of genera and species of these fishes, including those which bear a marked resemblance to the Characins from which they have clearly been derived. These ancestral Characins must have come from Africa, and, as far as the Indian region was concerned, were finally supplanted by the more specialised Cyprinids. At the time that Africa became detached from India it probably possessed no Cyprinids, and the multitude of species found in that country to-day, most of which belong to characteristic Indian genera, are the result of a comparatively recent immigration, when at the end of the Eocene period Africa became joined with India to Eurasia. Apart from the Carps, the other fishes common to India and Africa include Cat-fishes belonging to three families, Labyrinthic-fishes, Spiny Eels (*Mastacembelidae*), etc. Among those peculiar to Africa are the curious Mormyrids (*Mormyridae*), Bichirs (*Polypteridae*), certain families of Cat-fishes, and the toothless Moon-fishes (*Citharinidae*), related to the Characins. Apart from certain families of Cat-fishes there are no families peculiar to the Indian region, but there are numerous genera of specialised Carps, Suckers, Loaches, Labyrinthic-fishes, etc., found nowhere else, and a single genus of Cichlids.

The fish-faunas of the Palaearctic and Nearctic regions also exhibit certain definite resemblances, such important fresh-water families as the Carps (*Cyprinidae*), Pikes (*Esocidae*), Mud-fishes (*Umbridae*), and Perches (*Percidae*) being common to both (Fig. 101), although a number of characteristic North American families are absent in the Old World. The *Ostario-*

physi of the Palaearctic region are represented by comparatively few Cat-fishes, all of which belong to Indian genera, and a large number of Carps and Loaches. These must have spread northwards from their original headquarters, penetrating first into temperate Asia and later invading Europe. A fair number of Carps occur in Europe, a few Loaches, and one Cat-fish, the Wels or Glanis (*Silurus*), found only in the rivers east of the Rhine. In our own islands about twenty-two species of true fresh-water fishes may be recognised, of which fourteen belong to the order *Ostariophysi*. All of these are also found on the European continent, and a number extend eastwards into Asia. The importance of the Pyrenees mountains as a barrier is emphasised by the fact that only one of these fishes occurs in the Iberian Peninsula, although about half of them have succeeded in penetrating into Italy. Two species, the Burbot (*Lota*) and the Pike (*Esox*), occur also in North America. It is of interest to note that all the twenty-two species occur in Yorkshire, and nearly all in the Trent, the Ouse, and in Norfolk, but there are parts of the British Isles where the true fresh-water fauna is a very poor one. In Ireland there are only ten species, and in Britain there is a marked diminution in the number of species from south to north, culminating in a complete absence of true indigenous fresh-water fishes in the northern highlands of Scotland. A similar decrease in number of species is noticeable from east to west, and quite a number of them are absent from Wales west of the Severn system. The reasons for the very dissimilar distribution in the British Isles of certain species with a very wide and essentially similar distribution on the continent of Europe and Asia are to be found in the former connection of our islands with one another and with the mainland. The whole question of the origin and distribution of British fresh-water fishes has been dealt with in full by Dr. Regan in his book on *British Fresh-water Fishes*, to which reference may be made for further details. He points out that our islands

Fig. 102.

Restoration of Pleistocene Geography of the British Isles, showing the coast-line coincident with the contour of 80 fathoms. (After Jukes-Browne.)

must have been connected with each other and with continental Europe comparatively recently, "when our eastern, and probably our southern, streams were tributaries of continental rivers and received from them the fishes which they contained; only nine or ten of these had reached Ireland before it became a separate island, and the distribution of the rest in Britain at varying rates, according to circumstances has not yet proceeded long enough to spread them all over the island." The accompanying map (Fig. 102) will give some idea of the manner in which the fresh-water fishes reached our islands, and the main routes along which they must have travelled.

In addition to the families common to the temperate regions of the Old and New Worlds (*Esocidae*, *Umbridae*, *Cyprinidae*, *Percidae*, etc.), the Nearctic region possesses a number of families occurring nowhere else. These include the archaic Gar Pikes (*Lepidosteidae*) and Bow-fins (*Amiidae*), the Moon-eyes (*Hiodontidae*), Blind Cyprinodonts (*Amblyopsidae*), Trout Perches (*Percopsidae*), and Sun-fishes (*Centrarchidae*). The order *Ostariophysi* is represented in this region by a large number of genera and species of Cyprinidae, all of a similar type to those found in the Palaearctic region; the family of Suckers (*Catostomidae*), which, with the exception of two species found in China, is confined to North America; and the family of Cat-fishes (*Amiuridae*) variously known as Amiurids, Horned Pouts, Stone Cats, Channel Cats, Mad Toms, etc., of which only a single species is found outside North America. The Suckers and Cat-fishes have been established in this region for a considerable time, as fossil remains of genera and species not very unlike the existing ones occur in Eocene strata. The Cyprinids, on the other hand, appear to have arrived in the New World much later. It has been stated that during some part of the earlier Cretaceous period India became connected with Eastern Asia, thus allowing the Carps and their allies to spread northward, and there is good reason to believe that during the same time a bridge across the Bering Straits connected Asia with North America, probably serving as a passage for the Suckers and the ancestors of the Amiurids. During the subsequent Eocene period this bridge became broken, but the two continents were once again united during the Oligocene, and it must have been at this time that America received its Cyprinids from Asia, and Asia its two Suckers and one Amiurid from North America.

CHAPTER XIV

BREEDING

Reproductive organs. Fertilisation. Ancient theories of spawning. Spawning of Cod, Plaice, Herring, etc. Number of eggs produced. Spawning of Salmon. Of Sea Lamprey. Breeding habits of Fresh-water Eel. Of Cyprinids.

THE reproductive organs or gonads of fishes are of two kinds, ovaries in the female and testes or milt in the male, the former being popularly known as hard roes, the latter as soft roes. In most fishes these are elongate in shape, paired, and more or less intimately associated with the kidneys. The ovaries are pinkish or yellow in colour, granular in texture, and usually lie just below and behind the air-bladder when this is present (Fig. 103). As the breeding season approaches, the ovaries become much enlarged, fill a considerable part of the body cavity, and the separate eggs are plainly visible. The eggs may pass from the ovary to the exterior by way of a passage known as the oviduct, opening either by a special aperture or by one which it shares with the excretory duct, but in a large number of fishes no oviducts are developed, and the eggs simply drop into the main body cavity, passing out through pores in the body wall. The testes have much the same position as the ovaries, but are much smaller, paler in colour, and to the naked eye have a creamy rather than a granular texture. A narrow duct leads from each testis to the genital aperture. Occasionally, individuals are found in which both male and female organs are fully developed, this condition having been recorded in such well-known species as the Cod (*Gadus*), Herring (*Clupea*), and Mackerel (*Scomber*). Such individuals are clearly abnormal, but certain perch-like fishes are invariably hermaphrodite, and, further, are capable of self-fertilisation.

The act of reproduction, by which a new life is brought into being, will be associated by most people with such activities as courtship and pairing of male and female individuals, and with actual union of the two sexes. In fishes, however, such pairing is the exception rather than the rule, and in the majority of Bony Fishes the relations of the sexes at the breeding season are quite promiscuous. This is especially the case in those fishes like the Herring (*Clupea*) and Cod (*Gadus*), which congregate together in dense shoals at certain seasons for the purpose of spawning. The actual reproductive act is, of course, essentially similar to that of all the higher vertebrates, and consists in the fusion of two kinds of gametes or "marrying cells," the eggs or ova of the female and the spermatozoa or sperms of the male (sometimes referred to as the milt). The difference lies in the manner in which this fusion, or fertilisation, as it is called, takes place. Whereas, in the mammal this occurs within the body of the female as the result of conjugation between the sexes, and the fertilised egg develops within a special chamber in her body, in the generality of fishes the ova and sperms are merely shed into the water, where fertilisation takes place. Under such conditions it might reasonably be expected that the proportion of eggs escaping fertilisation would be rather high, especially where spawning takes place in the open sea. This is not the case, however, and in the Plaice (*Pleuronectes*), each female of which extrudes as many as from 250,000 to 500,000 eggs in a single spawning season, unfertilised eggs are very rarely found.

The difficulty of observing the actual process of spawning in certain fishes led to the advancement of some peculiar and generally highly inaccurate theories as to the manner in which they reproduced their kind by the older naturalists, and many of the explanations given by classical authors make amusing reading to-day. Oppian, for example, describes how fishes are overcome by the "passion of love," and the bodies of the male and female meet in the water and "exude mingled slime," which when swallowed by the female produces conception. The great Aristotle came little nearer to the truth. "In point of fact," he wrote, " some are led by the want of actual observation to surmise that the female becomes impregnated by swallowing the seminal fluid of the male. There can be no doubt that this proceeding on the part of the female is often witnessed; for at the rutting season the females follow the males and perform this operation, and strike the males with their mouths under the belly, and the males are thereby induced to part with the sperm sooner and more plentifully. And, further, at the spawning season the males go in pursuit of the females, and as the female spawns, the males swallow the eggs; and the species is continued in existence by the spawn that survives this process." Even Izaak Walton, writing in the seventeenth century, insisted on "spontaneous generation" to explain the propagation of certain fishes!

With regard to the time at which spawning takes place, this varies somewhat in different species, and naturally occurs at different seasons in various parts of the world. As far as our northern food-fishes are concerned, the majority breed in the first half of the year, the spawning season of the Plaice (*Pleuronectes*) extending from January to April, that of the Cod (*Gadus*) in the North Sea from February to May, and of the Sole (*Solea*)

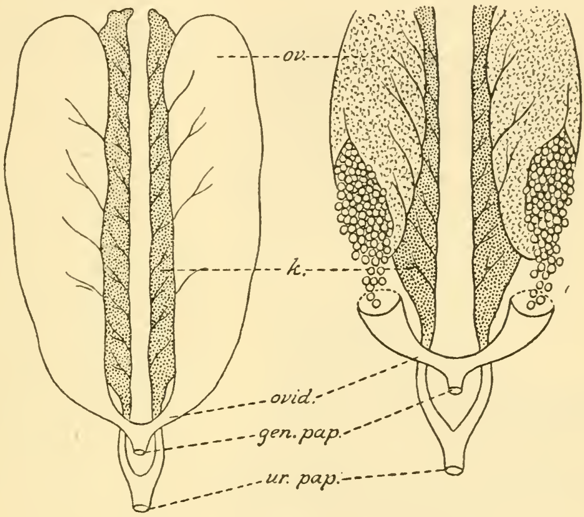


Fig. 103.

Reproductive and excretory organs of a typical Bony Fish (female); A. with oviducts continuous with the ovaries; B. with oviducts separated from the ovaries. (After Rey.)

from April to July. As was pointed out in the last chapter, each race of Atlantic Herring (*Clupea harengus*) has its own spawning season, and some deposit their eggs close to the shore in winter or spring, others in deeper water during the summer or autumn. By the spawning period or breeding season of a particular species or race is meant that period during which some individuals may be found to possess ripe ova or sperms, and this may last only for a few days or extend over as many weeks or even months.

As the time for spawning approaches the fish congregate in huge shoals in suitable localities, and on some grounds they may be very closely packed together at this season. Analysis of these shoals generally shows the females to be in greater numbers than the males, but this is by no means always the case. Here the individuals of both sexes simply discharge their ova and sperms into the water and the fertilised eggs are subsequently abandoned by the parents and left to the mercy of physical conditions. The actual rate at which the eggs are extruded varies a good deal in the different species, in some cases all or a large proportion of the ova being ripe for fertilisation at more or less the same time, while in others the process is comparatively slow and only a certain number ripen and are extruded at one time. In the Cod (*Gadus*) and Plaice (*Pleuronectes*), indeed, in all our food-fishes, with the exception of the Herring (*Clupea*) and Shad (*Alosa*), the eggs are minute and buoyant, and float at or near to the surface of the sea. Under such conditions the haphazard mode of reproduction must inevitably lead to a great waste of sex-cells, but this is diminished to a certain extent by the fact that the fishes are closely congregated and that both eggs and sperm will float roughly at the same rate and in the same direction. Drifting about in the sea at the mercy of the wind and currents, many of the eggs serve as food for other fishes, many are killed by changes of temperature and other physical catastrophes, and many more are cast on the shore by adverse currents. Mr. Masterman, writing of the Cod's eggs, remarks: "It is evident that for the successful development of the young fish a concatenation of favourable circumstances is necessary, which depends in the main upon

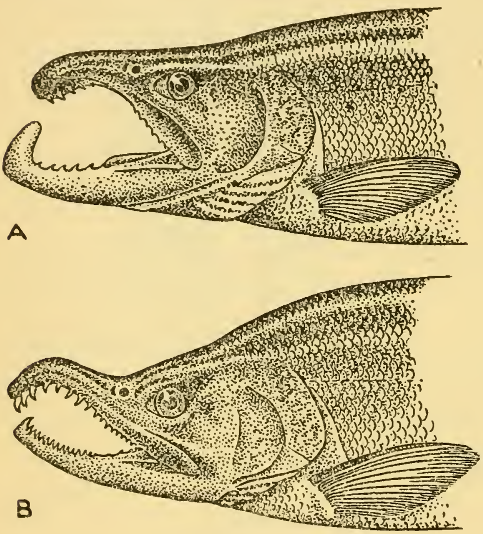


Fig. 104.
Heads of male breeding Salmon (*Salmo*).

A. Atlantic Salmon (*Salmo salar*), $\times \frac{1}{4}$; B. Pacific. Blue-back Salmon (*Salmo nerka*), $\times \frac{1}{6}$.

such essentially fickle phenomena as wind and temperature. Let the wind blow shorewards with abnormal strength and duration, and untold millions of unhatched Cod may perish, or let the temperature for a few weeks during the summer months be abnormally low, and the same fate may overtake hosts of embryonic Gurnards. Under such conditions it is only by the selection of suitable spawning sites, a prolongation of the spawning time (on the principle of not putting all the eggs in one basket), and other devices, that the pelagic spawning fishes have held their own." These enormous risks of destruction to which the larval fishes as well as the eggs are subjected, coupled with the difficulty of ensuring that every egg is fertilised after extrusion, have led to the production of huge numbers of eggs by fishes of this type. A single Ling (*Molva*), 61 inches long and weighing 54 lbs., was found to have 28,361,000 eggs in the ovaries, a Turbot (*Rhombus*) of 17 lbs. weight more than 9,000,000, and a Cod (*Gadus*), weighing 21½ lbs., 6,652,000; a Flounder (*Flesus*), however, produces a mere million of ova on the average, and a Sole (*Solea*) only 570,000. So great is the destruction of eggs and fry that it has been estimated that in the case of the Cod less than one egg in every million liberated ever becomes an adult fish.

The eggs of the Herring (*Clupea harengus*) are heavier than the sea water and are deposited in sticky clumps on shingly banks on the sea-floor. They thus escape many of the dangers to which the floating ova are subjected, but are still exposed to the depredations of hungry fishes of all kinds, and it is a common sight to see hoards of Haddock or other fish following close upon the spawning Herrings, greedily swallowing the newly fertilised eggs. The number of eggs produced by a single female is relatively small as compared with the fishes already mentioned, varying from 21,000 to 47,000.

Many marine fishes migrate to the quieter and shallower inshore regions to deposit their eggs, and others leave the crowded sea altogether, to seek greater safety for their offspring in the rivers. These anadromous fishes include such well-known forms as the Sea Lamprey (*Petromyzon*), Sturgeon (*Acipenser*), Shad (*Alosa*), Salmon and Sea Trout (*Salmo*). Most of them retain the old pelagic habit of leaving the eggs and larvae quite uncared for, and since these are still exposed to attacks by predaceous fishes and enemies of all kinds, the ova are produced in large numbers to compensate for the risks to which they are subjected. A mature female Salmon, for example, produces from 800 to 900 ova for every pound of her weight, so that a fish of 20 lbs. will have about 17,000 eggs. The breeding season of our own Atlantic Salmon (*Salmo salar*) extends from September to February, but these fishes approach the coasts and enter suitable rivers in almost every month of the year. While in the estuaries their ascent may be helped by the tide, but higher up they have to make their way unassisted, and so great is the urge for reproduction that they will display immense perseverance in negotiating obstacles such as falls or weirs lying in their path. Once in fresh water, active feeding is almost entirely given up, and as a result there is a gradual decrease in the weight of the fish after they leave the sea. When first entering the rivers fresh from a lengthy stay in the sea, with its rich and abundant food supply, the Salmon are in fine condition, and exhibit the graceful form and familiar silvery coloration so characteristic of the species, but with the approach of the spawning time they undergo very marked changes, particularly in their external appearance. The silver livery is replaced by one of a dull reddish-brown tint, and in the males the front teeth become enlarged, the snout and lower jaw are drawn out, and the latter is turned upwards at the tip to form a prominent hook (Fig. 104A). Further, the skin of the back becomes thick and spongy, so that the scales are embedded in it, the body becomes spotted and mottled with red and orange, and large black spots edged with white are also developed. Such male breeding Salmon are known as "Red-fish," and the ripe females, which are darker in colour, as "Black-fish." Another important change is in the character of the flesh. In a freshly run fish, that is to say, in a Salmon which has just left the sea, the muscles are firm and red, with a good store of fat in the tissues, but as the time for spawning draws near this fat is used up in the development of the organs of reproduction and the flesh itself becomes pale and watery. The suggestion has been made that this rapid transference of fatty substance from the flesh to the sexual organs is the cause of the difference between the sexes in the breeding season, the process leading to the formation of an excess of by-products which cannot all be excreted, and thus give rise to the growths at the ends of the jaws or appear as patches or spots of pigment in the skin.

Gravelly shallows where the stream runs fairly rapidly are selected as the spawning grounds, and on arrival the Salmon more or less segregate into pairs, the female setting to work to scoop out a shallow trough or trench by means of vigorous lashing movements of her body and tail, and depositing therein a few of her eggs. These are promptly fertilised by the male, sink to the bottom of the trench, and being somewhat sticky externally they adhere to the bottom. The female then loosely covers the eggs with fine gravel, through which they can be properly aerated by the swiftly flowing water of the stream. The whole process is repeated at intervals of a few minutes, the fish moving gradually farther up stream at each spawning, until at the end of a period of one or two weeks all the eggs have been extruded and fertilised. The spawning beds or troughs are known as "redds," and that of a single pair of fish may be several feet long. During the spawning period the males are generally very fierce, driving away intruders with great pugnacity and vigour or engaging in desperate combats with other males. They do not always succeed, however, in keeping away the Trout which sometimes attend the female Salmon on the spawning grounds, and these take any opportunity to fertilise the eggs in the temporary absence of the male Salmon.

The spawning process is a very exhausting one, particularly to the male fish, and few of the latter survive to breed a second time. The spent fish, which are known by the name of "kelts" or "slats," may be recognised by their large heads and general lean appearance. They are in a very enfeebled condition, and if the return journey to the sea be at all long or arduous many succumb to disease, injuries or starvation, or fall an easy prey to poachers, otters, or other enemies. Many females, however, succeed in regaining the sea, where regular feeding and abundant provender soon restores them to their normal condition, the silvery livery being again assumed and the prolongations of the jaws reduced by the absorption of the tissues composing them.

The majority of Salmon enter the rivers to spawn for the first time when three and a half years of age and in the autumn months: such fish are called "Grilse," and return to the sea as "grilse-kelts" in the following winter or spring. Many individuals, however, delay their ascent until the winter or spring, when they are nearly four years of age and are known as "Small Spring Salmon." Others, again, may pass through the Grilse stage in the sea, ascending the rivers for the first time as "Maidens" at the age of four, five, or even six years. A Salmon which survives to spawn more than once does not necessarily do so at regular intervals, and whereas some may actually spawn in successive seasons, spending only a few months in the sea to recover their condition, others miss a year or even allow two or more years to elapse before the call of reproduction once more urges them to enter fresh water. Few Salmon live beyond eight or nine years, and it is exceedingly rare for any individual to spawn more than three or four times in its life. It is of interest to note that with few exceptions Salmon always return to the same rivers from which they originally came, but this powerful homing instinct often receives a check nowadays owing to the poisonous chemical effluents poured into some of our Salmon rivers by factories. In former times the Thames was a famous Salmon river, but pollution of its lower reaches made the ascent impossible, and the last fish was captured here in about 1833. Every year, however, a few Salmon make their appearance at the mouth of the Thames, and there can be little doubt that were the water to become miraculously purified these fish would run up once more and spawn in the upper reaches.

The Salmon of the Pacific coast of North America, a natural group of five or six species (sub-genus *Oncorhynchus*) which includes the famous Quinnat or King Salmon [*S.* (*O.*) *tschawytscha*], have somewhat similar breeding habits, although many of the features of their spawning cycle are more accentuated. The Quinnat spawns in November at the age of about four years and at an average weight of 22 lbs., but the ascent of the rivers by these fish commences in the previous spring. Those individuals which run first have the greatest distance to travel, and in the Yukon the spawning grounds are situated near Caribou Crossing and Lake Bennett, a distance of no less than 2250 miles from the sea. The Blue-back Salmon or Red-fish [*S.* (*O.*) *nerka*] also runs in the spring, ascending the rivers for 1500 miles or more, but the remaining species—the Silver Salmon [*S.* (*O.*) *milktschitsch*], Dog Salmon [*S.* (*O.*) *keta*], Humpback Salmon [*S.* (*O.*) *gorbuscha*], and Masu [*S.* (*O.*) *masou*]—all ascend the rivers in the autumn. The differences between the sexes in the breeding season are very much more marked than in our own species, the males of the Quinnat or Blue-back being hump-backed, with sunken scales, much enlarged, hooked, bent or twisted jaws, and huge dog-like teeth (Fig. 104B). The reproductive act seems to be more exhausting to these fishes, for after spawning the male and female drift helplessly downstream tail foremost, and *no* fish, either male or female, succeeds in regaining the sea. If the spawning grounds lie far inland the bodies of the fish may be covered with bruises even before they reach them, and on these injuries patches of deadly fungus are developed; the fins may be mutilated, the eyes injured or destroyed, the gills heavily infested with parasitic worms, and the flesh white from loss of oil. Thus, as soon as the reproductive act is accomplished, sometimes even before, all of them die, and in some rivers the corpses of spent fish may be observed lining the banks for miles, piled, in some cases, to the height of several feet.

The Sea Lamprey (*Petromyzon*) will serve as another example of an anadromous fish whose spawning habits are of special interest. They ascend the rivers in spring or early summer, in the British Isles running up our southern rivers from February to May and those of Scotland from May or June to July. They not infrequently facilitate their journey by stealing a ride on some large fish bound in the same direction, attaching themselves to the unfortunate victims with their sucker-like mouths and feeding on their flesh *en route*! As in the case of the Salmon, the fish undergo considerable changes in colour at this time, and the two sexes differ markedly in appearance. They make their way to clear, shallow streams, where the bottom is sandy and strewn with pebbles and the current fairly rapid. Here a space is cleared in the bed by moving the stones a little way downstream. This so-called nest is usually oval or roughly circular in form, two or three feet in diameter, and slightly hollowed out, with a pile of stones just below it. Often the males are the first to arrive, and these commence nest-building on their own account: soon, however, each male is joined by a female who assists him in the operations. They move the stones by attaching themselves to them with their suctorial mouths, loosening them by powerful tugs and shakes, and finally dragging them to the pile below the nest. In rare cases a second female has been observed to assist the pair in this work, and the male has subsequently mated with both indiscriminately. The method of copulation is interesting, and takes place in the following manner. The female hangs on to a large stone by her mouth near the upper end of the nest, and the male seizes her by the top of the head in the same way, winding himself partly round her, the bodies of the two fishes being arranged so as to form an ellipse. They then vibrate the hinder parts of their bodies with great vigour, stirring up the fine sand in the process, and the ova and sperms are simultaneously extruded. The eggs are covered with a sticky substance to which particles of sand adhere, and they sink to the bottom of the nest. The fish now separate, and both at once commence to remove stones from above the nest and to place them on the pile below it, thus loosening a good deal of sand which is carried down by the stream and covers the fertilised eggs. The whole process is then repeated at short intervals until all the eggs have been extruded, when the parents leave the nest. They are by this time so exhausted by the reproductive act that they fall an easy prey to enemies of all kinds, including other Lampreys, the wounds inflicted upon one another during mating are attacked by fungus, which invades and ultimately destroys the tissues, and indeed they are so completely debilitated that recovery is out of the question and every one dies.

The Common or Fresh-water Eel (*Anguilla*) is another fish which undertakes a very extensive journey for spawning purposes, from which it never returns, but here the migration is in the opposite direction. Until quite recently the breeding habits of this species were a complete mystery, and some of the older naturalists were driven to advance the most extraordinary and unscientific theories as to the manner in which the Eels propagated their kind. So great was the interest in this matter that, from Aristotle downwards, almost every zoologist propounded his view as to when and where these fishes breed. Aristotle himself, pointing out that Eels had never been found with ripe milt or ova and seemed to possess no generative organs, argued that they must be derived out of "the bowels of the earth," presumably by some kind of spontaneous generation, a view which held favour with the great Izaak Walton. Oppian, as quoted by Mr. Radcliffe, had even more extraordinary views on the subject, but these may refer to the Lamprey.

> "Strange the formation of the eely race
> That know no sex, yet love the close embrace.
> Their folded lengths around each other twine,
> Twist amorous knots, and slimy bodies joyn;
> Till the close strife brings off a frothy juice,
> The seed that must the wriggling kind produce.
> Regardless they their future offspring leave,
> But porous sands the spumy drops receive.
> That genial bed impregnates all the heap,
> And little eelets soon begin to creep."

Pliny, asserting that the Eel has no sex, either masculine or feminine, suggests that, having lived their day, they rub themselves against rocks, and the pieces scraped off their bodies come to life! According to him, "they have no other mode of procreation." Other authors attributed the birth of Eels to the dews of May mornings, or to the transformation of hairs of horses which fell into the water, and others, again, decided that they sprang from the gills of other fishes. Still more extraordinary is the theory of a certain Mr. Cairncross, which appeared in 1862, this author being convinced that the "progenitor of the Silver Eel is a small beetle!" Even thirty years ago the matter still remained a mystery, and all that was known was that large numbers of adult Eels made their way to the sea every autumn, and that in the spring shoals of elvers or little eels, about two and a half inches in length, entered the rivers and made their way upstream. It was very naturally assumed that these elvers were the progeny of those adults that had descended to the sea a few months previously, and that breeding took place in the estuarine waters, a theory shown to be quite incorrect by subsequent discoveries. In comparatively recent years the whole matter has been cleared up by the patient and elaborate investigations of a Danish biologist, Dr. Johannes Schmidt, whose discoveries have provided one of the important biological events of this century. The life-history of the European Eel (*A. anguilla*) as elucidated by Dr. Schmidt may be briefly described, although consideration of the development and metamorphosis of the curious leaf-like larvae or Leptocephalids will be deferred until the next chapter (*cf.* p. 336).

Two distinct kinds of Eels may be recognised: Yellow Eels, representing individuals in their ordinary feeding and growing coloration, and Silver Eels, which are those in their special breeding livery. Yellow Eels are found in both salt and fresh water, inhabiting the regions among rocks and weeds close to the shore, in harbours, estuaries, rivers, lakes, small brooks and even isolated ponds. They vary in length from a few inches to five feet or more, and the females grow to a much larger size than the males. Towards the autumn a certain number of Yellow Eels assume their breeding livery and prepare to undertake the journey to the spawning grounds. Of these, the males are generally about eight to ten years old, the females several years older. They cease to feed, the eyes become enlarged, the lips thinner, the snout sharper, the pectoral fins more pointed and blackish in colour, and the yellowish or greenish coloration is replaced by a metallic silvery sheen on the sides with a deep blackish back (Fig. 105). All these characters become more and more accentuated as the time for breeding approaches, and internally a Silver Eel may be recognised by the riper reproductive organs and the shrunken alimentary tract. They make their way down the rivers in the late summer and autumn, and so powerful is the reproductive call that even those individuals isolated in ponds and lakes will make an effort to reach the sea if a river be fairly near at hand, wriggling across stretches of meadow at nights when the dew lies on the grass. Once in the sea our knowledge of their activities is more conjectural, but it is known that they migrate across the Atlantic Ocean to their breeding-ground, which lies in the Western Atlantic, south of Bermuda. It was formerly thought that the Eels from the countries bordering the Mediterranean spawned in the depths of that sea, but it is now known that even those from the farthest regions at the mouth of the Nile and the northern end of the Adriatic Sea make their way to the Atlantic for this purpose. This stupendous journey, which may be as much as three thousand or even four thousand miles, is undertaken because it is only in this particular part of the Atlantic that conditions suitable to the procreation of the species are to be found. It is believed that the Eels spawn at a depth of about four hundred metres below the surface, and that a fairly high temperature is required for the proper development of the eggs, as well as water of a certain salinity. Having completed the extrusion and fertilisation of the ova, the parents die, for it is not to be expected that such a journey could be undertaken more than once in a lifetime.

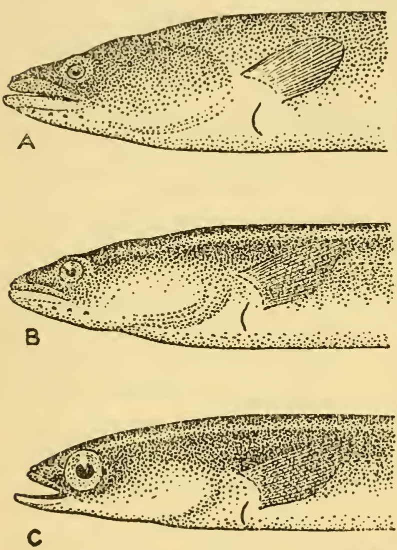


Fig. 105.

Heads of Fresh-water Eels (*Anguilla anguilla*), × ⅓. A. Yellow Eel; B. Silver Eel; C. Mature Eel.

The eggs float for a time, and the young, when hatched out, feed and grow at or fairly near to the surface of the sea, and gradually move in an easterly direction, approaching the coasts of Western Europe when about three inches long and a little more than two years old. They now undergo a metamorphosis and turn into little elvers or glass eels, about two and a half inches in length. These move inshore and commence the ascent of the rivers when about three years of age. The number of elvers passing up a river during these migrations or "Eel-fares" is enormous; upwards of three tons are said to have been captured in a single day in the Gloucester district in 1886, and it has been estimated that more than fourteen thousand individuals go to make a pound weight. Few obstacles seem too great to be overcome by the elvers in their ascent, and they will wriggle over weirs, etc., and even travel overland if the ground be wet in order to reach a suitable resting-place. Here they will feed and grow for some years until the time arrives for them to set off on their own breeding migration.

On the coasts and in the rivers of the Atlantic slope of North America is another closely related species of Eel (*A. rostrata*), distinguished from its European ally by the smaller number of vertebrae in its backbone. The breeding area of this species overlaps that of the European Eel, but its centre lies rather more to the south-west (Fig. 106). In the Western Atlantic, however, larvae of both species are found living together. How is it, then, that these larvae sort themselves out, one kind going to America, the other migrating across the Atlantic to Europe? The explanation lies in the fact that the American Eel grows more rapidly, and the development from egg to fully metamorphosed elver occupies only one year, as against three years in the case of the European species. Thus, if the larva of the European Eel travels in a westerly instead of an easterly direction it will reach the coast of America long before it is ready to change into an elver; and conversely, if the larva of the American Eel migrates in an easterly direction it will undergo its metamorphosis in the middle of the Atlantic. In other words, the larval life in each case is suited to the distance to be travelled, and the length of that of the European species is to be regarded as a special adaptation related to the great distance of the breeding-ground from the coasts.

Among the true fresh-water fishes the members of the large and varied Carp family (*Cyprinidae*) nearly all produce large numbers of ova, which adhere to weeds, stones, and other objects. After spawning no further care of the offspring is taken by the parents. A female Carp (*Cyprinus*) of four pounds weight has about four hundred thousand eggs, one of sixteen and a half pounds more than two million. The relations between the sexes in the breeding season may be described as polyandrous, for, although in certain species pairing may take

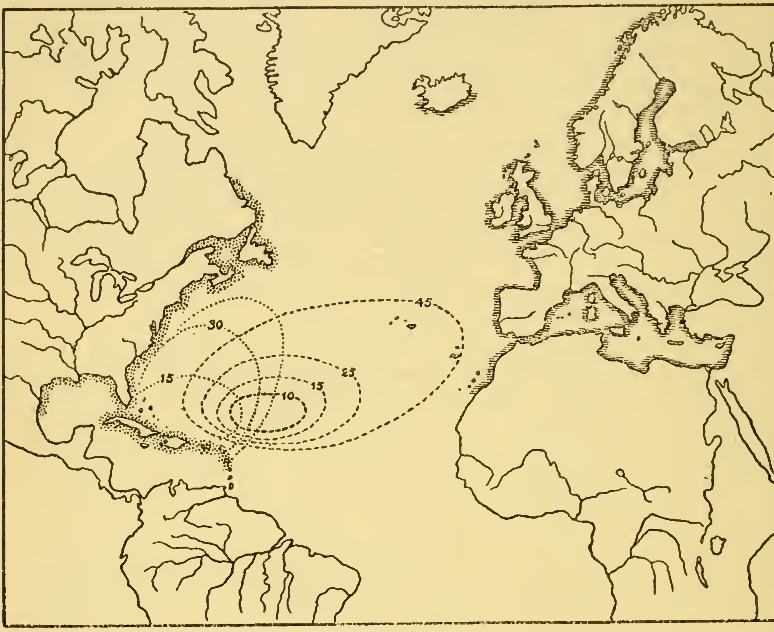


Fig. 106.

Breeding-grounds and distribution of the European Fresh-water Eel (*Anguilla anguilla*) and the American Eel (*Anguilla rostrata*).

The continuous curved dotted lines show the limits of occurrence of the larvae (the European species represented thus – – – – –, the American species thus . . . . . .). In the case of the European Eel, that marked 10 embraces an area that must include the actual spawning places of the species, for within it larvae less than 10 millimetres in length have been captured in large numbers, but never outside it. The numbers on the other curves denote the length of the larvae in millimetres captured therein. The adults of the European species occur in the countries outlined with short horizontal lines, those of the American species in the regions shown by dots outside the coast line.

place, in the majority each female is attended by two, three, or even more males, all of which take part in the fertilisation of the eggs when extruded. As a rule, the males develop hard, wart-like, nuptial tubercles at this season, which may be confined to the head or extend on to the skin of the back and sides. These excrescences, disappearing as soon as spawning has been completed, may be used in the battles between rival males, in nest building, or for a variety of purposes, including that of assisting to hold the female and to facilitate the extrusion of the ova by pressure on her body. All the Carps and their allies breed in spring or early summer, and even the most sluggish become intensely active under the stress of sexual excitement, sporting at the surface and sometimes leaping clean out of the water in their exuberance. As the time for spawning approaches they congregate into shoals, and usually move into quiet, weedy shallows near the banks of the rivers or in tributary streams. Roach (*Rutilus*) are said to mass so closely together that by their movements against one another they produce a kind of gentle, hissing noise. In Norfolk they have been described as crowding together among the rushes that fringe the banks in such dense multitudes "that every instant one may see small ones raised half out of the water by the passage of larger fish." Whilst engaged in spawning most Cyprinid fishes seem to be so intent on the business in hand that they are oblivious to all danger, falling an easy prey to foes of all kinds. The attendant males swim above or round the female, betraying great excitement, and even pushing her abdomen with their snouts in order to facilitate the extrusion of the ova, which are produced at the rate of four or five hundred at a time, each batch being promptly fertilised by the males.

CHAPTER XV

PAIRING, COURTSHIP, AND PARENTAL CARE

Intromittent organs: of Selachians, of Cyprinodonts. Breeding habits of Cyprinodonts. Secondary sexual characters. Courtship of Fighting-fish: of Dragonet. Pugnacity of males at breeding season. Parental care: primitive nests. Nests of Mud-fishes, Bow-fins, Cat-fishes, etc. Breeding habits of Three-spined Stickleback, of Fighting-fish and Paradise-fish, of Bitterling. Cichlids and Cat-fishes carrying eggs in the mouth and attached to the body. Care of eggs in marine fishes: Lump-sucker, Gunnel, *Kurtus*. Egg-pouches in Pipe-fishes. Parasitic males in oceanic Angler-fishes.

THOSE fishes in which there is a definite courtship, or at least a pairing of male and female during the breeding season, very often show marked differences in the two sexes. These may be of two kinds: (1) structural peculiarities directly concerned with the fertilisation of the ova, generally taking the form of special male organs for introducing the milt into the body of the female; and (2) structural differences, peculiarities of colour, etc., having no connection with sexual conjugation, but concerned more with courtship and display, or with the battles which take place between rival males. The so-called "claspers" of a Shark are examples of the first type, the horny tubercles on the snout of a Cyprinid at spawning time of the second.

In all Selachians the fertilisation of the ova takes place within the female's body, and there is consequently a definite sexual union. The mature males are provided with special organs, the "claspers" or mixopterygia, appendages of the pelvic fins (Fig. 107). Each has an internal cartilaginous skeleton, and along the whole length runs a groove or canal leading from a glandular sac at its base. During copulation the two grooves or canals are placed close together, both the claspers are thrust into the cloacal aperture of the female, and the seminal fluid is introduced into the oviducts. In addition to the mixopterygia which they possess in common with the Sharks and Rays, the Chimaeras (*Holocephali*) are provided with other claspers: the front portion of each pelvic fin is modified and separated off to form an organ provided with two large dermal denticles, which can be withdrawn into a shallow glandular pouch in front of the fin; the head is surmounted by a curious club-like appendage, the frontal or cephalic clasper, armed with a group of curved spines, and this can be lowered into a depression in the skin when not required (Fig. 80). Distinct marks and scratches that have been observed on the skin of female Chimaeras at the base of the dorsal fin are believed to have been caused by the frontal claspers of the males, who probably

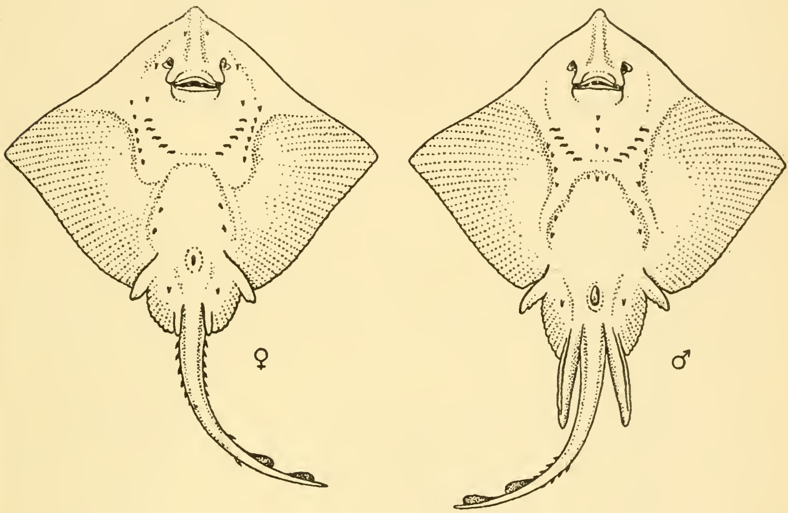


Fig. 107.

Thornback Ray (*Raia clavata*), × ⅛.
Ventral views of male and female.

make use of these organs to retain their hold when curling their bodies round those of their mates during coition.

Apart from the mixopterygia, sexual differences are rare in Selachians, but in many of the Rays (*Raia*) the males are provided with a patch of sharp spines on the upper surface of each pectoral fin, and this is entirely wanting in the other sex. These cannot play any part in grasping the female, and it seems likely that they serve as offensive weapons, for it is known that several males will pursue one female, fighting among themselves and buffeting each other with their fins. In some species the form and arrangement of the spines on the body and tail differs in the two sexes, and in the Thornback

Ray (*Raia clavata*) the teeth of the male are quite unlike those of the female, although alike in immature individuals of both sexes (*cf.* p. 127).

Among Bony Fishes intromittent organs (*i.e.* organs for introducing the spermatozoa into the body of the female) naturally occur only in those fishes in which fertilisation of the eggs is internal. A simple organ of this nature is provided by the prolongation of the genital or urino-genital orifice to form a conical papilla or a more or less lengthy tube. In some of the Toothed Carps or Cyprinodonts (*Cyprinodontidae*) the duct from the male reproductive organ is produced as a tube to the end of the anterior rays of the anal fin, and in the Four-eyed Fish (*Anableps*) this tube is covered with scales (Fig. 74D). The genital aperture of the female Four-eyed Fish is covered by a special scale, the foricula, which is free on one side but not on the other. In some individuals the opening beneath the scale is on the right side, in others on the left, while among the males some have the intromittent organ turned towards the right, some towards the opposite side. Thus, in order to transfer the milt to the genital duct of the female, copulation takes place sideways, and it is necessary for a right-sided male to pair with a left-sided female and *vice versa*.

In many South American and Central American Cyprinodonts (sub-family *Poeciliinae*) the males are provided with complicated intromittent organs developed in connection with the anal fin, which in these fishes is much modified and placed farther forward than usual. The third, fourth, and fifth rays of the fin are enlarged and produced, forming the margin of a groove or closed tube into which the genital duct opens. The rays may end in curved hooks, spines, or barbs, the function of which seems to be connected with keeping the organ in position during copulation. The whole organ is freely movable, and is supported internally by bony processes. The genital aperture is placed just in front of the base of the anal fin, and may be covered by the pelvic fins, which take part in conveying the seminal fluid into the groove. Another type of Cyprinodont (*Phallostethinae*), ranging from the Malay Peninsula to the Philippines, is remarkable for the possession by the male of a large fleshy appendage known as the priapium, which is situated below the head and chest. This appendage has a complicated internal skeleton of its own, and contains not only the ducts from the kidneys and reproductive organs, but also the terminal parts and openings of the intestine. In addition, there are external movable bony appendages which may serve to grasp the female during intercourse. As in the case of the intromittent organ of the Four-eyed-fish, the priapium is placed either to the right or to the left, but is never symmetrical in position.

The breeding habits of the Cyprinodonts are of great interest, and the small size and pretty appearance of the fishes, and the elaborate courtship in which many of them indulge, makes them great favourites with aquarium lovers of all countries, particularly as they will breed fairly freely in captivity. In the species in which they are brilliantly ornamented, the males will dart about with rapidity, displaying their manifold charms, and exhibiting a good deal of excitement. In some forms the females seem to encourage the advances of the males, but in others they may be very shy and their mates have to exercise great perseverance and not a little cunning in approaching them. It is of some interest to note that in those species in which the attentions of the male are encouraged by the female the intromittent organ is quite short, but where she endeavours, as it were, to make him keep his distance, it is much longer. Owing to the rapidity with which it usually takes place, the actual transference of the milt from the male to the female has rarely been observed in detail, but Dr. Philippi has described the process as it occurred in two species of *Glaridichthys* kept in his aquarium. He observed that during coition the male bent his anal fin round either to the right or to the left, so that its tip pointed forward and somewhat upward, and then darted towards his mate, touching her genital aperture with the processes at the extremity of the fin. The contact only took place for a moment or two, and the impetus of the rush on the part of the male carried him past the female. So rapid was the whole proceeding that it was impossible to see the spermatozoa actually transferred, but by taking a male fish and laying it on a glass slide Dr. Philippi found that by slight pressure on its body small lumps of milt were extruded which adhered to anything with which they came into contact. Examination of one of these lumps under a microscope showed that it was composed of spermatozoa surrounded by a sticky fluid, and the reproductive organs were found to be full of similar lumps. The formation of these masses or spermatophores is clearly designed to prevent the dispersal of the spermatozoa in the water, and when the intromittent organ is brought into contact with the body of the female as described above, some of these must be extruded, and are probably drawn into her body by some sort of sucking action.

All Cyprinodonts with complicated intromittent organs retain the fertilised ova within their bodies, and the young are brought forth alive, but there are a number of forms in which eggs are extruded and fertilisation takes place externally. Here the differences between the sexes are concerned merely with the coloration or with the shape of the fins (Fig. 108B), but there is a definite pairing of male and female, usually an elaborate courtship, and intercourse takes place in the following manner. The two fishes lie side by side, the heads looking in the same direction, and the male clasps his partner by folding his dorsal and anal fins

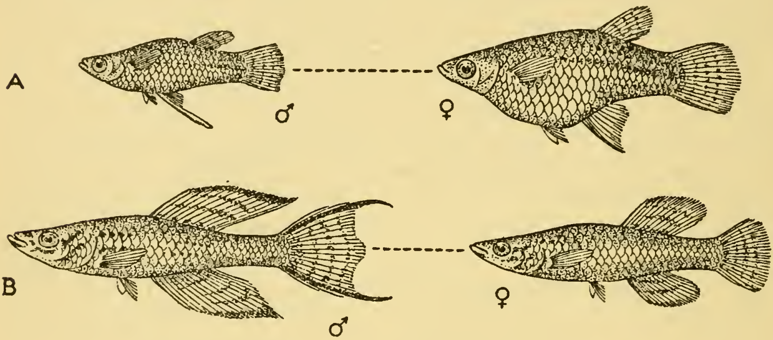


Fig. 108.—SEXUAL DIFFERENCES IN CYPRINODONTS.

A. Male and female of *Gambusia nicaraguensis*, × 1 ; B. Male and female of *Nothobranchius arnoldi*, × 1.

across her body, while the paired fins also may interlock. The ova and sperms are then extruded simultaneously in such close proximity that fertilisation of the vast majority of the eggs is certain. It seems probable that the curious forms with a priapium may take up a similar position during the sexual act, but the behaviour of these fishes in the breeding season has not yet been observed, and the actual function of the organ remains a matter for speculation.

The second type of differences between the sexes, the secondary sexual characters, which have no connection with actual union between male and female, may be present during the whole adult life of the male, but are frequently developed only as the spawning season approaches, and are discarded as soon as this is over. The difference in the size of the two sexes is worthy of notice. In the great majority of Bony Fishes the females are larger than the males, and in some Cyprinids she may be as much as six times as large as her mate, whilst in certain Cyprinodonts the disparity in bulk is even more marked. In some fishes, however, of which the Cod, Haddock (*Gadus*), and Angler (*Lophius*) may be mentioned, the males are slightly the larger. One of the commonest of the secondary sexual differences in fishes is concerned with the coloration of the body and fins, the males almost always having a brighter livery than their mates. This is the case in nearly all the Cyprinodonts, Cichlids, Labyrinthic-fishes, many Damsel-fishes (*Pomacentridae*), Wrasses (*Labridae*), and so on (*cf.* p. 223). Blue, red, green, black, and silvery-white pigments are especially characteristic of the males, whereas the females generally exhibit dull, olivaceous, or variously mottled hues. In some fishes, notably in some of the Wrasses (*Labridae*) and in the Dragonets (*Callionymidae*), not only are the colours different, but also the characteristic markings. In our own Cuckoo Wrasse (*Labrus mixtus*), to mention only one example, the male is yellow or orange tinged with red, with five or six blue bands radiating backwards from the eye; the fins are yellow or orange, with a large blue blotch on the front part of the dorsal fin. The female is reddish, there are no blue bands, but two or three large black spots are present on the back, below the hinder part of the dorsal fin. In many of the Cyprinids the males become much brighter during the spawning season, chiefly through the development of bright red or blue pigment, especially in the lower parts of the body, and these colours may become very much intensified during the actual courtship, with its attendant emotional excitement. In the little Three-spined Stickleback (*Gasterosteus aculeatus*) both sexes change their colours in the breeding-season, the dark greenish colour of the back extending on to the sides in the form of vertical bars, whilst the lower parts change from a silvery white to pale yellowish in the female and a brilliant red in the male. In the Ten-spined Stickleback (*G. pungitius*) the males change from a greenish-olive powdered with small black dots to a dark brownish. Among other changes in livery that of the breeding Salmon (*Salmo*) has already been described (*cf.* p. 284), and there are other examples too numerous and varied to be mentioned in detail here. The male Bow-fin (*Amia*) of North America may be recognised quite readily by his smaller size and by the presence of a deep black spot ringed with white at the base of the caudal fin, which, although present throughout the life of the fish, becomes much more intense as the spawning season draws near.

Differences in the form of the fins are nearly as common among fishes which indulge in pairing or courtship as differences in coloration, those of the male always being larger and more brightly marked. In many Cichlids and Cyprinodonts some of

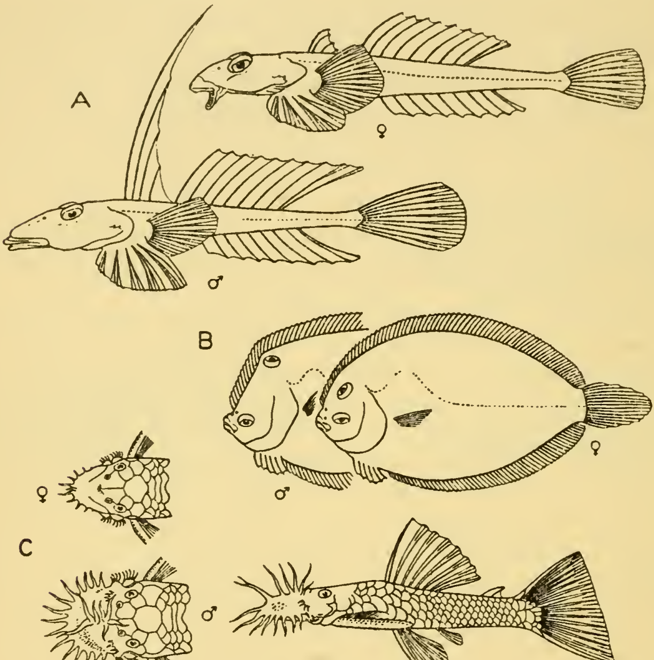


Fig. 109.—SECONDARY SEXUAL CHARACTERS.

A. Male and female of the Common Dragonet (*Callionymus lyra*) ; B. Female, and head of male of *Bothus podas* ; C. Male, and heads of male and female of Mailed Cat-fish (*Xenocara occidentalis*). All × about $\frac{1}{3}$.

the rays of the dorsal and anal fins may be prolonged to form fine streamers, and the membrane provided with eye-like spots of red, blue, or yellow. In some of the Mailed Cat-fishes (*Loricariidae*) the sexual differences are even more marked, affecting the shape of the snout, the form of the mouth and lips, the development of bristles on the head and fins, or of fleshy tentacles on the snout (Fig. 109C). In the Scald-fish or Lantern-fish (*Arnoglossus*), and in some other Flat-fishes, the first few rays of the dorsal fin, as well as some of the rays of the pelvics, are prolonged to form more or less lengthy filaments in the male; in the closely related genus *Bothus* the males are provided with spines on the snout and have the eyes much wider apart than the females, while the upper rays of the pectoral fin of the coloured side are frequently very elongate (Fig. 109B). The Sword-tailed Minnow (*Xiphophorus*) from Mexico and Central America, a favourite Cyprinodont for the aquarium, has the lower lobe of the caudal fin drawn out to form a long blade-like filament in the male, and in another member of the same family (*Mollienisia*) the dorsal fin is enlarged in the male to form a relatively huge, sail-like structure marked with brilliant ocelli.

Among the characteristic peculiarities of the males, developed only as the breeding season approaches, the horny tubercles on the head and body of many Cyprinids, and the hooked jaws and enlarged teeth of the Salmon have already been described (*cf.* pp. 92, 284). Many male Cichlids (*Cichlidae*) develop a huge fleshy hump on the forehead, which is gradually reabsorbed after spawning in some species and retained throughout life in others. Other Cichlids develop a much branched structure in the region of the vent, brilliantly coloured, generally with scarlet. It has been supposed that this is used for brushing the milt on to the ova, but its ornate appearance suggests that its function may be partly decorative. In the male of the South American Lung-fish (*Lepidosiren*) the pelvic fins are covered during the breeding season with bright scarlet processes, richly supplied with blood-vessels (*cf.* p. 305).

The courtship of the female by the male may consist merely in swimming round and round in her vicinity, betraying a varying degree of sexual excitement, or may take the form of a most elaborate display comparable to the nuptial antics of some birds. The relation, however, only appears to last for the period of pairing, or, at the most, for one breeding season, and there is nothing that can be described as personal affection between the two fish. The courting habits of the little Fighting-fish (*Betta*) of Siam are worthy of special mention. The brilliantly coloured male swims round and round his mate, his beautiful fins extended to their utmost, his mouth wide open, the gill membranes protruded and the bright-red gills visible beneath. During these preliminary movements the already vivid hues become even more intensified, and his body and fins have been described as "resplendent with iridescent colours and quivering with intense excitement." Should the female ignore his attentions, as sometimes happens, he becomes enraged, and not infrequently chases her until she is obliged to jump out of the water to escape him.

Among marine fishes courtship is rare, but the Common Dragonet (*Callionymus*) of our own coasts indulges in elaborate nuptial displays, yet afterwards leaves the eggs to float about in the sea, showing no concern whatsoever for the fate of the offspring. The male is about twelve inches in length, yellowish or orange, with two blue stripes along each side of the body and a row of light-blue or green spots above; the head is marked with spots or stripes of violet or blue, and the fins, which are larger than those of the female, the first dorsal being greatly prolonged, are variously spotted and banded with yellow, green and blue (Fig. 109A). The mature female is about eight inches long, dull yellowish-brown passing into white beneath, ornamented with greenish spots enclosed in dark-brown rings. So different are the two sexes that they were originally regarded as distinct species, and known as the Gemmeous and Sordid Dragonet respectively. At the time of courting the male rushes about in a state of great excitement, endeavouring to frighten other males in the vicinity; he then swims round the female, erecting all his fins, and displaying for her benefit his highly intensified colours. Finally, these antics excite her admiration, and she yields to his importunities. The male lifts his mate by placing his pelvic fin beneath hers, and the two fishes swim vertically towards the surface of the water side by side, the eggs and milt being extruded at the same moment; fertilisation takes place in the water, and the ova float to the surface.

In many species the males become very pugnacious during the breeding period, indulging in fierce combats for the possession of a favoured female or in defence of their nests. Thus, the Siamese Fighting-fish (*Betta*) are pitted against one another by the natives for sport, after the manner of fighting-cocks. Considerable sums of money, to say nothing of their own persons and families, are wagered on the results of the combats, and the issue of licences to exhibit "fish fights" provides a source of considerable revenue for the King of Siam. In a state of quiet the colours of this fish are rather dull, but if two be placed in the same aquarium, or if one sees its own image in the looking-glass, the fins and whole body shine with dazzling, metallic hues, and it will make repeated darts at its real or fancied antagonist.

The males of many of the Gobies (*Gobiidae*) also engage in hectic fights, rushing at each other and biting viciously, the victor afterwards spreading his fins and showing off his colours to the female. Some of the male Klip-fishes (*Clinus*) of South Africa seem to fight according to well-defined rules, the preliminary position adopted being either side by side or face to face; in the latter case the mouth is wide open and the gill-covers raised, so that the opercular spots look like a pair of eyes. They may engage in several "rounds" with short intervals of rest, but finally one of them backs away and leaves the field to his conqueror. The pugnacious habits of one of the Berycoid

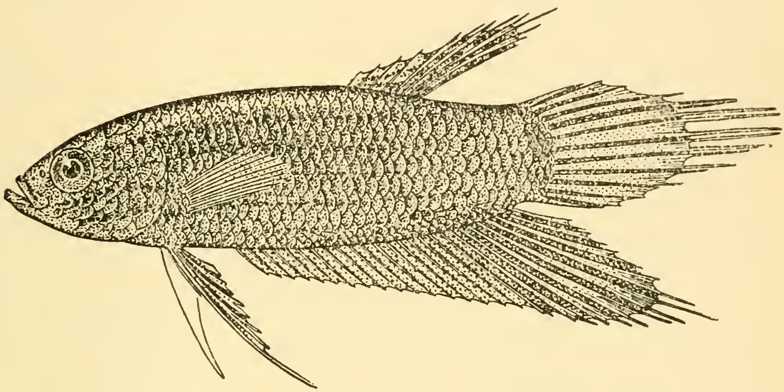


Fig. 110.

Siamese Fighting-fish (*Betta pugnax*), $\times \frac{3}{4}$.

fishes of Hawaii (*Myrispristis murdjan*), known to the natives as Uu, are turned to good account by fishermen. They catch a male and suspend it alive by a string in front of the crevices in the lava rocks inhabited by this species, where it remains with spread fins and flashing scales; other males approaching to fight the captive are promptly secured by concealed nets, another decoy is substituted, and the trick repeated. The little Three-spined Stickleback (*Gasterosteus aculeatus*) is perhaps the most pugnacious of all fishes at breeding times, the combats between rival males not infrequently ending mortally, one of the participants being literally ripped open by the sharp spines of his opponent. According to Dr. Regan, the two rivals make a rush at one another, "dealing violent strokes with their pelvic spines, and then hastily returning to the neighbourhood of their nests; after a few rounds one gives in and then the victor indulges in a splendid display of colours. . . ." Curiously enough, the colours of the unsuccessful fish become dull as soon as he retires from the combat, and for some time he is the constant object of persecution by his conqueror.

As a general rule, in those fishes in which courtship and pairing takes place at the breeding season the number of eggs produced by a single female is small or moderate, and these are cared for to a greater or lesser extent by one or both of the parents, generally the father. This parental care may take the form of constructing some sort of nest for the reception of the fertilised eggs, varying from a simple hollow scooped out in the gravelly bed of a stream to a beautiful and elaborate structure, or of some other precautions designed to ensure the safety of the eggs or offspring until they are old enough to take care of themselves.

The Darters (*Etheostominae*), pretty little fishes of the family *Percidae*, found in the rivers of eastern North America, congregate together in gravelly shallows at the spawning season, the larger males each selecting a suitable place which they regard as their own domain, repelling with vigour any attempt by a rival male to dispute their claim. Any female entering the domain is allowed to remain, and she constructs a kind of trough with her body into which she sinks as the eggs are extruded. These are promptly fertilised by the male, and being covered with a sticky substance, they adhere to the stones. The extent to which the Salmon and Trout care for their offspring is almost equally primitive, and has been already described. Dr. Semon has recorded the breeding habits of a species of Cat-fish (*Arius*) found in the Burnett River of Queensland, in which a further advance in the protection of the prospective family is exhibited. The nests of this fish consist of circular excavations, about twenty inches in diameter, scooped out in the bed of the river. The fertilised eggs are covered with a layer of large stones, but, this being done, the parents take no further interest in the fate of their offspring. Many of the North American Cyprinids, known as Chubs and Shiners, construct somewhat more elaborate nests composed of large heaps of stones, some of which may weigh nearly eight ounces, but the eggs are here again left to the mercy of physical conditions, to say nothing of predaceous fishes.

The fresh-water Sun-fishes (*Centrarchidae*) scoop out a shallow basin-like nest, from the bottom of which all pebbles are carefully removed, leaving a layer of fine sand or gravel to which the fertilised eggs adhere. The work is carried out entirely by the male, who remains to guard the eggs until the young are hatched. In many of the Cichlids (*Cichlidae*) the male constructs a similar kind of nest, but both parents assist in the task of guarding the eggs. Other fresh-water fishes make a nest by clearing a space among aquatic vegetation. That of the African Osteoglossid (*Heterotis*) is built in about two feet of water, is as much as four feet across, and the walls, which are several inches thick, are made up of the stems of grasses removed by the fish from the centre, the floor being formed by the smooth, bare ground of the swamp. One of the Mormyrids (*Gymnarchus*) constructs a floating nest of large size, the walls projecting several inches above the surface of the water at two sides and one end, the opposite end, forming the entrance, being some six inches below the water. One of the Mud-fishes (*Protopterus*) scoops out a hole in the mud of a swamp, surrounded by long aquatic weeds and grasses, the male alone being responsible for the preparation of the home and for the subsequent care of the eggs. Not only does he defend these assiduously against the depredations of hungry fishes, but, aerating the surrounding water by lashing vigorously with his tail, he keeps the eggs well supplied with the oxygen necessary for their development. The related Lung-fish of South America (*Lepidosiren*) has a nest which takes the form of a burrow excavated in the peaty soil of a swamp, varying in length from three to five feet. The entrance is four or five inches wide, and the burrow consists of a short vertical part and a much longer horizontal portion, at the blind end of which the eggs are deposited. The blood-red filaments developed during the breeding season on the pelvic fins of the male (*cf.* p. 301) probably have a respiratory function, enabling the fish to remain in the burrow to guard the eggs without coming to the surface to gulp air, and perhaps even serving to aerate the stagnant water surrounding the eggs. The male Bow-fin of North America (*Amia*) constructs a crude, circular nest, usually placed at the swampy end of a lake where there is an abundance of aquatic herbage, and when this is completed he is attended by one or more females, the fertilised eggs adhering to the leaves and roots at the bottom of the hollow. They are guarded henceforward by the male, who remains constantly either on the nest itself or in a passage through the reeds leading to it. After the young are hatched they are said to leave the nest in a body, still under the protection of the watchful father, who keeps them together in a compact mass by circling slowly around them. Many of the Cat-fishes (*Amiuridae*) of North America excavate a rude nest in the mud, a labour in which both parents share, and which may mean two or three days of incessant work. Sometimes this nest is placed in crevices in the river banks, beneath logs, stones, or even in pails or other receptacles lying in the water.

The Three-spined Stickleback (*Gasterosteus aculeatus*) constructs a much more elaborate nest, and as the breeding habits of this fish are of especial interest, they may be described in some detail. The construction of the home is undertaken entirely by the male, who sets about this duty before courtship is begun, selecting a suitable site, such as one among the stems of aquatic plants where the water flows regularly but not too swiftly, in quiet shallows, or in rock-pools which are only reached by the sea at high tides. He then collects pieces of the roots and stalks of water plants, or any other vegetable rubbish, and cements them together by means of threads of sticky substance secreted by his own kidneys. Describing the building of a nest in Vancouver Island, Mr. Lord writes: "During this operation he swims against the work already done, splashes about, and seems to test its durability and strength; rubs himself against the tiny kind of platform, scrapes the slimy mucus from his sides, to mix with and act as mortar for his vegetable bricks. Then he thrusts his nose into the sand at the bottom, and bringing a mouthful, scatters it over the foundation; this is repeated until enough has been thrown on to weight the slender fabric down and to give it substance and stability. Then more twists, turns, and splashings to test the firm adherence of all the materials that are intended to constitute the foundation of the house that has yet to be erected on it. The nest or nursery, when completed, is a hollow, somewhat rounded, barrel-shaped structure, worked together much in the same way as the platform fastened to the water plants; the whole firmly glued together by the viscous secretion scraped from off the body. The inside is made as smooth as possible by a kind of plastering system; the little architect continually goes in, then, turning round and round, works the mucus from his body on to the inner sides of the nest, where it hardens like tough varnish." Having finished the home, which often takes several days to complete, he goes in search of a mate, and having selected one, goes through an elaborate process of courtship, and finally conducts her to the nest. He swims round her in evident pleasure, trying to persuade her to enter through the circular aperture in the side, aiding her entrance by poking her vigorously with his snout, or, if she be slow, even using his spines. She proceeds to deposit two or three eggs within, finally boring through the wall of the nest on the side opposite to the entrance and swimming away. While she is in the nest the male swims round and round in great excitement, butting and rubbing his snout against the fabric. He then enters, deposits his milt on the eggs and departs through the back door. Next day he seeks out another female, and repeats the whole process with her, and so on, with one after another, until sufficient eggs have been deposited. The male now mounts guard over the entrance, defending his charge with vigour against all comers for nearly a month, furiously attacking any other Stickleback that attempts to approach the nest. From time to time he repairs any damage to the walls, and Mr. Frank Buckland describes how in a nest which he watched the little sentry kept "constant watch over the nest, every now and then shaking up the materials and dragging out the eggs, and then pushing them into their receptacles again, and tucking them up with his snout, arranging the whole to his mind, and again and again adjusting it till he was satisfied." The two doorways allow a constant current of fresh cool water to bathe the eggs within the nest, but he may assist this process by placing himself at the entrance and vibrating his pectoral fins. Even when the young hatch out his task is by no means done, but no the contrary his vigilance is increased and his duties multiplied. He pulls down the upper part of the nest, leaving the foundations as a kind of cradle for the fry, which he continues to guard as before, preventing any attempts on their part to leave the nest by seizing the truants in his mouth and returning them to their quarters. As soon as they can swim strongly, however, he gradually relaxes his attentions, although still keeping a watchful eye on them as they swim about in the water, until finally they are left to fend for themselves. The Fifteen-spined Stickleback (*Spinachia*), an exclusively marine form, builds an elaborate nest from a suitable branch of seaweed, binding the fronds of weed with the sticky secretion from the kidneys. The threads are passed round and round the fronds until they are finally bound together into a roughly pear-shaped structure of about the size of a man's clenched fist.

Many of the Labyrinthic-fishes (*Anabantidae*) make a most unusual type of nest, the male blowing bubbles of air and sticky mucus, which adhere together to form a floating mass of foam, dome-shaped or more or less flat on the upper surface. In the case of the little Fighting-fish (*Betta*), the elaborate courtship is followed by the surrender of the female, who approaches her mate and is suddenly turned upon her side: he then tightens his body around her, and turns her upside down, but in a few moments the pressure is relaxed and the male takes up his position below. The eggs are extruded, and after being held for a few moments by the female to ensure fertilisation, are allowed to drop, and being heavier than the water, they sink downward towards the waiting male. He catches the eggs in his mouth, and swims upwards, gives them a coating of mucus, and sticks them to the under side of the mass of foam. From three to seven ova are extruded at a time, and the process is repeated until some one hundred and fifty or two hundred are produced. They are then guarded by the father, who is obliged to keep a watchful eye on his mate, who is not averse to eating them, if permitted. The larvae remain adherent to the foamy nest for some time after hatching, and if any of them should show a tendency to sink, they are caught and replaced by the watchful male, until they finally drop off when old enough to find food for themselves. The related Paradise-fish (*Macropodus*) has very similar breeding habits, but here the eggs are lighter than the water, and thus rise to the mass of bubbles without the intervention of the male. The female is completely inverted while the eggs are extruded, and any which fail to adhere to the nest are collected by one or both of the parents and placed in position.

The Bitterling (*Rhodeus*), a small Cyprinid found in the rivers of Central Europe, takes remarkable precautions to ensure the safety of its offspring. The oviduct of the female fish is drawn out to form a long tube, acting as a kind of ovipositor, by means of which she deposits her eggs within the valves of fresh-water pond mussels, where they are out of reach of enemies. In this situation they undergo their development, the respiratory current of water produced by the Shell-fish serving to aerate the ova, and the fry finally leave their temporary host about a month after the deposition of the eggs. The male fertilises the eggs after they have been extruded, and, as Professor Cunningham remarks, "it is a most curious case of adaptation of sexual instincts that the male is sexually excited, not by the presence of the female of his own species, but by the sight of the mussel in which the eggs have been deposited."

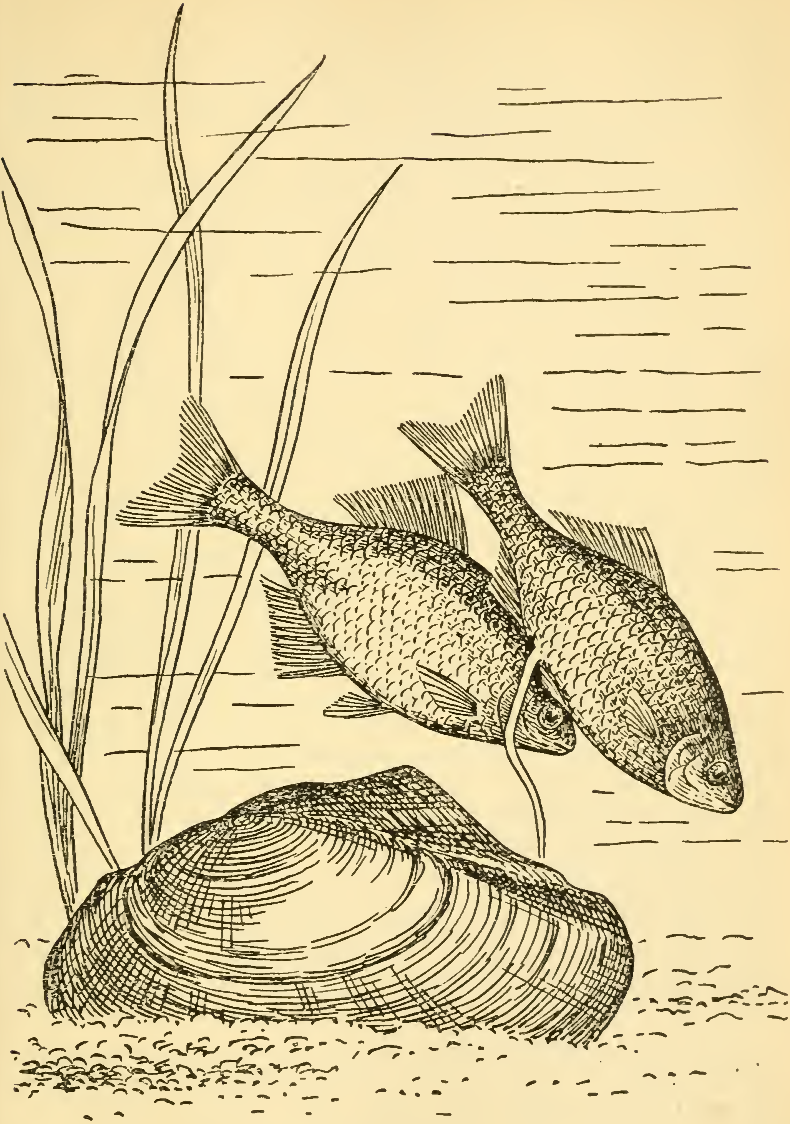


Fig. 111.

Male and Female Bitterling (*Rhodeus amarus*) with fresh-water Pond Mussel, $\times \frac{2}{3}$. (From a photograph.) The female fish is about to deposit her eggs.

Another remarkable fact lies in the manner in which the mussel is able to reciprocate the attentions of the fish. Its own breeding season coincides with that of the Bitterling, and it is in the habit of throwing off its own embryos into the water, where they become attached to the adult fishes and undergo their early stages of development.

Many of the Cichlids (*Cichlidae*) protect their eggs by carrying them in their mouths, thus ensuring their safety and perfect aeration at one and the same time. This duty is nearly always undertaken by the mother, and even after hatching the young fry do not leave the shelter of her mouth. Later, they swim about in the water, keeping always within easy reach of her head, and should danger threaten they return to their refuge with extraordinary rapidity. When still more developed, the fry may be observed swimming about in a small shoal accompanied by the parents, the female generally in the middle and the male circling around them. Most of the Sea Cat-fishes (*Ariidae*) found on the coasts and in the rivers of North and South America have similar habits, but here it is always the male who undertakes the care of the eggs. These are produced in small numbers, and are of remarkable size, measuring as much as seventeen or eighteen millimetres in diameter in a species growing to a length of three or four feet. The eggs are carried about until hatched, and the unfortunate father does not appear to take any food during this period. Another Cat-fish (*Platystacus*), of the rivers of Brazil and the Guianas, exhibits a different method of caring for the eggs, but here the female is entirely responsible for their safety. During the breeding season the skin of the lower surface of her body becomes very swollen and tender, assuming a soft, spongy condition. As soon as the eggs have been extruded and fertilised, she lies on them, presses them into this soft tissue, and each egg becomes attached to the skin by a small, stalked cup, remaining thus fixed until hatched. As soon as this takes place, the skin shrinks to its original size, and the abdomen is once again perfectly smooth.

Apart from the Sticklebacks, nest building is the exception rather than the rule among marine fishes, and any sort of parental care is very rare. Some of the Wrasses (*Labridae*) are said to construct rude nests of seaweed, shells, or stones, an operation in which both sexes take part. Many of the Gobies (*Gobiidae*), Blennies (*Blenniidae*), Bull-heads or Sculpins (*Cottidae*), and Cling-fishes (*Gobiesocidae*), nearly all of them inhabitants of rock-pools between tide-marks, provide for the safety of their eggs by depositing them in the dead shells of mussels, oysters, etc., in crevices in the rocks, on the under sides of stones, on fronds of seaweed, or even within the broken "bulbs" of the familiar Bladderwrack. The male usually mounts guard, and in the case of some of the Sculpins (*Cottidae*) may actually "brood" over them, clasping the egg-masses with his pectoral and pelvic fins, the inner surfaces of which are provided with asperities or hooks to enable him to obtain a firmer grip. Aeration of the eggs is another duty falling upon the father, and is generally accomplished by fanning the surrounding water with the pectoral fins. The Common or Sand Goby (*Gobius minutus*) of our own shores makes a more elaborate shelter, the male first seeking a suitable shell, generally a cockle or small scallop, which he turns over so that the concave side is downwards. He then gets underneath it, clearing away the sand with his tail, until a neat little chamber has been constructed, communicating with the exterior by a single tunnel-like opening. Finally, he covers the whole structure with fine loose sand, and sets off in search of a suitable mate.

The Lump-sucker or "Cock and Hen Paddle" (*Cyclopterus*) generally deposits its spawn in crevices in the rocks above the level of low water at spring tides. The large masses, containing anything from 80,000 to 136,000 eggs, vary in colour from dark brown to red, pink or pale yellow. For a portion of each tide the eggs are, of course, uncovered, and are preyed upon by numerous enemies in the shape of starlings, rooks, seagulls, and rats, whilst at high water they may be devoured by various fishes. It is doubtful, however, whether there are many better cases of parental devotion than that of the male Lump-sucker. For weeks and even months he devotes himself to the care of the eggs, fasting rather than leave his post, from time to time pressing his head into the clump of spawn to allow the water to penetrate to the centre, and thus ensuring the proper aeration of the eggs, a process which he further helps by blowing upon them with his mouth and fanning them with his pectoral fins. He removes any animals such as crabs, star-fishes, and shell-fish which may crawl on to the spawn, and defends it with intense vigour against foes both large and small. One individual male, kept under observation for several weeks, was seen to be faithful to his charge during the whole of this period, even though exposed for a considerable time twice daily at ebb-tide. While on guard the males have been described as being attacked by rooks and carrion crows, which thrust their sharp beaks through the abdominal wall and feast on the liver of the unfortunate fishes. If removed from the eggs and then released, they will at once rush back to their posts, and after a heavy storm that has swept masses of eggs from their normal positions high up on to the beach, as soon as the sea becomes calm again the parents may be seen anxiously seeking for their charges.

The Gunnel or Butter-fish (*Pholis*), an elongate Blenny-like fish, some ten inches in length, is in the habit of rolling its mass

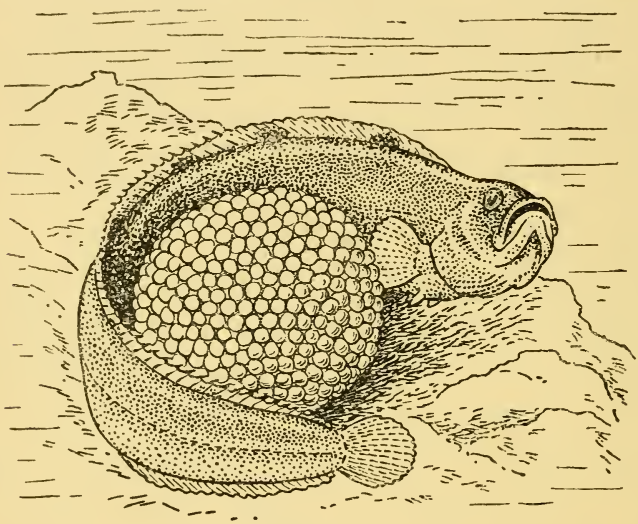


Fig. 112.

Gunnel or Butter-fish (*Pholis gunnellus*) with mass of spawn, $\times \frac{1}{2}$.

of spawn into a ball, about the size of a Brazil nut, an operation in which both parents may assist. Afterwards, one of them remains on guard, coiled round the eggs, but it is not certain whether this is the male or the female, or whether both take their turn. Often the mass of eggs, accompanied by the parent fish may be found between the valves of empty oyster shells, or in the holes made by boring molluscs in the rocks (Fig. 112).

In the Indo-Pacific genus *Kurtus*, the male is provided with a bony hook projecting from the forehead, supported by a special process of the skull. The mass of eggs is produced in two bunches connected by a string, and this becomes attached to the hook in such a manner that one bunch of eggs lies on either side of the male as he swims about in the water.

In the Pipe-fishes (*Syngnathidae*) the care of the eggs and fry is always undertaken by the male fish, who carries them about until hatched, either "glued" to a simple groove lined with soft skin in the lower surface of the abdomen, or in a special pouch closed by flaps of skin and situated on the under side of the trunk or tail (Fig. 113d). In the Florida Pipe-fish (*Siphostoma*), in which the whole process has been accurately observed, the reproductive act is preceded by an elaborate courtship, the

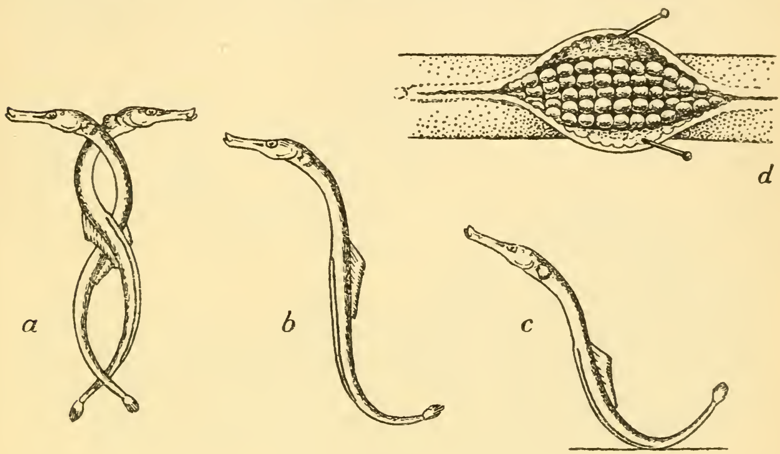


Fig. 113.

Breeding habits of Florida Pipe-fish (*Siphostoma floridae*).

a. Position of fishes during transfer of eggs ; b. Attitude assumed by male while moving eggs backward in the pouch ; c. Position of male during period of rest following several transfers, × about ¼. (After Gudger); d. Portion of pouch opened to show eggs.

two fishes swimming round in nearly vertical positions, but with the head and shoulder region bent forward. They then swim slowly past one another, their bodies come into contact, and the male demonstrates his affection by contortions of the body, caressing his mate with his snout. Just before the actual transfer the male becomes violently excited, wriggles his body about in corkscrew fashion, and rubs the belly of the female with his snout. This demonstration is repeated several times, the fishes becoming more and more excited, until finally the nuptial embrace (Fig. 113a) occurs, after which the fishes separate, to commence the process again after an interval of a few minutes. During the embrace, when the bodies of the two fishes are intertwined, the protruding oviduct of the female is rapidly thrust into the small opening at the front end of the male's pouch, and the eggs are thus transferred. By a series of contortions the male then succeeds in moving the eggs to the hinder end of the pouch (Fig. 113b), and then the whole process is repeated until the pouch is full, after which the male appears to be very exhausted and remains quiescent for some time (Fig. 113c).

The eggs remain in the pouch until hatched, but even after this event the fry may occupy it for some time, and, when they are able to swim freely in the sea, will still return to its shelter when danger threatens. Dr. Smitt has described a male Broad-nosed Pipe-fish (*Siphonostoma*) which opened the pouch (marsupium) by a downward movement of the tail, whereupon the young fishes crept out one after another. "As soon as I tried to capture the male," he writes, "it made a sudden movement, at the same time bending the body in an arch upwards, and the young crept into the marsupium, the lids of which were then shut."

It is of interest to note that something of the habits of the Pipe-fish, the *Belone* of the Greeks and the *Acus* of the Romans, was known to Aristotle, although his interpretation of the facts may have been rather wide of the mark. "That fish which is called *Belone*," he states, "at the season of reproduction, bursts asunder, and in this way the ova escape; for this fish has a division beneath the stomach and bowels like the serpents called typhlinae. When it has produced its ova it survives and the wound heals up again."

In a related family (*Solenostomidae*) the female takes care of the eggs, keeping them in a pouch formed by the pelvic fins, the inside of the chamber being provided with numerous long filamentous processes, which serve to assist in retaining the eggs in position. In the Sea Horses (*Hippocampus*), as in the Pipe-fishes, it is the father who looks after the eggs and young, the former being received into a brood-pouch beneath the tail, where they remain until hatched. At the breeding season this pouch becomes thickened and well supplied with blood-vessels, thus being prepared for the reception of the eggs and the nutrition of the embryos. At the same time the cloaca of the female becomes somewhat extended to form a genital papilla, which acts as a kind of intromittent organ for the transfer of her ova to the male. The final extrusion of the young fish from the pouch is a much more difficult matter than in the Pipe-fishes, and may occupy several hours, only five or six individuals being set free at a time. The small aperture of the sac-like pouch makes it impossible for the young to return to its shelter, and it is probable that they are retained for a longer period than in the case of the Pipe-fishes.

Finally, mention must be made of the Ceratioid Angler-fishes (*Ceratioidea*), inhabitants of the mid-waters of the oceans, in which the relationship between the sexes is unique among fishes, and indeed among all vertebrates. The discovery of these relations was made only two or three years ago, and provides

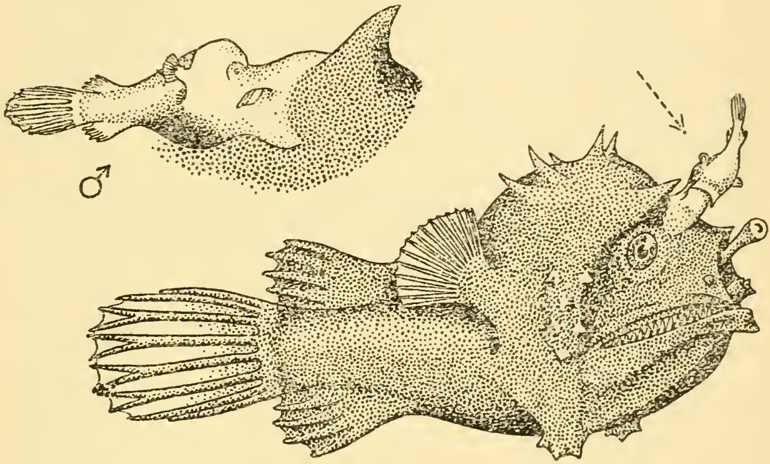


FIG. 114.

Photocorynus spiniceps: female with parasitic male, × 1½. (Male × 3.)

one of the startling biological events of the present century. All the large free-swimming individuals that have been captured have proved to be females, and it has been shown that the males are mere dwarfs and spend the greater part of their lives as parasites upon the females. A fish taken near Iceland was forty inches in length, and the attached male was about four inches, the one, therefore, being one thousand times the size of the other. Another female measured no more than about two and a half inches, and had a tiny male, two-fifths of an inch in length, attached to the top of her head above the right eye (Fig. 114). This remarkable relationship seems to have been evolved in relation to the habits and conditions of life of the fishes. Living as they do in the comparative darkness of the middle layers of the oceans, sluggish in their movements and solitary in their habits, the chances of a mature fish finding a mate of its own species might be somewhat slender. This difficulty is overcome by the males, almost as soon as they are hatched, seeking the females and each holding on to his selected mate, and remaining attached to her body for the rest of his life.* The site selected for attachment is quite haphazard, sometimes being on the abdomen, sometimes on the sides or on the head, or in the region of the gill-opening below the spine on the praeoperculum: occasionally more than one male becomes attached to a single female. Having gripped the female with his mouth, the lips and tongue of the male apparently unite with her skin, and the two become completely fused. The mouth, jaws, teeth, fins, and gills of the tiny male—indeed, almost all the organs except those connected with reproduction—degenerate, and thereafter he is nourished by the blood of the female (the two vascular systems being connected).

* It has quite recently been suggested that the small Ceratioids without line and bait, and with the eyes and nostrils enlarged (*cf.* p. 183), may be the free-swimming males which have not yet become attached to females.

CHAPTER XVI

DEVELOPMENT

Gametes. Eggs of Cyclostomes and Selachians. Eggs of Bony Fishes: pelagic and demersal eggs. Segmentation. Yolk. Embryonic development. Viviparous fishes. Connection between embryo and parent. Embryonic development of a Shark. Development of Salmon. Larvae and larval organs: *Ammocoetes*; external gills. Larval Sun-fishes, Deal-fishes, "Sword-fishes," Gar-fishes, etc. Larval development and metamorphosis of Fresh-water Eel. Metamorphosis of Flat-fishes. Hybrids.

By the term development is understood all those changes that take place in the egg or ovum from the moment it is fertilised until maturity. As has been already pointed out, the process of fertilisation consists in the union of the two kinds of sex-cells or gametes, the ovum of the female and the spermatozoon of the male. The early history of these gametes cannot be detailed here, and it must suffice to point out that these are at first similar to the ordinary body-cells, but later become specialised for the duty of perpetuating the race. Thus, each gamete is a single cell, consisting of a clear ground substance or cytoplasm with its contained nucleus. The ovum is large, being distended with yolk, and is immobile. The spermatozoon, on the other hand, has no such food reserve, and is consequently very much smaller: it consists of a head, which may be globular, elliptical, wavy, or rod-like in shape, and is composed largely of nuclear material; and a propelling, whip-like tail (Fig. 115), which enables it to seek out the ovum. The latter is generally provided with a minute aperture or micropyle in its surrounding membrane, situated at one of the poles, through which the head of the spermatozoon makes its entry, the tail, having played its part in bringing the two together, being left outside to die. The entry of the male element stimulates the ovum into activity, and it begins to divide into two, four, and eight cells, and so on, until gradually the embryo is built up. Another important feature of fertilisation lies in the fact that the fusion of the nuclei of the two gametes results in the mixing of the characters of the two parents in the offspring, these characters being believed to be carried by the microscopic bodies known as chromosomes, which form an important part of every cell nucleus.

The eggs of fishes present great diversity, not only in size and shape, but in the manner in which they are protected (Fig. 116). In the Cyclostomes there is a very striking difference in the characters of the eggs in the two families. In the Lampreys (*Petromyzonidae*) they are minute, spherical, and enclosed in delicate membranes, the average size being about one millimetre (one-twenty-fifth of an inch) in diameter. In the Hag-fishes (*Myxinidae*) on the other hand, they are large, roughly spindle-shaped, and enclosed in tough horny capsules, measuring up to thirty millimetres in length and ten millimetres in width (Fig. 116E). At the end of the capsule is a tuft of horny processes, each of which ends in a tiny anchor-like hook,

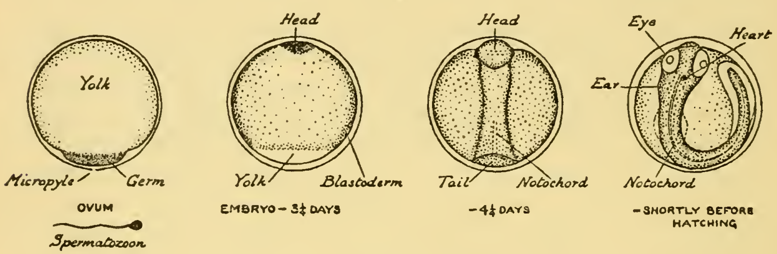


Fig. 115.

Development of egg of Flounder (*Flesus flesus*). Much enlarged. (After Johnstone.)

and in the middle of one of the tufts is the micropyle: the whole of this end of the capsule is thrown off like a cap at the time of hatching, thus allowing the young Hag-fish to make its escape. The eggs are extruded one at a time, but are afterwards linked together by means of the hook-like processes to form long strings or bunches, usually attached to pieces of seaweed at the bottom of the sea. Like all other large eggs, those of the Hag-fish consist almost entirely of yolk, the essential portion containing the nucleus being represented by a small hillock at the end nearest to the micropyle.

The Selachians may be oviparous or viviparous: that is to say, they either produce eggs which are fertilised and left to develop in the sea, or this development takes place in the oviduct of the female, the young being finally born alive in an advanced condition. The former is without doubt the more primitive method, for in many, if not in all, viviparous Sharks and Rays

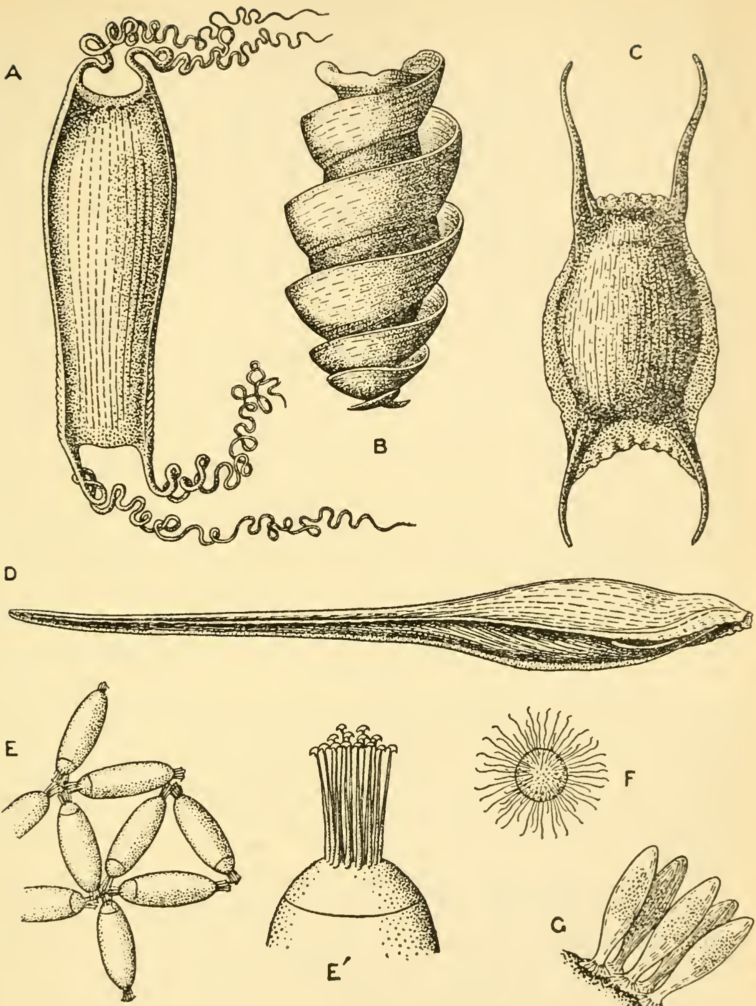


Fig. 116.—EGGS AND EGG-CAPSULES.

A. Egg-capsule of Spotted Dog-fish (*Scyliorhinus sp.*), $\times \frac{1}{2}$; B. Of Port-Jackson Shark (*Heterodontus phillippi*), $\times \frac{1}{2}$; C. Of Spotted Ray (*Raia maculata*), $\times \frac{1}{2}$; D. Of Chimaera (*Chimaera phantasma*), $\times \frac{1}{2}$; E. Eggs of Californian Hag-fish (*Polistotrema stouti*), $\times$ about 5 ; E′. Animal pole of a single egg, greatly enlarged ; F. Egg of Gar-fish (*Belone belone*), $\times$ about $2\frac{1}{2}$; G. Eggs of the Black Goby (*Gobius niger*), $\times$ about 10.

a rudimentary capsule is at first formed round the egg, this being later absorbed. The eggs are large and filled with yolk, and fertilisation takes place in the upper part of the oviduct. In the oviparous forms, the eggs, as they pass down the oviducts, are enclosed in a shell or envelope of horny texture, tough but not brittle, and of a flattened, oblong shape, which besides the egg, contains a certain amount of semi-fluid, albuminous material. The capsule is formed by a special gland peculiar to Selachians, situated in the oviduct, and it varies somewhat in pattern according to the species. In Sharks (*Pleurotremata*) the outer surface may be quite smooth, or delicately ribbed (Fig. 116A), and the four corners are usually drawn out into long tendrils, which become coiled round pieces of seaweed, rocks, stones, and other fixed objects, and serve to anchor the egg during development. They may also assist the extrusion of the capsules themselves, for as these project from the oviducts through the cloaca of the female fish, the tendrils become entangled with objects on the sea-floor and thus help to pull the eggs out. As might be expected where such elaborate precautions for the safety of the embryos are taken, the eggs are always few in number, and are deposited one or two at a time over a long period. The Bull-headed Sharks (*Heterodontidae*) of the Pacific produce eggs of unique shape, these being of relatively large size, and protected by an elongate cone-shaped capsule with very thick walls, provided with two broad flat flanges twisted spirally round it, and two long, coiled filaments at the pointed end (Fig. 116B). The Greenland or Sleeper Shark (*Somniosus*), alone among Selachians, produces small eggs, and these are deposited in the sea quite unprotected by a horny envelope.

The oblong capsules of the Skates and Rays (*Raiidae*) are essentially similar to those of the Sharks, but instead of the coiled tendrils, the corners are produced to form more or less stiff, pointed horns (Fig. 116C). These are known variously as "skate barrows," "sailors' purses," "mermaids' purses," and "mermaids' pin-boxes," and may frequently be picked up on the shore after storms. The horns of the capsule are hollow and provided with small slits, through which a current of water passes to the contained embryo. The period of incubation lasts from four and a half to nearly fifteen months, and the little fish finally makes its escape through a slit in one end of the capsule, as in the Sharks. The capsules vary in shape and size in the different species, the largest being one hundred and eighty millimetres in length and about one hundred and forty millimetres in width, the smallest sixty-three millimetres and thirty-seven millimetres respectively. They are generally deposited on muddy or sandy flats, and the more convex surface is provided with a sticky substance, to which small pieces of stone, shell, seaweed, etc., adhere, and thus help to anchor the capsule.

The capsules of the Chimaeras (*Holocephali*) are essentially similar to the above, but of somewhat different form, being spindle-shaped in outline and bordered by a broad fringe (Fig. 116D). In the Californian Chimaera or Spook-fish (*Hydrolagus*) they are about six inches long, and one end is produced into a lengthy "tail," which sticks into the mud of the sea-floor when the egg is deposited. The shape of the Chimaeroid capsule is adapted, not to the egg as it exists when the capsule is formed, but to the later developed embryo, and the interior cavity may be divided into three distinct chambers, each of which corresponds in shape and size to a definite portion of the embryo fish. There is a row of small slits along each side of the envelope, closed by membrane when the egg is first extruded, but by a process of gradual weathering and decay these become open at a later stage of development, thus allowing currents of air to flow through the case and provide the growing embryo with the necessary oxygen. The upper and lower halves of the capsule are at first united by a membrane, but at the time of hatching they separate at one end, leaving an opening through which the fish can make its escape.

The eggs of Bony Fishes are enclosed only in a vitelline membrane, formed from the ovary itself, and varying from a tough and almost leathery structure to a very fine and fragile membrane. As a rule, the shape of the egg is spherical, and although always provided with some yolk, is never as large as that of the Selachians. Two main types of eggs may be recognised, according to their structure and the manner in which they undergo development: pelagic eggs, which are buoyant and generally provided with a thin and non-adhesive membrane; and demersal eggs, which are heavy and sink to the bottom, and have a hard and smooth or adhesive membrane. Marine fishes may produce eggs of one type or the other, but with very few exceptions, the eggs of fresh-water fishes are demersal. Most of our well-known food-fishes have pelagic eggs, only the Herring (*Clupea harengus*), Wolf-fish (*Annarrhichas*), Sand Eel (*Ammodytes*), and a few others depositing their spawn on the sea-floor. No evident connection seems to exist between the habits of a particular species and the nature of its eggs, for whereas the pelagic, plankton-feeding Herring (*Clupea harengus*) produces demersal eggs that are deposited in adhesive masses among gravel and shingle on the sea-bottom, the closely related Sprat (*Clupea sprattus*), with exactly the same habitat, as well as the Pilchard (*Sardina*) and the Anchovy (*Engraulis*), have typical pelagic eggs which float separately near the surface. The Angler (*Lophius*), a typical ground-dwelling form, has pelagic eggs, but the Wolf-fish (*Anarrhichas*), also living on or close to the bottom, has large demersal eggs.

Pelagic eggs are very much smaller than those of the demersal type, and it is their small size and glassy transparency when in the sea that helps to render them inconspicuous to other fishes. Those of the Plaice (*Pleuronectes*), which are to be regarded as giants of their kind, never exceed two millimetres in diameter. Eggs of this type when developing in the ovaries or roes are pinkish, opaque objects, but as they mature the granules of yolk disappear and both they and their capsules become quite translucent. A conspicuous feature of many pelagic eggs is the presence of a single large oil-globule, forming a glistening object moving about freely on the surface of the yolk. In others the yolk itself may be partially or completely broken up into small masses, giving the egg a characteristic appearance. For the most part, they are non-adhesive, floating freely and separately at or near the surface of the sea, but those of the Angler (*Lophius*) are invested by a gelatinous outer coat and unite together to form a transparent mass, which may be as much as one hundred feet square in area. The little fish known as *Fierasfer* also has adhesive floating eggs, forming a mass of cylindrical shape, two or three inches in length.

Of the fishes with demersal eggs, those breeding in fresh water have, as a general rule, larger eggs than those spawning in the sea. Among the largest are those of *Gymnarchus* of Africa, which measure about ten millimetres in diameter, and those of some of the Sea Cat-fishes (*Ariidae*), occasionally exceeding fifteen millimetres. Among marine fishes, those of the Lump-sucker (*Cyclopterus*) are about two and a half millimetres in diameter, and of the Wolf-fish (*Anarrhichas*) about six millimetres. Demersal eggs may also be quite free and separate, as in the Salmon (*Salmo*), Shad (*Alosa*), and other anadromous fishes, in which case they are usually provided with fairly tough and smooth outer membranes: more usually, however, they have adhesive surfaces, and stick to one another as well as to fixed objects. The spawn of the Smelt (*Osmerus*), which adheres to the gravel bottom in estuaries, or to the piles of harbours and piers, is peculiar in its manner of attachment. After extrusion, a portion of the surrounding membrane of the egg breaks away and becomes turned back, remaining attached to the egg at one point, and it is by this piece of membrane that the egg is fixed. In some of the Gobies (*Gobiidae*), Blennies (*Blenniidae*) and other shore-dwelling fishes the eggs may be oval or pear-shaped, and attached to rocks, stones, pieces of seaweed, shells and the like by one end, and this end may be provided with a bunch of adhesive filaments (Fig. 116G). The eggs of the Skippers (*Scombresocidae*), Gar-fishes (*Belonidae*), and Flying-fishes (*Exocoetidae*) have sticky threads developed from opposite points on their surfaces, which either serve to anchor them to foreign objects or become entangled with those of other eggs of the same species (Fig. 116F). The eggs of nearly all fresh-water fishes are adhesive, being attached to rocks or stones on the river bed or to the leaves or stems of aquatic plants. The eggs of the Perch (*Perca*) are held together by a membrane, and form long, floating bands, attached at one end to water-weeds in fairly still water.

It will be impossible to follow in detail the manifold and complex series of changes by which the fertilised egg is transformed into a mature fish. Briefly, development starts by a simple cleavage of the ovum into two halves, each of which soon divides into two again, so that by a process of repeated division, or segmentation, accompanied by regular growth, a hollow ball of cells, the blastula, is formed, the walls of which are made up of a single layer of cells. When the amount of yolk present is very small and evenly distributed throughout the egg, the cleavage occurs more or less uniformly all over, but where the amount of food material is more or less abundant, as is the case in most fishes, this may influence the segmentation in one of two different ways. The yolk may tend to become accumulated at one end of the ovum, the vegetative pole, and the essential protoplasmic portion containing the nucleus to be reduced to a relatively small cap situated at the opposite end or animal pole. Thus, in the more primitive Bony Fishes (Sturgeons, Bow-fins, Gar Pikes, Lung-fishes) the segmentation starts at the animal pole, and always proceeds here at a faster rate than at the vegetative pole, so that when the blastula is formed, the cells are much larger and fewer in number in the latter region. In all other Bony Fishes, as well as in the Selachians, the amount of yolk present is usually so great that it prevents segmentation altogether in the vegetative region of the ovum, and cleavage is restricted to the small cap of protoplasm, the germinal disc, at the animal pole. There is, however, no hard and fast line between the two types of segmentation, certain species of fish providing transitional stages. After the blastula has been formed, by the inpushing of one side, this is converted into a double-walled cup, the gastrula, the central cavity of which becomes the alimentary canal. From this stage onwards growth proceeds rapidly, and each of the cells of the two layers goes on dividing. Concurrently, groups of cells become specialised for the performance of particular duties, and give rise to the various tissues and organs—alimentary canal, notochord, brain, muscles, gill-slits, and so on—the mouth and vent are formed, and the embryo comes into being.

The early stages of development just described may conveniently be termed embryonic, in contrast to the post-embryonic or larval development which takes place after the egg is hatched. Such a division of development into two stages is, of course, merely arbitrary, and the whole process from the fertilised egg to the mature fish goes on without a break. In a large number of fishes the development may be almost entirely embryonic, the young fish, when hatched, being a replica of its parents, except in size. In others, on the other hand, the young fish is obliged to leave the shelter of the egg before it has reached this stage, and has to undergo a further series of changes, constituting the larval development, before its bodily structure is that of a mature fish. There is an important relation between the size of the egg and the condition of the young fish on hatching. As a general rule, in those fishes producing large eggs the young are hatched in a fully developed condition, and have little, if any, larval development. In those with small eggs, on the other hand, the post-embryonic or larval stage is more or less prolonged. This relation is clearly connected with the amount of yolk present in the egg. In the case of the oviparous Selachians, with their large and heavily yolked eggs, the abundance of food enables the embryo to remain within the egg for a long period, and when hatched it has reached an advanced stage of development. Thus, a Black-mouthed Dog-fish (*Pristiurus*) hatches out about nine months after fertilisation, a Spotted Dog-fish (*Scyliorhinus*) about seven months. In the case of small pelagic ova, the amount of yolk available for the nutrition of the embryos is comparatively small, and consequently only suffices to support embryonic development for a short time.

In viviparous fishes the development is necessarily almost wholly "embryonic." The majority of Selachians produce their young alive, and of the order of Rays (*Hypotremata*) only the true Skates and Rays (*Raiidae*) and a few allied forms are oviparous. The number of young produced at a birth varies. Thus, the Spiny Dog-fish (*Squalus*) produces only 7 or 8, the Monk-fish (*Squatina*) 25, and as many as 32 have been counted in a single Tope (*Eugaleus*). In nearly all viviparous Selachians some sort of connection is established between the growing embryo and its mother, serving to aid its respiration and nutrition, and in its more elaborate forms recalls the complicated placenta developed in mammals. During the early stages of development the embryo is nourished by the yolky portion of the ovum, which, after a time, comes to lie in a flask-like bag or yolk-sac, attached to the under surface of the body of the embryo by a long and narrow neck (Fig. 117). When first formed the contents of the yolk-sac pass directly into the alimentary canal, but at a later stage the connection between the two is interrupted and the last remains of the yolk are absorbed by the blood-vessels alone. In many Selachians the walls of the lower part of the oviduct (*i.e.* the uterus), in which the embryos develop, throw out long filamentous processes known as uterine villi or trophonemata. These are richly supplied with tiny blood-vessels and secrete a creamy nutritive fluid, which is either absorbed by the blood-vessels of the embryonic yolk-sac, and thus passed to the embryo itself, or is taken up in a more direct manner. In some of the tropical Sting Rays (*Trygonidae*) and Eagle Rays (*Myliobatidae*) the fluid seems to be taken into the alimentary canal of the embryo directly through the mouth or spiracles. In the Butterfly Rays (*Pteroplatea*) the villi from the walls of the uterus are particularly long, and these are gathered into two bundles which pass through the very large spiracles into the pharynx of the embryos, of which there may be one to three, and it is probable that the secretion is first digested in the alimentary canal and afterwards taken up in the embryonic blood-vessels. In a few Sharks such as certain of the Smooth Hounds (*Mustelus*) another type of connection is established between embryo and parent when the food material in the yolk-sac is nearly used up. The walls of the yolk-sac are abundantly supplied with blood-vessels, and special folds or processes of these walls become adherent to or penetrate into the walls of the uterus, which are similarly highly vascular, and through the conjoined vessels the blood of the mother passes to her offspring. Even after birth young Sharks may carry, for some time, the pendent yolk-sac, and continue to derive some nourishment from that source (Fig. 117A, III).

The actual extrusion of the young in Sharks and Rays has rarely been observed, so that the observations made by Mr.

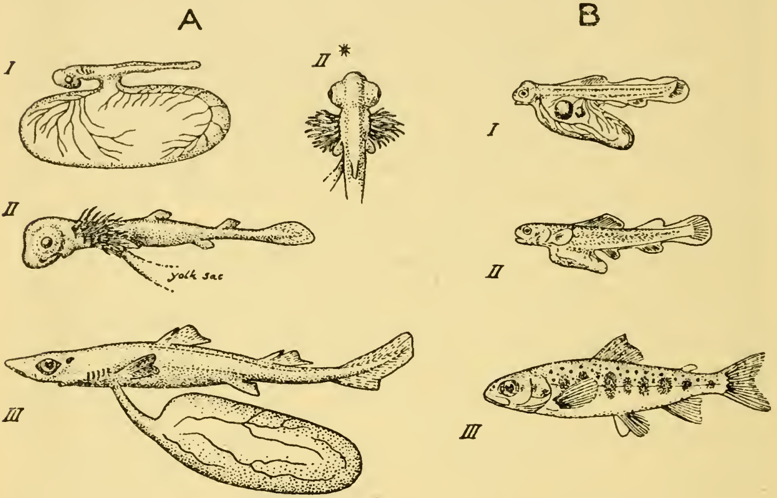


Fig. 117.—DEVELOPMENT OF SHARK AND BONY FISH.

A. Three stages in the development of the Spiny Dog-fish (*Squalus acanthias*). I and II—nat. size; III—× about ½. (I. After Balfour); B. Three stages in the development of the Salmon (*Salmo salar*). I and II—Alevins, nat. size; III—Parr, × ½.

Coles on the birth of a Devil-fish (*Manta*) off the coast of Florida are of particular interest. "Almost immediately after being struck by the harpoon," he writes, "the *Manta* made the sideways revolution alongside the boat, and just before the tail had reached the perpendicular an embryo was violently ejected to a distance of about four feet. The embryo appeared tail first, folded in cylindrical form, but it instantly unfolded, and its pectorals, moving in bird manner, retarded its descent until the mother fish had disappeared below the surface. I was almost in the act of securing this embryo when it was swept below by the pectoral of the large male mate which was near the big female. The embryo was well advanced, with a width of more than three feet and a tail approximating eight feet in length." It must be borne in mind that this extrusion took place after the severe wounding of the mother fish, and may not represent the normal process of birth. The embryos of Saw-fishes (*Pristis*) are generally produced in fairly large numbers, as many as twenty-three having been taken from a female fifteen and a half feet in length caught off the coast of Ceylon. The saw seems to remain more or less soft and flexible until after birth, and the process of parturition is assisted by the fact that the teeth along the margin of the saw at first scarcely project through the membrane enveloping them.

Among Bony Fishes viviparous forms are comparatively rare, occurring only among the Cyprinodonts (*Microcyprini*), the Surf-fishes (*Embiotocidae*) of the North Pacific, the Blennies and their allies (*Blennioidea*) and the Mail-cheeked Fishes (*Scleroparei*). In the Blennioids viviparous forms are found in three widely separated families, but all the remaining members of the suborder are oviparous. The specialised blind Cave-fishes, both Cyprinodonts (*Amblyopsidae*) and Brotulids (*Lucifuga*, *Stygicola*), are all viviparous. The eggs of Bony Fishes bringing forth their young alive are fertilised while still either in ovisacs in the walls of the ovaries or within the cavity of the ovary itself, and may undergo their development in either position. As usual, the embryos are nourished by the yolk contained originally within the ova, but this may be supplemented, or even to a large extent replaced, by certain nutritious secretions from the walls of the ovaries or of the ovisacs, as in the Surf-fishes, where this ovarian secretion is swallowed by the embryos and absorbed by villi on the inner surface of their intestines. The oxygen necessary for respiration is supplied by the blood of the mother.

The number of young produced at a single birth naturally varies considerably. In the Surf-fishes (*Embiotocidae*) it varies from three to forty or fifty; in most of the Cyprinodonts from fifteen to twenty-five, although the Four-eyed Fish (*Anableps*) may have only four or five; in the Viviparous Blenny or Eel Pout (*Zoarces*) of our own shores (Fig. 118) a female of seven or eight inches in length produces twenty to forty young, one from eight to ten inches, from fifty to one hundred and fifty, while larger specimens have been found to contain more than three hundred. It has been estimated that the Norway Haddock

(*Sebastes*), a member of the family *Scorpaenidae*, may have as many as one thousand embryos in each ovary. The eggs of the Eel Pout hatch in about twenty days, but the young do not leave the body of the mother until some four months after fertilisation: they are then about one and a half inches in length, and, externally at least, closely resemble their parents.

The accompanying figures (Fig. 117A) have been selected to show three of the main stages through which the developing embryo passes in a typical Selachian, and to a large extent explain themselves. As in any other vertebrate, the head of the early embryo is very large in proportion to the body, and is bent downwards at an angle, forming the cranial or cephalic flexure (I). As development proceeds, this angle becomes less and less marked (II). The median fins appear at an early stage, and take the form of a continuous membranous fold surrounding the trunk, which later becomes split up into the

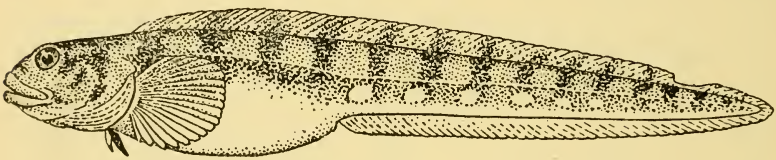


Fig. 118.

Viviparous Blenny or Eel Pout (*Zoarces viviparus*), $\times \frac{3}{8}$.

dorsals, anal, and caudal of the mature fish (*cf.* p. 55). Concurrently with this differentiation of the median fins, the first rudiments of the pectoral fins make their appearance, and soon afterwards the pelvics also appear. At the same time, the head commences to take on the form of that of the adult, accompanied by marked changes in the form of the mouth and gills, and the lateral line appears. An interesting feature of Selachian embryos is the presence of the so-called external gills (*cf.* p. 43), long, filamentous processes developing from the walls of the branchial clefts and protruding through the external gill-openings (II). Their function appears to be twofold: they assist the embryo to breathe, and may also aid in the absorption of nutriment. Having served their purpose, they completely disappear. The last figure shows a final larval stage, in which all the external features of the mature fish are recognisable, and only the pendent yolk-sac remains as a legacy from the embryonic life (III).

Turning to the Bony Fishes, it will be found that in its essential details the development follows much the same course as in the Selachians, but, as the amount of yolk available is considerably less, the larva hatches out in a much less advanced condition. The Salmon (*Salmo*) will serve to illustrate the development of a typical Bony Fish with fairly large and well-yolked demersal ova (Fig. 117B). As compared with that of a pelagic egg, the incubation period is long, and varies from five weeks to more than five months, being very much slower when the temperature of the surrounding water is low. In this connection it may be mentioned that the successful introduction of Salmon and Trout into such distant countries as Australia and New Zealand is made possible by the fact that the development of the fertilised ova may be artificially prolonged by keeping them on ice. Normally, however, the eggs of the Salmon hatch out at the end of winter, and the fry or alevins, about sixteen millimetres in length, remain for some time hidden away in the spaces between the stones on the spawning bed. They are weighed down at this stage by the large yolk-sac, which is relatively smaller than that of the embryo Shark, and is packed away beneath the body instead of being pendent (I, II). This provides the fry with nutriment during the early part of their lives, but at the end of a month or two all the yolk has been absorbed and they have to fend for themselves. By this time they have grown to about twenty-six millimetres in length, but thereafter growth is rapid, and they normally attain to three or four inches in a year, and five or six inches in two years. During the first two years of their life, when they live in fresh water, feeding on small crustaceans, insects, etc., they are known as Parr (III), and may still be regarded as larval fishes. The Parr are especially distinguished by the bluish or purplish colour of the back, and by the presence of seven to eleven oblong or oval spots of the same hue, the "parr-marks," along the middle of each side. At the end of the two years, or a little later, another change occurs, and the Parr become transformed into Smolts. A bright silvery livery is assumed, the parr-marks are obscured, and the smolts drop down the rivers and migrate rapidly out to the open sea, where they soon assume all the characters of the adult fishes.

In those fishes with small pelagic eggs, the period of incubation, although varying considerably in the different species, is always very much shorter. As far as our own food-fishes are concerned, this period rarely exceeds two weeks, and the Anchovy (*Engraulis*) and Sprat (*Clupea sprattus*) actually hatch out from two to four days after fertilisation. As in the case of the demersal eggs, a low temperature delays hatching, and it has been found that the eggs of the Herring (*Clupea harengus*) will hatch in eight or nine days in water kept at a temperature of 52° to 58° F., but will take forty-seven days in water of 32° F. (*i.e.* just freezing). As might be expected, the newly hatched larvae of these fishes are very small, sometimes only three millimetres in length, and are imperfectly developed. At the same time, the remainder of the development is sometimes crowded into an incredibly short space of time, and the three-millimetre larva hatched on the fourth day may have assumed the essential features of the all but mature fish before a month has elapsed, and before it is much more than ten millimetres in length.

As a general rule, the larva hatched from a pelagic egg is transparent, with the pectoral fins developed to a greater or lesser extent, and with a continuous median fin-fold along the back, round the tail, and along the lower edge of the body as far forward as the vent or even farther: this fold has the form of a simple membrane, and is not yet supported by rays. The mouth is frequently not yet formed, the blood is quite colourless, and even the gill-clefts may be still wanting. In this condition nourishment is provided by the remains of the yolk, but as this is used up the mouth is developed and the larva begins to feed on the minute organisms of various kinds found near the surface of the sea. At a later stage the continuous median fin becomes split up into its definitive components, and the pelvics make their appearance. By degrees, the form, proportions, and structure of the adult fish are assumed, and, as a rule, all the essential organs, including the bony internal skeleton, are developed before the fish is much more than an inch in length. It may be noted here that the fins vary a good deal in their development in different species, the dorsal appearing before the anal in some, the anal before the dorsal in others. In the members of the Herring tribe (*Clupeidae*) the dorsal is completely developed well back, and then migrates forward to its final position in the middle of the length of the fish.

Frequently special larval organs are developed, which disappear when the more permanent organs have been acquired. Such structures are for the most part concerned with feeding, respiration, or locomotion, and may give the larva an appearance so unlike that of the mature fish that it has sometimes been mistaken for a distinct species.

In the Lampreys (*Petromyzonidae*), for example, the newly hatched larva is so unlike the parents that it has received distinct generic and specific names (*Ammocoetes branchialis*), and is popularly known as a Pride or Niner. It is curiously worm-like in form, and differs from the adult in having rudimentary eyes buried beneath the skin, a horse-shoe shaped mouth, with a small transverse lower lip and a hood-like upper lip, and no teeth (Fig. 119): the entrance to the mouth is surrounded by a number of fringed barbels forming a perfect strainer. The small external gill-openings lie in a marked groove. The Prides are hatched some ten to fifteen days after fertilisation of the eggs, and remain in the nest for about thirty days. They then wander down the stream, and having selected a suitable spot, burrow in the sand or mud. They live buried in tubes for three or four years, quite blind, and feeding on minute organisms or on organic matter contained in the mud. In their mode of life, and particularly in the manner in which they obtain their food, these larvae bear a marked resemblance to the little sand-dwelling Lancelet (*Amphioxus*) and to the other very lowly vertebrates, the Sea Squirts or Ascidians. The minute particles comprising the food are carried through the mouth into the pharynx by currents of water produced by the action of special ciliated cells working in unison. The particles become entangled in strings of mucus, secreted in a groove (endostyle) in the floor of the pharynx (which, in the higher vertebrates, becomes the thyroid gland), and are swept into the stomach by bands of cilia. At the end of three to five years a metamorphosis occurs, and the larva quite suddenly assumes the characters of the

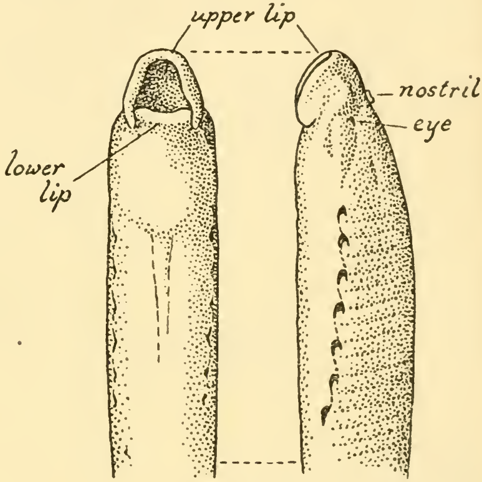


Fig. 119.

Two views of the head of the larval Lamprey or Pride (*Ammocoetes branchialis*), × 4.

adult. First the eyes appear, the mouth is contracted and takes on the suctorial disc-like form so characteristic of the Lampreys, the tongue and horny teeth are developed, and the branchial groove disappears. At the same time important changes take place in the form of the skeleton, gill-pouches, alimentary canal, kidneys, etc., the whole process occupying about two months.

Among other examples of larval or provisional organs, the adhesive or cement organs and the external gills may be mentioned. In the Lung-fishes (*Dipneusti*) the newly hatched larva is not unlike the tadpole larva of the amphibian: there is no yolk-sac, the small amount of food-material still present being distributed over the lower region of the body. The resemblance is further strengthened in the African (*Protopterus*) and South American (*Lepidosiren*) forms by the presence of four pairs of feathery external gills, projecting freely from the gill-arches, and of a glandular adhesive organ situated behind the mouth. In the South American species the gills disappear during the metamorphosis (Fig. 19A), being replaced by the internal gills and lungs, but in the African species vestiges are retained throughout life (Fig. 99A). In the larval Bichir (*Polypterus*) there is a single pair of fringed pinnate external gills (Fig. 19B), which generally disappear completely during the metamorphosis, but occasionally one or both are retained for a further period. Some others of the more primitive Bony Fishes have been described as possessing larval external gills (*Mormyridae*, *Osteoglossidae*, *Cobitidae*, etc.), but these are merely the ordinary gill-filaments which are excessively long and prolonged to the exterior. The development of these structures is always correlated with life in badly aerated, tropical swamps, and there can be little doubt that they assist the respiration of the larvae until the permanent breathing organs are developed. The larval Bow-fins (*Amia*) or Gar Pikes (*Lepidosteus*), hatched in the more temperate climate of North America, and in better aerated water, do not possess external gills. They are, however, provided with cement organs, but instead of being placed behind the mouth, these are situated at the end of the snout, a position occupied by similar organs in the larval Ascidian. Traces of the sucking disc are to be found in the larval Sturgeon (*Acipenser*), in the form of a shallow pigmented groove in front of the mouth, but such a structure is never present in the larvae of any of the higher Bony Fishes. Its function is to enable the larvae to attach themselves to weeds and other fixed objects when at rest, and it has been found that artificially hatched Gar Pikes will adhere by their discs to the sides of a glass jar.

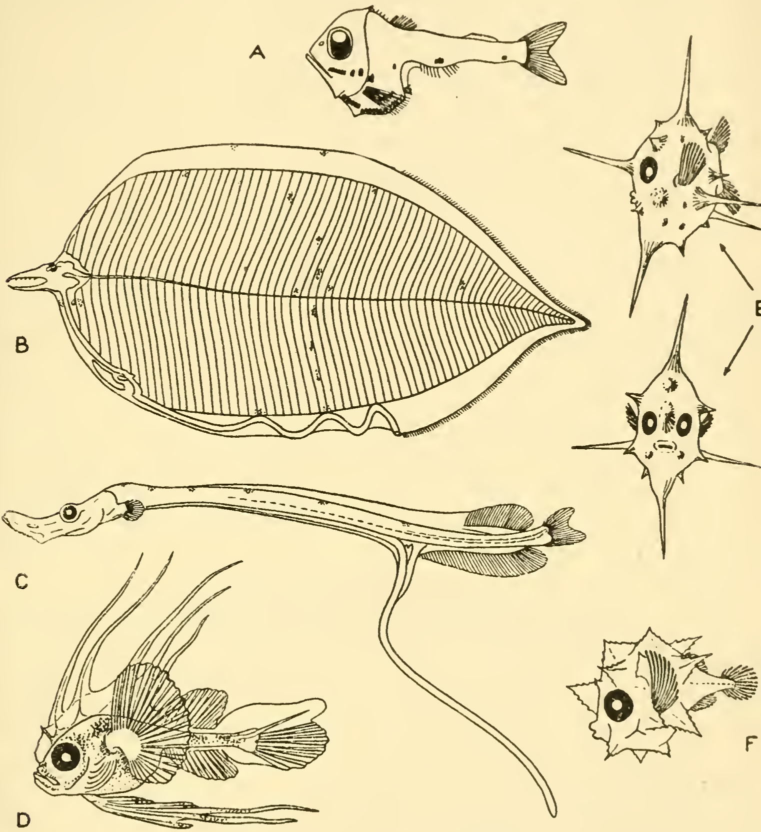


Fig. 120.—LARVAL FISHES.

A. *Argyropelecus aculeatus*, × 4. (After Brauer); B. *Leptocephalus sp.*, × 1½. (After Roule); C. *Stylophthalmus macrenteron*, × 2½. (After Regan); D. Angler (*Lophius piscatorius*), × 2½. (After Tåning); E. Sun-fish (*Mola lanceolata*), × 2½. (After Schmidt); F. Truncated Sun-fish (*Ranzania truncata*), × 8. (After Schmidt.)

Some pelagic larvae and young fishes also possess curious structures that disappear altogether later, and the larvae may be so different from the adults that they have been described as distinct species or even genera. In the oceanic Sun-fishes (*Molidae*), for example, the newly hatched larva is quite normal, but soon loses its caudal fin and acquires a regular armour of strong spines projecting in every direction all over the body, which serve to protect it during a period of helplessness (Fig. 120F). Five of these spines afterwards grow out into long "horns," one of which projects from the middle of the back, one from the snout, one from the chest, and one from each side of the body (Fig. 120E). A little later the fish undergoes a remarkable change in shape, the body actually becoming deeper than long; the spines shorten, and a new tail-fin develops which connects the abbreviated dorsal and anal. The fish is now about half an inch in length, and from this stage onwards it gradually assumes the form of the adult.

The young of the Deal-fish (*Trachypterus*) is remarkable for the extraordinary development of the fin-rays, those of the front part of the dorsal, of the pelvics, and of the lower lobe of the caudal being produced into very long filaments, which may be many times longer than the body and are ornamented with lappet-like membranous processes (Fig. 121 BI). As the fish grows these filaments get progresively shorter and the lower lobe of the caudal fin disappears (BII). The Deal-fish is an oceanic species, and it seems probable that the young live at some considerable depth where the water would be fairly calm, for the currents prevailing at or near the surface of the sea would soon damage such delicate structures.

The Sword-fishes (*Xiphiidae*) and their allies, the Sail-fishes and Spear-fishes (*Istiophoridae*), are distinguished by having the snout prolonged to form a long flat or rounded spear or sword, and the changes undergone by these fishes during development are very striking. The young of the Sail-fish (*Istiophorus*) have been beautifully illustrated by Dr. Günther, whose figures are reproduced here. In the first stage (Fig. 121 AI), an individual nine millimetres in length, both jaws are equally produced and armed with pointed teeth; the edge of the head above the eye is provided with a series of short bristles; and from the back of the head project, above and below, long pointed spines. The dorsal fin is a long low fringe, the pectoral is large and truncated, and the pelvics are represented by a pair of short buds. In the next stage (AII), a fish fourteen millimetres long, the dorsal has increased enormously in size, the pelvics have grown out into long filaments, and the pectorals have changed their shape. The spines on the head are still prominent, but the bristles above the eyes have disappeared, and the upper jaw has grown a little longer than the lower. At the third stage (AIII), when the fish has grown to a length of sixty millimetres, even more marked changes have occurred. The dorsal fin has become differentiated into an anterior portion of great size and a smaller posterior part; the upper jaw has grown out still farther

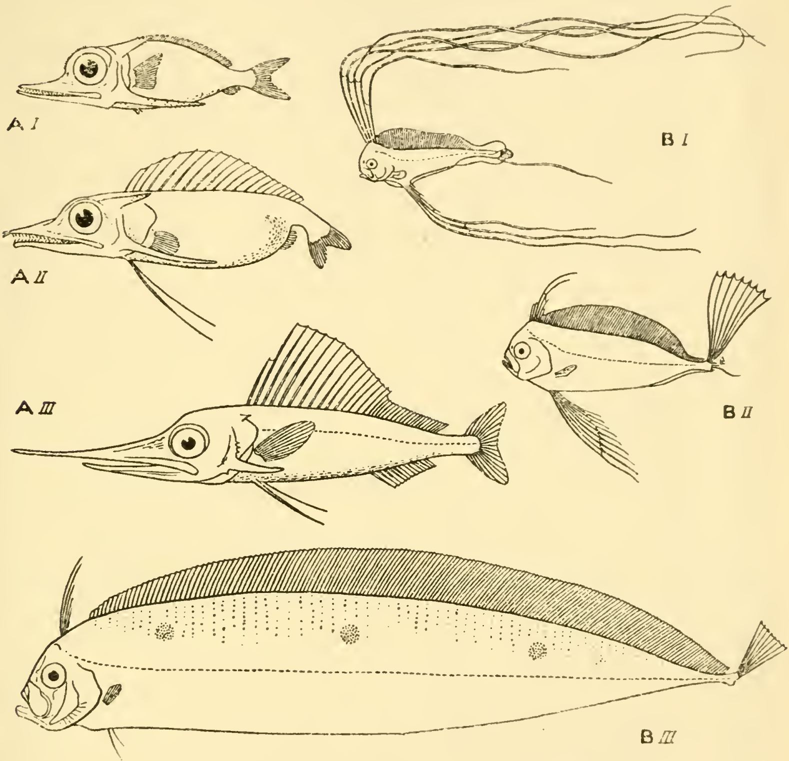


Fig. 121.—DEVELOPMENT OF SAIL-FISH AND DEAL-FISH.

A. Three stages in the development of the Sail-fish (*Istiophorus*, *sp*.). (After Günther.) (I) 9 mm., $\times 3\frac{1}{2}$; (II) 14 mm., $\times 3\frac{1}{2}$; (III) 60 mm., nat. szie. A full-grown specimen is shown in Fig. 6A. B. Three stages in the development of the Deal-fish (*Trachypterus arcticus*). (After Emery and Smitt.) (I) 16 mm., $\times 1\frac{1}{4}$; (II) 100 mm., $\times \frac{1}{4}$; (III) 1000 mm., $\times \frac{1}{10}$.

and now projects considerably beyond the lower, and the teeth have all but disappeared; the long spines from the back of the head have been reduced to comparatively minute proportions, and the filamentous pelvic fins are much smaller. It will be observed that the eye is progressively smaller at each stage. The young Sword-fish (*Xiphias*) undergoes a very similar series of changes, but the body is covered with small, rough warts arranged in regular lengthwise rows, these being still apparent after the individual has assumed all the other features of the mature fish.

The Gar-fishes (*Belonidae*) also possess long beak-like jaws, but a study of the development of these fishes reveals the fact that it is the lower jaw which is first prolonged and the upper afterwards grows out to equal it. Thus, during its development the Gar-fish passes through a temporary stage in which, as far as the jaws are concerned, it is exactly like the adult Half-beak (*Hemirhamphus*). It might be assumed that the Half-beaks are ancestral to the Gar-fishes, but it is more probable that the unequal jaws of the larval Gar-fish are associated with some specialised feeding habit, and that this condition was later retained by some of the primitive Half-beaks in the adult stage.

In the Ten-pounders (*Elops*), Lady-fishes (*Albula*), and in all the Eels (*Apodes*), the larvae are of a peculiar, transparent, leaf-like form, quite unlike the mature fishes, and the period of larval life is greatly prolonged. Further, these larvae may grow to a relatively large size, in certain species attaining to a length of a foot or more. This type of larva is known as a *Leptocephalus* (leaf head), and the first specimen of its kind was discovered by a naturalist called Scopoli in 1777, but he regarded it as representing a distinct group of fishes. The first British *Leptocephalus* was discovered in 1763 by one William Morris near Holyhead, but this was not described until 1788, when Gmelin named it after the finder, *Leptocephalus morrisii*. It was not until 1861 that Carus first recognised that these creatures were larval forms, but he was mistaken in regarding them as young Ribbon-fishes. In 1864 Gill expressed the view that they were larval Eels, and established the fact that *Leptocephalus morrisii* was the young stage of the Conger Eel (*Conger*). Dr. Günther accepted this explanation, but held that they were abnormally developed forms, "arrested in their development at a very early period of their life . . . and perishing without having attained the character of the perfect animal." This view was soon disposed of, when the French scientist, Yves Delage, succeeded in keeping a specimen of the Conger larva alive in an aquarium for seven months, and watched the whole process of transformation into the adult state. The next step in the solution of what came to be known as the "Eel question," occurred when an Italian naturalist, Raffaele, described the eggs of five species of Eels, which he succeeded in hatching and

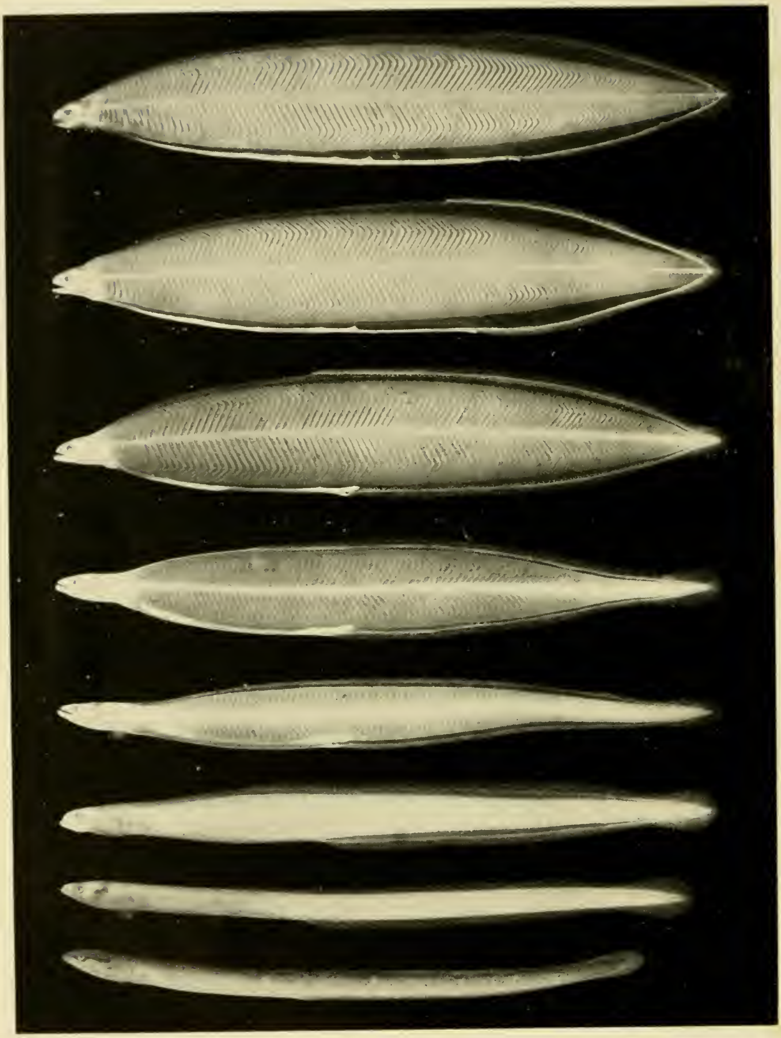


Plate IV.

Stages in the metamorphosis of *Leptocephalus brevirostis*, the larva of the European Fresh-water Eel (*Anguilla anguilla*).

By permission of Dr Johannes Schmidt.

kept the larvae alive for about two weeks. Next, two other Italian investigators, Grassi and Calundruccio, made a thorough study of the *Leptocephali* of the Straits of Messina, and were able to trace the transformation of several kinds of larvae into their respective species of Eels. They showed beyond any doubt that the larva which had been named by Kaup, *Leptocephalus brevirostris*, was the young of the Common or European Fresh-water Eel (*Anguilla anguilla*), thus establishing that fresh-water as well as marine forms pass through the same larval history. They concluded that the European Eel bred in deep water near the coast, and that the larvae lived at considerable depths, being brought to the surface in the Straits by the agency of the strong currents and whirlpools prevailing there. This explanation was ingenious, and not surprising in view of the data at their disposal, but, as has been already pointed out (*cf.* p. 289), was still far from the truth. Finally, the whole life-history of the European Eel has been elucidated by Dr. Johannes Schmidt, who has traced the larvae on their long journey across the Atlantic, and has examined them at almost every stage of their development. He has also paid considerable attention to the American Eel (*Anguilla rostrata*), and is at present engaged in investigating the life-histories of some of the species inhabiting the Indo-Pacific region. Curiously enough, the egg of the European Eel has yet to be described, but four years ago an American expedition to the Atlantic procured five eggs which were hatched out in the laboratory, and these are confidently believed to be those of the American species.

The larval history and metamorphosis of the European Eel may be briefly summarised. The breeding-grounds lie in the Western Atlantic, south-east of Bermuda (*cf.* p. 290), and the eggs hatch out some time in the spring. The larvae or *Leptocephali*, living in the upper layers of the ocean, are provided with curious long, needle-like teeth, which may assist them to seize the minute organisms believed to form their food. They at once commence the long homeward journey, the majority travelling north-eastward with the Gulf Stream, floating at a depth of about one hundred fathoms, in water of a temperature of about 68° F. They grow rapidly during the first few months, averaging about twenty-five millimetres in length in their first summer, and are to be found at this time in the Western Atlantic west of 50° W. Longitude. From now onwards they inhabit the upper strata of the sea, sometimes being found actually at the surface, and by the second summer most of them have reached the Middle Atlantic, and have grown to fifty to fifty-five millimetres. They finally arrive off the coasts of Europe when fully grown, about three inches in length, and a little over two years old. They are now ready to undergo the metamorphosis, and this takes place in the autumn. The larvae cease to feed, the needle-like teeth are lost, and a progressive shrinking takes place both in length and depth, until they assume a cylindrical, although still perfectly transparent form, about two and a half inches long. These Elvers or Glass Eels at once acquire a fresh set of teeth, small and conical, and quite unlike those of the larvae, and are ready to commence the ascent of the rivers. Considering this account of the larval history with that of the breeding of the adults given on page 290, it will be seen that the remarkable life-story of the Eel may be divided into four chapters. These are: (1) a pelagic larval stage—a period of active growth and passive migration; (2) the metamorphosis into the Elver; (3) the growth of the ordinary Yellow Eel; and (4) the change into the breeding Silver Eel, and the migration to the spawning-ground, which ends in death.

The true Flat-fishes (*Heterosomata*) are distinguished from all other fishes by having both their eyes on the same side of the head: the upper or eyed side only is coloured, the lower or blind side being white. The larval history and metamorphosis of these fishes is very remarkable, and throws considerable light on the evolutionary history of the group. The eggs are pelagic and are hatched in a very few days. The newly hatched larvae are quite symmetrical, with an eye on each side of the head as in any other fish, and they swim at or near the surface of the sea. After a time, when the larvae have grown to half an inch or more in length, one eye moves round to the upper edge of the head and finally round to the opposite side, where it comes to lie close to its fellow; at the same time, the dorsal fin is prolonged forward, and as soon as the eye has moved round the fin grows along the edge of the head above it. In some species the migration of the eye is delayed until the dorsal fin has grown forward on to the head, and the eye is then obliged to push its way through between the base of the fin and the edge of the head. While these important changes are taking place the little fish sinks to the bottom of the sea, and thereafter lies or swims at or near the bottom with the eyed side uppermost. The twisting of both eyes to the one side of the head leads to radical changes in the symmetry of the skull, and it is of great interest to note that, if the migration of the eye is the effect of habit, as

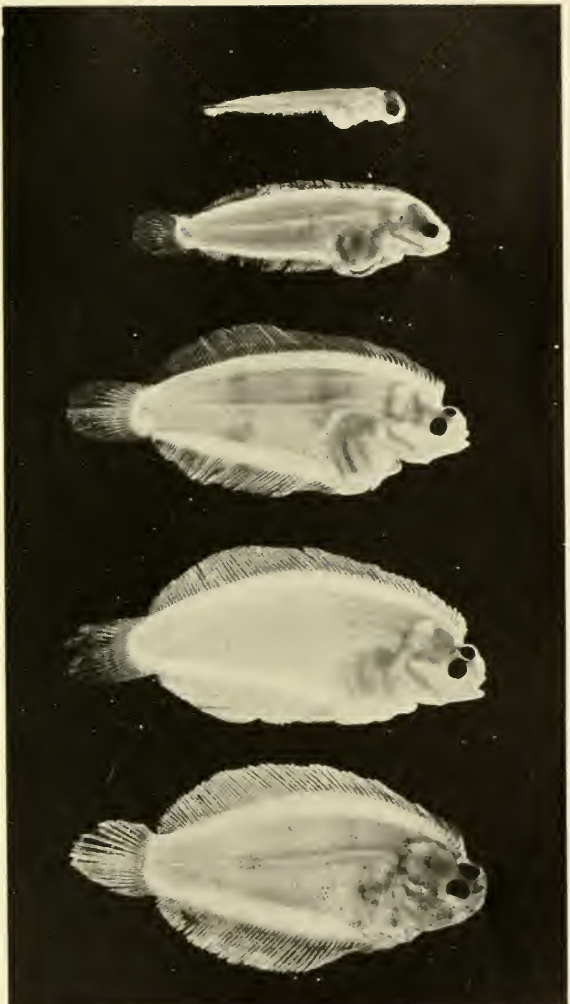


Plate V.

Stages in the metamorphosis of the Plaice (*Pleuronectes platessa*).

Photograph by Mr H. H. Goodchild.

is generally and probably rightly supposed, then it is an inherited effect which is so strongly impressed on the constitution of the fish that preparations for the event begin almost as soon as the fish is hatched. The skull is at first cartilaginous as in any other larva, and there is a curved bar of cartilage above each eye: long before the young fish settles on the bottom, the bar above the eye destined to migrate is absorbed, so that there shall be no obstacle in its path.

In concluding a chapter on development, it may be convenient to mention very briefly the question of hybrids, that is to say, of individuals that have sprung from an ovum fertilised by a spermatozoon of an alien species. Such cases are comparatively rare in marine fishes, as far as our knowledge goes, but are not uncommon between the various members of the Salmon family (*Salmonidae*), as well as among the members of the Carp tribe (*Cyprinidae*). The best-known crosses occurring in a state of nature in the former group are Salmon and Trout and Trout and Char, and these are easily made by artificial fertilisation. It has been shown experimentally that the hybrid offspring of Salmon and Trout are deficient in vitality, and seldom—in the case of males never—come to maturity. Dr. Day remarks, concerning the handsome Zebra hybrid of the Trout (*Salmo trutta*) and the American Brook Trout (*Salvelinus fontinalis*) that the developing eggs show a very high mortality, and that the resulting offspring are frequently deformed in one way or another. In the *Cyprinidae* hybrids have been described between Bleak and Chub, Bleak and Dace, Bleak and Roach, Bleak and Rudd, Bleak and White Bream, Bream and Roach, Bream and Rudd, Carp and Crucian Carp, Roach and Rudd, White Bream and Roach, and White Bream and Rudd in the British Isles alone. In these cases the resulting offspring seem to be quite healthy, and, as in the case of the Salmon and Trout, generally exhibit more or less equally the characters of both parent species. In other fishes the characters of the hybrids may be very variable, sometimes resembling one parent, sometimes the other.

CHAPTER XVII

FOSSILS AND PEDIGREES

Taxonomy and the science of palaeontology. Stratified rocks. Geological record. Fossil Marsipobranchs: Ostracoderms. *Palaeospondylus*. Placoderms: Arthrodira and Antiarcha. Fossil Selachians: *Cladoselache*, *Climatius*, *Pleuracanthus*, etc. Origin of Bony Fishes. Palaeopterygii: Palaeoniscids, Platysomids, Catopterids, Chonodrosteids, etc. Crossopterygii: Rhipidistia, Actinistia, and Dipneusti. Neopterygii: Semionotids, Pycnodonts, Eugnathids, Pachycormids, etc. Primitive modern Bony Fishes.

An important branch of the science of fishes is that known as taxonomy, which is concerned with the arranging or classifying in natural sequence of the multitude of diverse forms of animal life together constituting the three great vertebrate classes here grouped together under the general name of fishes. A century or so ago any scheme of classification was mainly artificial, being constructed in the belief that the world had come into existence quite suddenly, and that the different kinds of animals inhabiting it were separately created in the beginning and have remained unchanged ever since. Such a view has now been shown to be untenable, and slowly and steadily a mass of evidence has been accumulated which shows beyond any shadow of doubt that the existing species of animals have all been produced from earlier and simpler types by a process of racial evolution, all life having a common origin. It has been demonstrated that the birds and mammals have sprung from the cold-blooded reptiles, the reptiles from the amphibians, the amphibians from some of the primitive fishes, while the fishes themselves have arisen from some even more primitive type of vertebrate, itself presumably derived from an invertebrate stock. The same evidence also shows that the fishes living to-day, multitudinous and diverse as they may be, represent but a proportion of the total number of fishes that have flourished in the seas and rivers since they were first evolved. The existing forms may be compared to the topmost and finest branches and twigs of the fish "family tree"; they are the successful forms that have succeeded in adapting themselves to present-day conditions, and have accordingly triumphed in the struggle for existence. There are innumerable other branches, some short and simple, others long and further branched, representing forms that have flourished for a time but finally passed away: of these, some failed to adapt themselves to changed conditions and so perished, others became variously changed and modified, to give rise to new and perhaps more successful types.

The main diverging branches of such a genealogical tree are called phyla, and the term phylogeny is applied to the study of the pedigrees of living animals, as opposed to ontogeny, concerned with the development of the individual from the egg to the mature animal: the one deals with the history of the race, the other with the history of the individual. The business of the systematic zoologist is to study and compare the existing fishes, in an endeavour to make out their affinities one to the other, and to discover the lines of descent that connect the various branches of the "tree" upon which his classification is based. A perfect taxonomy is one that would express all the known facts in the evolution and development of the various forms. The evidence upon which it would be based would be drawn mainly from two sources, namely, comparative anatomy and embryology, but there is a third science which provides definite and irrefutable evidence of the truth of racial evolution. This, the science of palaeontology, is concerned with the remains of extinct animals and plants buried in the rocks, and no scheme of classification, nor any genealogical tree that may be composed to illustrate the lines of descent of a particular group of animals, is worthy of serious consideration until it has been tested by a study of the record provided by the rocks. It is reasonable to suppose that if, as every scientific man believes to-day, evolution is an established theory and not a mere hypothesis, the series of fossils excavated by the palaeontologist should provide some evidence of this process, and that it should be possible to reconstruct from these remains, if not some of the ancestral types themselves, at least some of their near relations. To give any sort of detailed account of the large number of fossil fishes that have now been described would be altogether beyond the scope of this work, and it will be possible only to survey very briefly some of the more interesting forms, and to consider their affinities with living fishes.

As the result of many years of study of the organic remains contained in the fossil-bearing rocks of the world, most of these rocks have now been assigned to their correct place in the geological record, and the history of the earth has been split up into a series of divisions of various grades, corresponding to the chapters, sections, and paragraphs of a book. The names given to the different kinds of rock by the geologist, such as the Chalk, Cambridge Greensand, Oolite, Red Sandstone, London Clay, etc., may be ignored here, but the main divisions and subdivisions into which geological time has been split up are of greater importance, as it will be necessary to mention these by name in the course of this chapter. The main divisions are known as eras, each era being subdivided into several periods, which may be further split up into epochs. Just as it is customary to speak of ancient, mediaeval, and modern history of the human race, so do geologists refer to the Palaeozoic, Mesozoic, and Tertiary (or Caenozoic) eras in the history of the earth. In the accompanying diagram (Fig. 122) the earliest era, the Archaean or Pre-Cambrian, has been largely omitted, for although it may represent more than the half of geological time, and correspond to about thirty-two miles of thickness of strata (all the remaining fossil-bearing rocks representing about twenty-one miles), this time was passed before there were any living organisms with structures sufficiently hard to form fossils. The rest of the divisions from the Cambrian to the present day are all included, and the sizes of the spaces in the diagram represent very approximately the relative length of the periods in geological time. Some idea of the time-scale may be gained from the fact that it has been estimated that the lower layers of the Triassic period, during which mammals first made their appearance on earth, were deposited somewhere in the neighbourhood of 175,000,000 years ago. Fishes first made their appearance during the Silurian period, and became very abundant during Devonian and Carboniferous times, when they were the dominant type of animal life and had already produced a large number of diverse types.

It must not be supposed that the fossil-bearing strata always have the regular arrangement depicted in the accompanying diagram, or that the record of the rocks provides a continuous story, in which the history of all the main groups of animals and their lines of descent may be deciphered with the aid of a complete series of well-preserved fossil remains. Quite often the proper arrangement of the layers has been much disturbed, the rocks being variously tilted, buckled, twisted, broken, or even turned wrong way up, as a result of the shrinkage of the earth's crust when cooling down. The reading of the story of the earth's history may be likened to the reading of a book, but a book which has been extensively damaged by fire, water, and decay, so that many of its pages are altogether missing, while others are variously torn, dog-eared, crumpled, and their contents rendered illegible. The following passage emphasising the imperfection of the geological record was written in 1898 by Sir Arthur Smith Woodward, one of the leading authorities on fossil fishes, but in spite of many discoveries made since that date, its substance remains fundamentally true to-day. "We may, in fact, without exaggeration declare that every item of knowledge we possess concerning extinct plants and animals depends upon a chapter of accidents. Firstly, the organism must find its way into water where sediment is being deposited and there escape all the dangers of being eaten; or it must be accidentally entombed in blown sand or a volcanic accumulation on land. Secondly, this sediment, if it eventually happens to enter into the composition of a land area, must escape the all-prevalent denudation (or destruction or removal by atmospheric or aqueous agencies) continually in progress. Thirdly, the skeleton of the buried organism must resist the solvent action of any waters which may percolate through the rock. Lastly, man must accidentally excavate at the precise spot where entombment took place, and someone

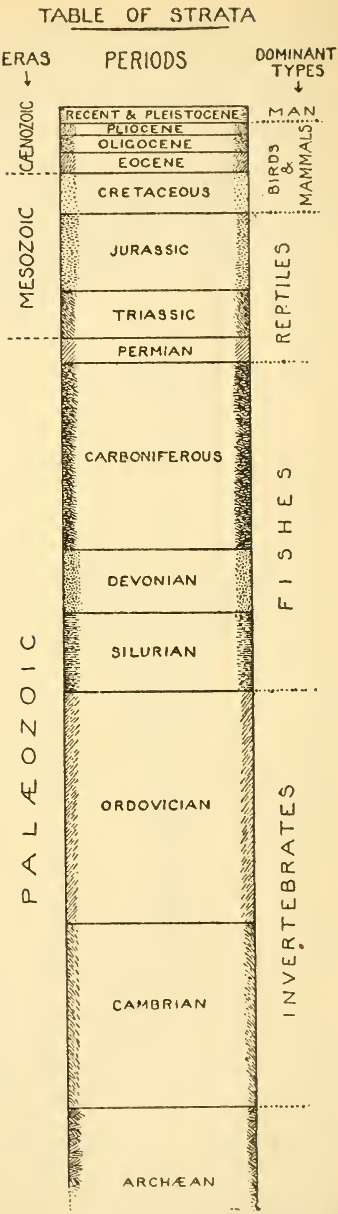


Fig. 122.—TABLE OF BRITISH STRATA, SHOWING APPROXIMATE THICKNESS.

must be at hand, capable of appreciating the fossil, and preserving it for study when discovered."

The geological record has so far provided no evidence as to the origin of the three vertebrate classes here grouped together as fishes, and at the time when fish-like fossils first made their appearance in the rocks the Marsipobranchs, Selachians, and Bony Fishes are not only already differentiated from each other and firmly established, but are represented by a number of diverse and often specialised types, a fact that suggests that each of the classes had already enjoyed a respectable antiquity. It will be convenient, therefore, to consider the fossil history of each separately, commencing with the Marsipobranchs as being admittedly the most primitive.

In the Marsipobranchs (pouch-gills) the gills are contained in a series of separate muscular pouches, which expand and contract during respiration, and are quite unlike those of any other fish (*cf.* p. 37). This character, coupled with the complete absence of jaws and of gill-arches, serves to distinguish them from both Selachians and Bony Fishes. It had formerly been supposed that these characters represented secondary modifications brought about by the highly specialised, semi-parasitic habits of the existing Cyclostomes, but the past history of the group, recently correctly interpreted for the first time, effectually disposes of this view, and places beyond all doubt that the differences between the Marsipobranchs and other vertebrates in the structure of the mouth and gills are truly fundamental. It must be understood, of course, that the fossil remains furnished by the Silurian and Lower Devonian rocks provide few clues as to the lines of descent of the existing forms, these archaic forms being quite as specialised in many respects as are their descendants living to-day. At the same time, however, they are of very great interest, and show in their anatomy undoubted evidence of descent from the same stock.

These fossil Marsipobranchs, the oldest fish-like vertebrates known, were formerly grouped together with other superficially similar forms under the name of Ostracoderms, but three main groups are now recognised, each ranking as a distinct sub-class, the fourth sub-class, the Cyclostomes, being reserved for the existing forms. The *Anaspida* have a typical fusiform body, covered with series of small scale-like plates, the head being armed with numerous plates of a similar nature, but less regularly arranged (Fig. 123A). Immediately behind the head on either side is a row of gill-openings, and special plates and small spines posterior to these are believed to represent the pectoral fins. Anything less like a Lamprey it is scarcely possible to imagine, but a closer study of these Anaspids reveals several striking

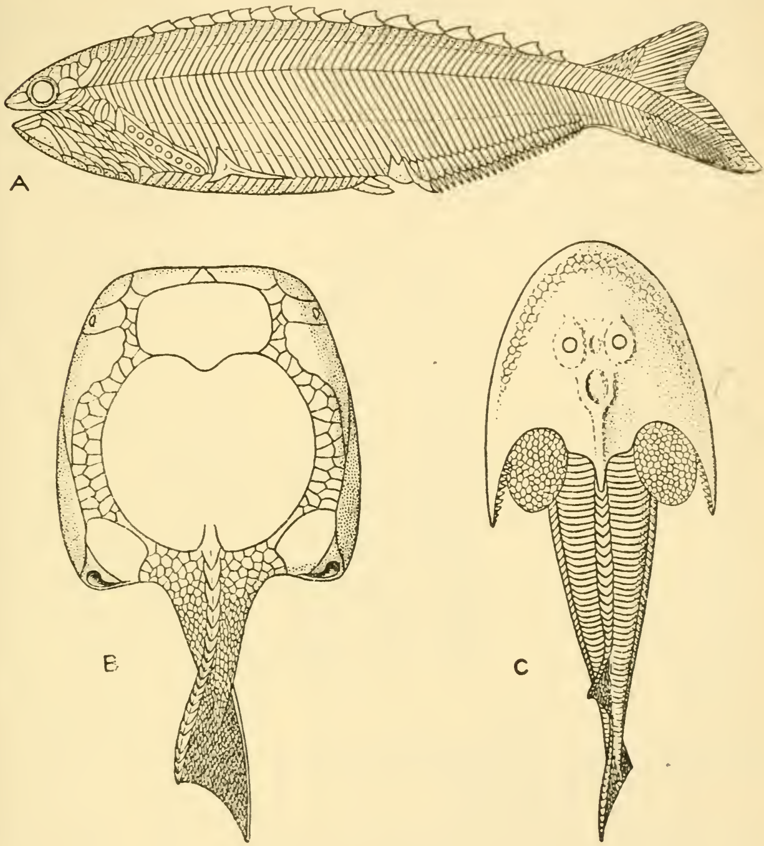


Fig. 123.—RESTORATIONS OF SILURIAN AND DEVONIAN MARSIPOBRANCHS.

A. *Rhyncholepis parvulus*, $\times 1\frac{1}{2}$. (After Kiaer); B. Upper view of *Drepanaspis gemundenensis*, $\times \frac{1}{5}$. (Modified from Traquair); C. Upper view of *Cephalaspis lyelli*, $\times \frac{1}{2}$. (After Traquair.)

points of resemblance. In both there is a pineal organ between the eyes and a single unpaired nostril in front of it (Fig. 124). Unfortunately, the form of the mouth cannot be determined in the fossils, and it seems probable that the terminal portion of the snout was soft, and therefore was not preserved. The tail of the Anaspids, of a reversed heterocercal type, with the fleshy lobe turned *downwards* and bearing the fin on its upper edge, is unique among fishes, but such a tail occurs as a transitory structure in the larval stages of the existing Lampreys.

The flexible body and fusiform shape suggests that the Anaspids must have been good swimmers, and probably lived at or near the surface of the water. Of very different shape are the members of the next group, the *Cephalaspida*, occurring in the Upper Silurian and Lower Devonian rocks. These were first discovered in the British Isles, the finest specimens of the characteristic genus *Cephalaspis* occurring in Forfarshire and the west of England, while others are found in Europe and Canada. Quite recently remains of these fishes have been excavated in Spitzbergen, and some of these are so perfectly preserved that it is possible to make out their internal anatomy almost as accurately as if fresh specimens were available for dissection. Like other fossil Marsipobranchs, the Cephalaspids were of smallish size, few of them exceeding a length of a few inches. The head is flattened and covered over with a large bony shield, rounded in front, and with the hinder corners generally produced to form pointed "horns" (Fig. 123c). The body is sheathed in numerous hard, bony plates, not unlike those of the Anaspids, arranged in regular rows, those on the sides being high and narrow. Beneath the head-shield there is an internal skeleton, at least partly composed of bony tissue, and all the blood-vessels and nerves penetrating this or lying in contact with it are contained in hard limy tubes, which are preserved in the fossils. Owing to this wonderful state of preservation of anatomical details, coupled with the immense

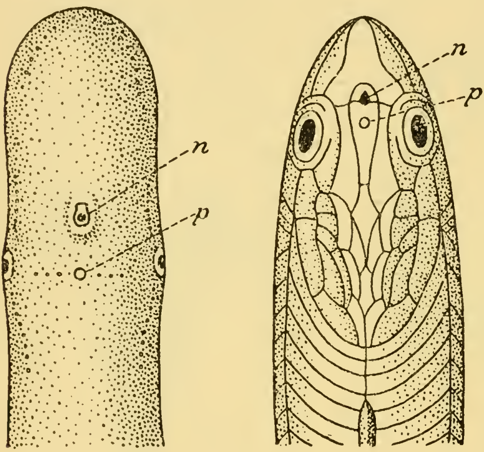


Fig. 124.

Head of *Rhyncholepis* compared with that of Lamprey (*Lampetra*) ; *n.*, nostril ; *p.*, pineal organ. (After Kiaer.)

skill and patience displayed by Dr. Stensiö, who has made a special study of these remains, it is possible to see that the arrangement of the nervous and vascular systems bears some marked resemblance to that of existing Cyclostomes. Dr. Stensiö believes that the very large nerves which extend upwards and outwards from the hinder part of the brain supplied electric organs, probably embedded in the head-shield. On the lower surface of the shield is a series of separate gill-openings on each side, and from the evidence supplied by markings on the inner side of the shield it appears certain that the gills themselves were contained in pouches. An important feature of these structures is the position of the first pair of pouches, which is in advance of that occupied by the jaws in other vertebrates. The significance of this becomes clear when it is considered that in the Selachians and Bony Fishes the modification of one pair of gill-arches into biting jaws has entailed the disappearance of the gills in front of them, and it follows, therefore, that the Cephalaspids cannot have possessed true jaws, nor can they have been descended from animals with such jaws. As in the Anaspids, there is a single nostril in the middle of the upper surface of the head-shield. In the auditory region there are only two semicircular canals, as in the existing Lampreys, the horizontal canal of other fishes being undeveloped. A study of the development of the Lamprey provides still more evidence of its relationship to these Palaeozoic forms, for the plate of so-called mucous cartilage which arises in the head region of the larva corresponds remarkably closely, both in form and position, with the head-shield of *Cephalaspis*—a very striking example of recapitulation! The Cephalaspids were doubtless sluggish creatures that lived on the bottom, and in their shape and manner of life bear much the same relationship to the Anaspids as do the Rays to the Sharks. Towards the middle of the Devonian they gradually decreased in abundance, became comparatively rare during the latter half of that period, and finally became extinct before the beginning of the Carboniferous. The causes which led to their disappearance from the face of the earth must remain a matter for speculation, but several similar cases occur in other groups of fishes, where elaborate, clumsily built, over-armoured creatures have quite suddenly died out, giving place to less specialised and less protected, but more active forms.

The last sub-class of Palaeozoic Marsipobranchs, the *Heterostraci*, likewise occur in Silurian and Devonian strata. They have the head and trunk enclosed in bony plates, those on the hinder part of the body being small and having the general appearance of scales. The best-known genus is *Pteraspis*, in which the form of the mouth has been recently made out. This is a transverse slit on the lower surface of the head, surrounded by bony plates bearing minute denticles, but with no trace of any structures that might be interpreted as true jaws. Unlike the other two sub-classes, the gills open to the exterior by a single aperture on either side, as in some of the existing Hag-fishes (*Myxine*), and the nostrils are paired—a primitive feature. Several curious types of *Heterostraci* have been described, some of them box-like, with broad rounded snouts and short thick tails (Fig. 123B), others with the head-shield prolonged to form a pointed rostrum. Their generally flattened form and rigid head and trunk are evidence of sluggish habits, and they probably lived, like the Cephalaspids, at or close to the bottom.

Before leaving the Marsipobranchs mention may be made of a curious little organism found in large numbers in the Caithness Flagstones (Lower Devonian) near Thurso. This is generally an inch or two in length, and has been named *Palaeospondylus gunni*. The fossils are well preserved, and this creature can be seen to have a circular mouth surrounded by barbels, and to possess no traces of jaws or paired fins, features which have led to its being associated with the Cyclostomes. At the same time, however, the caudal fin is large, with elaborately bifurcating supports, the vertebrae are stout and ring-like, and the skull complex, with what appear to be relatively enormous auditory capsules. On the whole, its affinities with the Lampreys are *non proven*, and *Palaeospondylus* must be regarded as one of the puzzles of palaeontology as yet unsolved.

Before passing to the Selachians proper, another interesting group of extinct fishes is worthy of consideration. Their remains occur in Devonian and Lower Carboniferous strata, and their anatomy has been recently elucidated by Dr. Stensiö. They were formerly regarded as archaic Lung-fishes, but it is now certain that they are in no way related to the Bony Fishes, but represent an independent offshoot from the main stem of primitive Sharks, a stem which became extinct during the early part of the Carboniferous period. They might well be placed in the class of Selachians, but it is perhaps better to regard them as constituting a distinct class, the Placoderms, of which two sub-classes may be recognised, *Arthrodira* and *Antiarcha*. These fishes have a stout external skeleton of bony plates, a character at once distinguishing them from the Selachians, but the underlying skull and brain are essentially Shark-like. A curious feature is the presence of a joint or hinge in the neck region, the armour of the head and trunk being quite distinct, and the head consequently freely movable on the body. The Arthrodires have a somewhat large mouth, armed with formidable crushing or cutting teeth. Pelvic fins can be seen in some specimens, but the pectorals may or may not have been developed. Like many other archaic fishes, the front part of

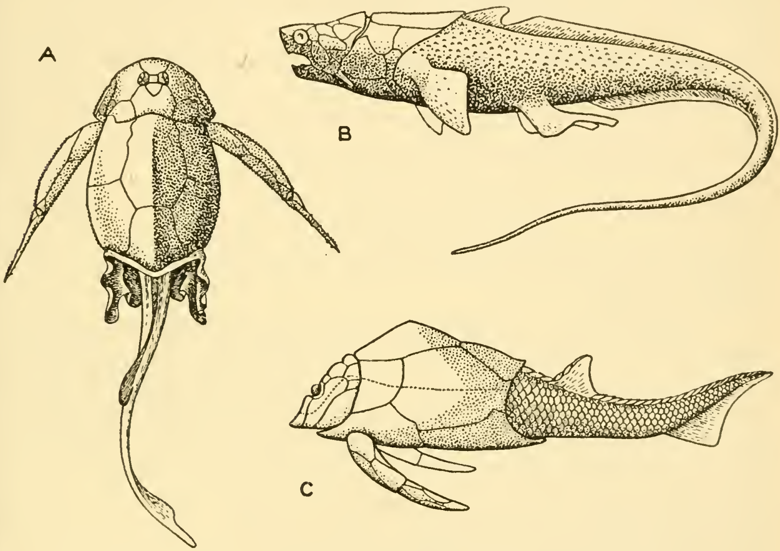


Fig. 125.—RESTORATIONS OF PLACODERMS.

A. *Bothriolepis canadensis*, × ¼. (After Patten); B. *Coccosteus decipiens*, × ⅙. (After Jaekel); C. *Pterichthys milleri*, × 1½. (After Traquair.)

the body is heavily cuirassed, but the hinder part is quite unprotected. *Coccosteus* is perhaps the most familiar genus, a comparatively small fish, occurring in Europe and particularly abundant in the Old Red Sandstone of Scotland (Fig. 125B). The members of this genus varied in size from about twelve to eighteen inches in length, but certain Arthrodires (*Dinichthys*, *Titanichthys*) from North America rival some of the largest of the existing Sharks, attaining to a length of twenty feet or more. The great variation in the form and dentition of these fishes suggests that their habits were equally varied, and the group includes fusiform pelagic types as well as flattened ray-like creatures.

Even more remarkable are the members of the sub-class *Antiarcha*, of which *Pterichthys* from the Old Red Sandstone of Scotland and the Devonian rocks of Eifel, and *Bothriolepis* of North America, are characteristic genera. The mouth is small, the eyes are placed close together on the upper surface of the head, there are no pelvic fins, and at the front end of the body there is a pair of curious two-jointed and freely movable appendages, not unlike the limbs of a crustacean in appearance, which are entirely without parallel in vertebrate animals (Fig. 125A, C). Each of these appendages is quite hollow inside, and is encased in a number of bony plates. Their function remains problematical, and it is by no means certain that they correspond to the pectoral fins of other fishes. These rather grotesque creatures, bearing a curious resemblance to turtles, must be regarded as being in the nature of fantastic evolutionary experiments, which flourished for a time, but were doomed to extinction under stress of competition with later developed types.

The origin of the Selachians is obscure, and our knowledge of the early history of this class is based only on a large number of fragmentary remains and a few well-preserved skeletons. The earliest traces of these fishes take the form of isolated spines, or ichthyodorulites, as they are sometimes called—teeth, dermal denticles and the like, from the Upper Silurian and Lower Devonian rocks, interesting enough in themselves, but giving no clue to the structural features of their owners. Their diversity, however, is evidence that there must have existed, even at this period, a wealth of genera and species, and that the Selachians had already been in existence for a long time. The late Professor Bashford Dean suggests that they probably reached the zenith of their differentiation in the Carboniferous period, "when specialised sharks existed whose varied structures are paralleled only by those of existing bony fishes—sharks fitted to the most special environment; some minute and delicate; others enormous, heavy, and sluggish, with stout head and fin spines, and elaborate types of dentition." In the most recent classification, the group of Selachians is divided into five main sub-classes, but it may be necessary to erect a sixth to include a remarkable Shark (*Cratoselache*) recently described from the Carboniferous rocks of Belgium. The first three sub-classes contain only extinct forms, the fourth, the *Euselachii*, includes all the existing Sharks and Rays, and the fifth, the *Holocephali*, the Chimaeras, and their allies.

The best-known member of the first sub-class, the *Pleuropterygii*, is *Cladoselache*, occurring in the Upper Devonian strata of Ohio. Besides being one of the more complete of the oldest fossils, this Shark is by far the most primitive yet discovered, and may be regarded as ancestral to most of the later types. It varies in length from two to six feet, and in shape and general appearance is not very unlike a modern Shark (Fig. 23D). The mouth, however, is terminal, and the teeth closely resemble the dermal denticles of the skin. The paired fins are little more than balancers, have broad bases, and may be looked upon as the remnants of once continuous fin-folds (*cf.* p. 55). The internal structure of these fins is equally primitive (Fig. 25), the basal elements of the pelvics being quite separate, and the pectorals are scarcely more advanced in structure. These broad-based, pointed fins, taken in conjunction with the strongly heterocercal tail, suggest that *Cladoselache* was a pelagic Shark and a strong swimmer. Unlike all the existing Selachians, there are no "claspers."

Numerous and diverse fragments of the members of the next sub-class, the *Acanthodii*, occur in the strata from the Upper Silurian to the Lower Permian, but more complete or well-preserved remains are comparatively rare. Each of the fins of these Sharks, both paired and unpaired, has a strong spine at its anterior edge, and in the genus *Climatius* from the Lower Devonian of Forfarshire there is a row of spines on each side of the body between those supporting the pectoral and pelvic fins, providing additional evidence as to the existence of continuous lateral fin-folds in their ancestors (Fig. 23E). The body is encased in an elaborate armour, the dermal denticles having been modified to form a closely fitting mosaic of minute, flat, diamond-shaped scales, and some of these in the region of the head have become fused to form a series of separate bony plates for the protection of the skull. The teeth are few in number and degenerate in structure. The known fossils are all of small size, and, like the members of the preceding group, show no trace of "claspers." These Sharks cannot be regarded as ancestral to any of the existing forms, but are rather a highly specialised and terminal branch springing from near the base of the Selachian "tree." Their extreme specialisation, coupled with their small size, may have been the cause of their comparatively early extinction.

The third sub-class, the *Ichthyotomi*, is distinguished by the presence of "claspers," a feature that suggests that these Palaeozoic forms and the existing Selachians sprang originally from a common stock. *Pleuracanthus* is the best-known genus, and well-preserved skeletons have been found in the Carboniferous and Permian rocks of Europe, Australia, and North America. Although Shark-like in many respects, there are certain features in which it bears some resemblance to the Bony Fishes. It has a long dorsal fin, two small anals, and a long tapering tail, fringed above and below by a continuous caudal fin (Fig. 126). The paired fins are unique among Selachians, being paddle-shaped, and with the supporting basals forming a jointed central axis with the radials arranged on either side (Fig. 25). Dermal denticles, as such, do not appear

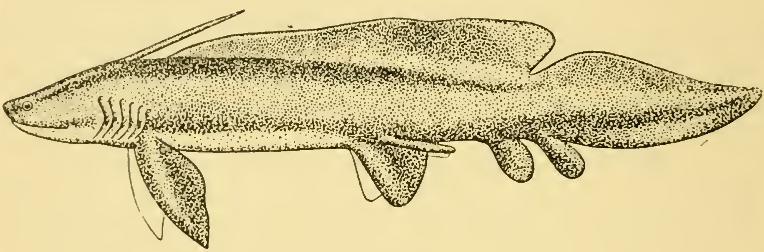


Fig. 126.

Restoration of *Pleuracanthus gaudryi*, $\times \frac{1}{6}$. (After Hussakof.)

to be present, those on the head region having been transformed into roofing bones for the skull. The mouth is terminal and the teeth shark-like. A curious feature is the presence of a long median spine projecting from the back of the head. In size, *Pleuracanthus* ranged from eighteen inches to six feet or more, and the form of the fins and tail suggests that it was a slow swimmer and lived at or close to the bottom.

No remains that can definitely be ascribed to the members of the sub-class *Euselachii* have yet been discovered in rocks earlier than those of the Triassic period, but many of the fragments of teeth and spines from Carboniferous and Permian strata may have belonged to such Sharks. All the families of existing Selachians, with the sole exception of the Blue Sharks and their allies (*Carcharinidae*) and the Sting Rays (*Trygonidae*), include genera which have been found fossil in Cretaceous rocks, and such specialised forms as the Monk-fish (*Squatina*) and Guitar-fish (*Rhinobatus*), as well as the Comb-toothed Sharks (*Hexanchidae*), Bull-headed Sharks (*Heterodontidae*), and some of the Dog-fishes (*Scyliorhinidae*), date back to the Jurassic period. Indeed, so little have some of these changed in course of time, that well-preserved remains of *Squatina* or *Rhinobatus* from the Lithographic Stone (Jurassic) of Bavaria are almost indistinguishable from their descendants of the present day. The curious Elfin Shark (*Scapanorhynchus*) was first found in a living condition in deep water off Japan in 1898, but the same genus had long been known from fossil remains in the Cretaceous rocks. An interesting Shark (*Protospinax*) has recently been described from the Jurassic, and seems to bear the same relation to the Saw Sharks (*Pristiophoridae*) as does the Guitar-fish (*Rhinobatus*) to the ray-like Saw-fishes (*Pristidae*). It has a pointed rostrum, not yet armed with teeth at the sides, but, apart from the more primitive character of the median fins, it is very like the Saw Sharks, to which it was probably ancestral.

The *Holocephali* also date from the Triassic period, and reached their zenith during the Cretaceous and Eocene. Some of the Devonian and Carboniferous ichthyodorulites may have belonged to ancient members of this sub-class, but this is by no means certain. The comparatively few existing Chimaeras, etc., may be looked upon as the degenerate descendants of an important group, the members of which were once numerous and diverse. The living forms rarely exceed a length of three or four feet whereas the extinct genus *Edaphodon* attained to relatively gigantic proportions.

As in the case of the Selachians, little is known of the actual beginnings of the class of Bony Fishes (*Pisces*), although it is fairly certain that these arose as an offshoot from the primitive Sharks at some time during the Silurian period. A modern taxonomist divides the Pisces into three main groups or sub-classes: *Palaeopterygii* (ancient fins), *Crossopterygii* (fringed fins), and *Neopterygii* (new fins). The differences between them are of a technical nature, involving the form of the skeleton and scales and the structure of the fins. It may be noted that, as far as the living representatives are concerned, the three groups are vastly different in size: the first and second together include some ten existing genera with less than fifty species all told, whereas the Neopterygian sub-class contains numerous genera and probably at least fifteen thousand species. In the past, however, at a time when the modern Bony Fishes had not yet come into existence, the first two sub-classes were spread all over the world, and were represented by a large number of species and individuals. The fact that during the Devonian period these groups were already represented by several diverse forms, suggests that the Pisces had had a long history, even at this time, and had undergone considerable differentiation.

The earliest members of the *Palaeopterygii* were a family of fishes known as Palaeoniscids, which had their beginnings in the Lower Devonian, attained their maximum development during the Carboniferous and Permian periods, and finally became extinct towards the end of the Jurassic. They ranged over the major part of the globe, fossil remains having been found in the British Isles, various parts of Europe, South Africa, Australia and North America. The *Palaeoniscidae* exhibit such a combination of what may be regarded as primitive features that they may be looked upon as the ancestors of all other Bony Fishes, with the exception of the Crossopterygians. They are mostly elongate fishes, fusiform in shape, with a large heterocercal tail and a single dorsal fin (Fig. 127A). The body is ensheathed in a complete armour of small, closely fitting, diamond-shaped, ganoid scales, the shining surfaces of which are often elaborately sculptured; the head is protected by a series of bony plates. The mouth is rather large, and usually armed with sharp, pointed teeth, while above it projects a short and blunt snout. From their general build there can be little doubt that some of these were fast-swimming, predaceous fishes.

During the Carboniferous period a branch of the Palaeoniscids gave rise to the *Platysomidae*, which flourished with them until late Permian times. They are of very different shape, with a deep, compressed body, larger dorsal fin, smaller mouth and blunt, crushing teeth: the scaly covering of the body is still of the ganoid type (Fig. 127B). These fishes held their own for an enormous period of time, but their record is actually a shorter one than that of the parent stock from which they sprang, and they do not appear to have given rise to any later forms. Another offshoot (*Catopteridae*) from the Palaeoniscids during the Triassic period, are small fishes found in the rocks of North America, Europe, Africa, and Australia. The same ganoid armour still persists, but the upturned end of the tail is very much shorter. The *Belonorhynchidae* also arose from the main stem during this period, and these are characterised by the very long snout and lower jaw, and by the disappearance of nearly all the ganoid scales, which are replaced by four rows of scutes running along the body, rather like those of the existing

Sturgeons (*Acipenseridae*). Unlike the other families mentioned above, some of which survived until the Cretaceous, the Belonorhynchids died out during the Jurassic period. As the *Palaeoniscidae* were approaching extinction during the Liassic or Lower Jurassic epochs, their place was taken by another family, the *Chondrosteidae*, arising from the main Palaeoniscid stem and eventually leading on to the living Sturgeons, which

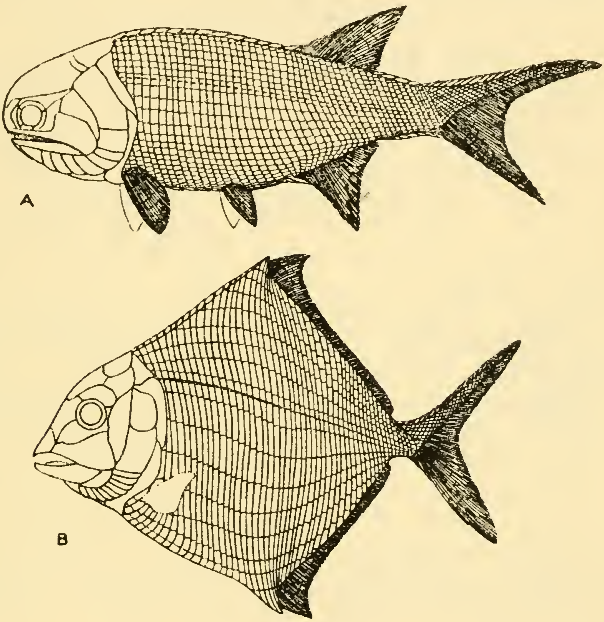


Fig. 127.—PRIMITIVE PALAEOPTERYGIANS.

A. Restoration of *Stegotrachelus finlayi* (Palaeoniscidae), × $\frac{3}{4}$. (After Woodward and White); B. Restoration of *Cheirodus granulosus* (Platysomidae), × about $\frac{1}{2}$. (After Traquair.)

first made their appearance during the Tertiary era. Here again the ganoid scales have undergone considerable degeneration, and, apart from the presence of a series of branchiostegal rays and one or two other minor characters, *Chondrosteus* and its allies are not very unlike their existing descendants.

The Bichirs (*Polypterus*) and their eel-like relative (*Calamoichthys*), which live in the rivers and swamps of tropical Africa, and are the only existing members of the last Palaeopterygian order, the *Cladistia*, were, until quite recently, regarded as belonging to the next sub-class, but in the presence of ganoid scales, and in the form of the head-skeleton, pectoral arch, etc., they bear a marked resemblance to the Palaeoniscids, from which they are probably descended. Unfortunately, no fossil remains connecting the Bichirs with their Palaeozoic forebears have yet been discovered.

The Palaeopterygian Bony Fishes were dominant during Palaeozoic times, held on during the Mesozoic era, during which nearly all the orders became extinct, and are represented to-day by a few scattered remnants, such as the Sturgeons (*Acipenseridae*), Spoon Bills (*Polyodontidae*), and Bichirs (*Polypteridae*). The history of the sub-class *Crossopterygii* followed exactly the same course, the surviving members being the three genera of Lung-fishes found to-day in Australia, Africa and South America respectively. Three orders of Crossopterygians may be recognised, of which the first two, the *Rhipidistia* and *Actinistia*, contain only extinct forms, while the last, the *Dipneusti*, includes the existing Lung-fishes as well as a number of fossil genera. Representatives of the first and last of these orders were already in existence in the Middle Devonian epoch, and were contemporaneous with the earliest Palaeoniscids.

The *Rhipidistia* occur in Devonian and Carboniferous strata, and include a family, the *Osteolepidae*, the members of which are of particular interest as representing the probable ancestors of the four-footed, terrestrial vertebrates. The paired fins are rounded and lobe-like, the body is covered with ganoid scales, and the teeth in the jaws are of simple form. In the arrangement of the bones of the skull these fishes present certain resemblances to the earliest known Amphibians, and it is not very difficult to see how their pectoral fins might have been converted into five-toed limbs. The characteristic genus, *Osteolepis*, occurs in the Old Red Sandstone of Scotland, other members of the family being found in the rocks of Europe and North America. A closely related family, *Holoptychiidae*, shows the same heterocercal tail and two small dorsal fins, but the pectorals have a long, blade-like form, and the ganoid scales have given place to overlapping cycloid scales (Fig. 128A). *Holoptychius* was widely distributed in the Devonian period, remains occurring in the British Isles, Europe, Greenland, and North America. A portion of a slab from the Old Red Sandstone of Scotland, preserved in the British Museum, contains a large number of remains of these fishes, lying so close together as to suggest that they must have been simultaneously overwhelmed by some sudden catastrophe, and their bodies rapidly interred by the settling of vast quantities of sediment. The *Rhizodontidae* represent another allied family, but the teeth are of a still more specialised pattern and the scales of the cycloid type. The genus *Eusthenopteron* (Fig. 128B) also shows many Amphibian-like characters, and has the curious double tail (see below).

The second order, the *Actinistia*, includes a number of specialised fishes derived from the *Rhipidistia*. The *Coelacanthidae* are interesting forms, which, according to Sir Arthur Smith

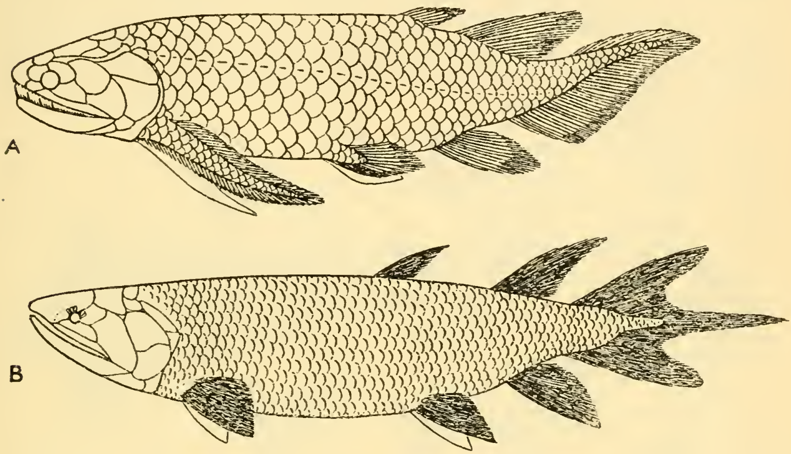


Fig. 128.—PRIMITIVE CROSSOPTERYGIANS.

A. Restoration of *Holoptychius flemingi* (*Holoptychiidae*) $\times \frac{1}{8}$. (After Traquair); B. Restoration of *Eusthenopteron fordi* (*Rhizodontidae*), $\times \frac{1}{6}$. (After Whiteaves.)

Woodward, enjoy the distinction of having "perhaps the most remarkable range of all known extinct fishes, occurring almost unchanged throughout the whole series of formations from the Lower Carboniferous to the Upper Chalk." The genus *Coelacanthus* is found in the Carboniferous or Permian rocks of England, Scotland, Europe, and North America, and other important genera include *Undina*, a Jurassic fish (Fig. 129), *Diplurus* from the Carboniferous of North America, and *Macropoma* from the Cretaceous of England and Europe. The double nature of the tail in *Undina* and *Diplurus* has been described in detail in an earlier chapter (*cf.* p. 62). The scales of the Coelacanths are cycloid, the paired fins rounded and lobe-like, and an important feature of their internal anatomy is the transformation of the walls of the air-bladder into bony tissue. Quite recently one of these fishes was described, in which the remains of several embryos could be seen *in situ*, thus indicating that the manner of reproduction was viviparous.

The *Dipneusti* may be readily distinguished by the character of the teeth, which take the form of a pair of large plates with coarse ridges situated on the roof of the mouth, and a similar plate on the inside of each lower jaw (Fig. 130). Like the *Rhipidistia* they flourished throughout the Palaeozoic era, but dwindled during the Triassic period, from which time onwards they were represented by forms not very unlike the existing Lung-fish (*Epiceratodus*) of Australia (Fig. 99C). One of the earliest members of the order is the interesting *Dipterus*, found

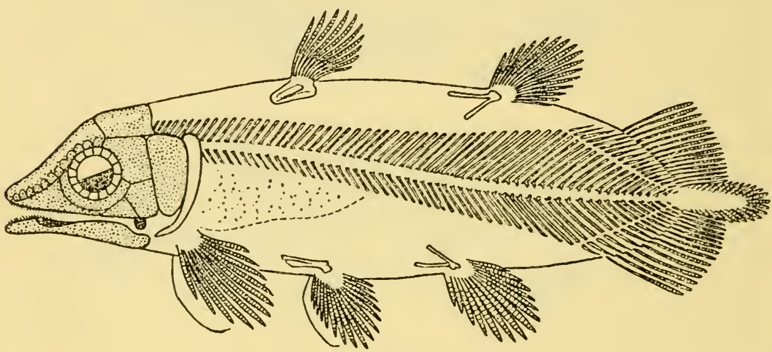


Fig. 129.

Restoration of *Undina gulo* (Coelacanthidae), × about $\frac{1}{7}$. (After Woodward.)

in the Old Red Sandstone of Scotland along with the early Rhipidistians and Palaeoniscids. In the ganoid scales, heterocercal tail and two dorsal fins, this fish resembles the Osteolepids, and the head is covered with a number of small bones. The later Lung-fishes of the *Ceratodus* type appear to have been almost world-wide in their distribution during the Triassic period, teeth and other fragments having been found in England, Europe, South Africa, India, and North America. The surviving Australian genus (*Epiceratodus*) occurs only in the fresh-water portions of the Burnett and Mary Rivers of Queensland, but the presence of teeth of this genus in the later Tertiary deposits of New South Wales indicates a wider distribution in comparatively recent times. The other existing Lung-fishes were probably derived from some form like *Ceratodus*, but no remains have yet come to light which give any clue to the lines of descent of these more specialised types.

The cartilaginous nature of a large part of the skull, coupled with the continuous median fins and the apparently symmetrical tail, led many of the older authorities to suppose that the existing Lung-fishes were the most primitive members of the group, and more nearly related to the ancestral stock than the Palaeozoic forms, like *Dipterus*, which were regarded as highly specialised offshoots. More recently, however, Professor Dollo has shown fairly conclusively that evolution has taken place in exactly the opposite direction. The existing Lung-fishes, according to his view, have been derived from the archaic forms by a process of gradual degeneration, accompanied also by some specialisation, and they appear to stand in much the same relation to the *Dipterus*-like forms as do the Sturgeons to their Palaeoniscid ancestors. Commencing with *Dipterus*, it is possible to select a series of genera, living and fossil, which not only fall into place in the scale of geological time, but at the same time illustrate the probable line of descent of the living forms.

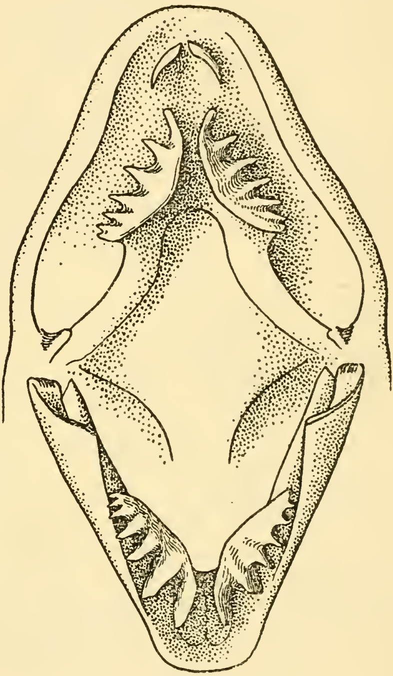


Fig. 130.
Jaws and teeth of the Australian Lung-fish (*Epiceratodus forsteri*), $\times \frac{1}{2}$.

In addition to the reduction in the number of dermal bones of the skull, other features of degeneration (or specialisation) are exhibited by the gradual assumption of a more eel-like shape, the extension of the median fins and their union to form a continuous fold round the hinder end of the body, the change in the tail from a heterocercal to an outwardly symmetrical form, and the replacement of ganoid plates by thin, cycloid scales. In the existing African (*Protopterus*) and South American (*Lepidosiren*) Lung-fishes the story has been carried a step or two further, the body being even more eel-shaped, the paired fins reduced to whip-like vestiges, and the small scales so much embedded in the skin as to be invisible externally (*cf.* Figs. 99A, B).

The sub-class *Neopterygii* had its origin in later Permian times, and includes the vast majority of the Bony Fishes living to-day. The main orders and sub-orders into which these fishes are grouped will be discussed in the next chapter, and it must suffice here to describe very briefly some of the earlier families, and to indicate their relationship to the more generalised of the modern Bony Fishes. The earliest family is represented by the *Semionotidae*, which flourished during the Triassic and Jurassic periods. They seem to have sprung from the Palaeoniscid stem, and although there are a number of differences between the two types, Dr. Regan has suggested that nearly all these can be interpreted as being related to a change in the mode of life. The Palaeoniscids, it will be remembered, were active, predaceous fishes, with a large mouth and strong teeth, whereas the Semionotids were comparatively slow swimmers, feeding at the bottom on shell-fish and the like, and had a small mouth armed with teeth of a more specialised type. Just as the differences in the mouths and dentition can be shown to be related to a change in the diet, so those concerned with the form of the skull, pectoral arch, median fins, etc., seem to be connected with a change in the swimming habits: at the same time, however, other differences, among which the structure of the scales may be mentioned, do not appear to be so related. The family includes a number of diverse genera from such widely separated localities as England, Europe, South Africa, India, Australia, and North America. Some had a typically fusiform shape, others were deep bodied: nearly all were covered with ganoid scales (Fig. 131A, B).

During Triassic and Jurassic times the Semionotids gave rise to a number of important offshoots, most of which flourished for some time, but all became extinct before or during the Cretaceous period, with the sole exception of the Bow-fin (*Amia*) and Gar Pikes (*Lepidosteus*), still living in North America. The *Pycnodontidae* were remarkable fishes, bearing a superficial resemblance to some of the modern File-fishes, with a deep body, small mouth and specialised crushing teeth. They ranged from the Jurassic to the Lower Eocene. The *Eugnathididae* were large mouthed, predaceous forms, which made their first appearance during the Triassic and flourished throughout the

Jurassic. They have a fusiform body, strong jaws armed with sharp teeth, and a forked tail (Fig. 131C). Many have a covering of ganoid scales, but in others these are replaced by thin, cycloid scales. From this family sprang the *Amiidae*, a tribe dating back to the Jurassic, and differing from the Eugnathids in the large dorsal fin, rounded tail, and thin, rounded, overlapping scales. The sole living representative of this family, the Bow-fin (*Amia*), is to-day confined to the fresh waters of North America, but this, or some nearly related species, has been found fossil in European strata as late as the close of the Lower Miocene

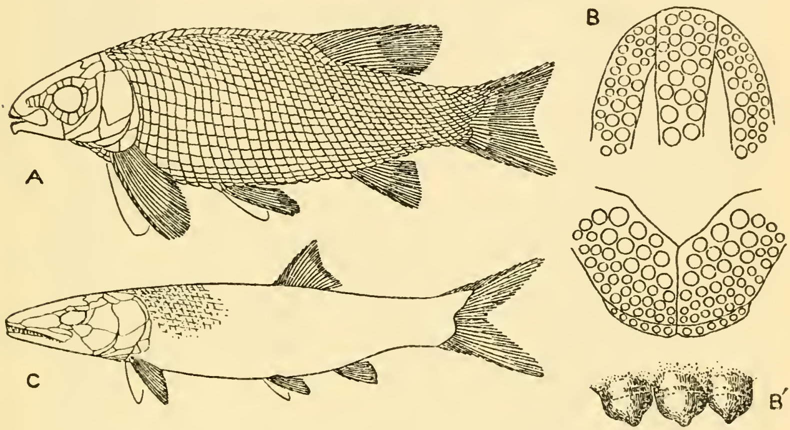


Fig. 131.—PRIMITIVE NEOPTERYGIANS.

A. Restoration of *Lepidotus minor* (Semionotidae), $\times \frac{1}{4}$; B. Dentition of *Lepidotus mantelli* . . . B′, three teeth enlarged; C. Restoration of *Eugnathus orthostomus* (Eugnathidae), $\times 1\frac{1}{4}$. (All after Woodward.) The scales have been omitted in figure C.

epoch. The *Pachycormidae* have also been derived from the Eugnathids, and were large-mouthed, predaceous fishes, not unlike the modern Mackerels (*Scombridae*) in appearance. The *Aspidorhynchidae* were long-bodied fishes, with the jaws prolonged to form a beak as in the existing Sword-fishes. These are not closely related to the Gar Pikes (*Lepidosteus*), as was formerly supposed, the latter having been derived from the main stem at an earlier period, and probably descended direct from the Semionotid stock. The Gar Pikes were abundant in Europe during the Eocene and Miocene periods, but to-day are confined to North America, where they made their appearance during the Eocene.

During the Jurassic period an offshoot of Herring-like fishes, the *Pholidophoridae*, arose from the Semionotid stem, and in general form and in the shape of the fins these bear a markedly close resemblance to the modern Herring-like fishes. The presence of minute teeth in the jaws indicates that these extinct forms were probably plankton-feeders. They gave rise towards the end of the Jurassic to another family, the *Leptolepidae*, the first Bony Fishes with a homocercal tail. These were very like the existing Ten-pounders (*Elops*), a genus abundantly represented in Cretaceous times, but now reduced to a few species, which are to be regarded as the most primitive of living Bony Fishes of the modern type. The *Leptolepidae* were the earliest members of the first of the great orders of modern Bony Fishes, namely, the *Isospondyli*, a group which includes all the Herrings, Salmon, Trout and their allies, as well as the Osteoglossids, Mormyrids, and other related forms. During the Cretaceous period this order underwent considerable evolution, and several important offshoots made their appearance, including the earliest members of the order *Iniomi* and the first Eels (*Apodes*), as well as the first spiny-rayed fishes in the form of primitive Berycoids. There is a slab of rock in the British Museum containing the remains of numerous individuals of one of these early Berycoids named *Hoplopteryx*, which are preserved in a most extraordinary manner, and seem to represent part of a shoal suddenly overwhelmed by some catastrophe. The fishes are lying one upon the other, their bodies frequently twisted or contorted in various ways, the mouths and gill-covers gaping wide, and the fins erect, conditions which suggest sudden asphyxiation (Pl. VI).

No true Perch-like fishes make their appearance until towards the end of the Cretaceous, but from this time onwards their evolution is very rapid. It will be impossible to follow the history of modern Bony Fishes any further here, especially as their geological history is often far from complete. It is known that most of the modern families began somewhere in the early part of the Eocene, for remains of Scorpion-fishes, Sucker-fishes, File-fishes, Mackerels, Sword-fishes, and Anglers have been found in the rocks of that period.

Plate VI.

Slab of Chalk (Sussex) with remains of *Hoplopteryx superbus*.

From a specimen in the British Museum (Natural History).

CHAPTER XVIII

CLASSIFICATION

Phylogenetic trees. Species and their origin. Races, sub-species, and varieties. Genera and sub-genera. Nomenclature. Classification of Marsipobranchs, of Selachians, of Bony Fishes.

Classification is the sorting of different kinds of individuals into groups of varying size and importance, and, as has been already pointed out, the classifications of most of the older naturalists were necessarily of an artificial nature. They were well aware of the existence of natural affinities, and of the fact that individuals fall naturally into groups, which in turn may be linked together into larger categories, and so on, but the units of classification which they used remained convenient pigeon-holes and little more. The doctrine of evolution has changed all this, and the modern systematist endeavours to arrange his animals into groups which are in accord with their natural relationships. Such a classification may be visualised as a tree, and the mere fact that living organisms can be arranged in this manner provides striking evidence in support of the view that they themselves have been produced by tree-like evolution. The roots of such a genealogical or phylogenetic tree are deeply buried far back in geological time, and in each succeeding period of the earth's history its branches have become more and more ramified. The existing fishes are represented by the topmost and youngest twigs of the fish "tree," and in spite of the knowledge of the past provided by a study of the fossils, most of the branches connecting the living twigs with the lower parts of the tree may be said to have died out, leaving little, if any, trace of their former existence. It is this dying away of the older parts of the tree, the connecting links, as it were, that makes it possible to sort the living fishes into groups, for if it were possible to examine at one time all the individuals, both past and present, existing and extinct, each would be found to be linked up with the others by a complete series of small gradations. In the accompanying diagram of a typical "tree" the continuous black lines represent existing species, the dotted lines extinct stems and unsuccessful branches

(Fig. 132a). The branches marked A and B are totally extinct, while that marked C is moderately successful and represented at the present day by a few species. The remaining branches, D and E, have been most successful, and the topmost twigs show an abundance of closely allied living species. The second diagram (Fig. 132b) represents a part of one of these end branches in greater detail, and illustrates the manner in which species may become separated by the dying out of connecting links. Here the dark lines represent the separate individuals, and the enclosed areas are the limits of existing species. All the individuals within each of these areas, although differing from one another in minor characters, are fundamentally alike,

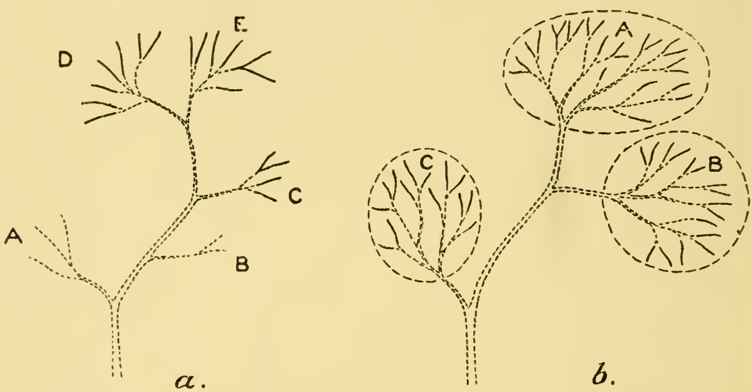


Fig. 132.

DIAGRAMS OF PORTIONS OF TYPICAL PHYLOGENETIC "TREES."
(For explanation see text.)

and the three groups of individuals shown in the diagram have become well differentiated by the dying away of the branches from which they sprang. Further, the two on the right, marked A and B, may be seen to diverge from a common stem at a point not very far down the tree, whereas that marked C joins the same branch at a point nearer to the base. The species A and B, therefore, might reasonably be expected to resemble each other more closely than either resembles C, and they are consequently to be regarded as representing one genus, while C forms another.

The lowest unit in any classification is, of course, the individual, and these must first of all be grouped into larger units or species. The Latin word *species* means literally a particular kind, and the average observer familiar only with the better known fishes will perhaps say that he experiences little difficulty in arranging these into more or less well-defined groups. He will be able to distinguish, say, a Roach from a Bream, Chub, or Barbel, and something in the general appearance of these fishes will suggest that they are fairly closely related to one another, but widely separated from such forms as the Salmon or Perch. The task of the systematist, studying every kind of fish from all parts of the world, is by no means as easy as this, however, and he may experience considerable difficulty in distinguishing the species in some groups of fishes, besides constantly coming across intermediate forms or connecting links between two species.

A great deal has been written, not only on the subject of what does and what does not constitute a species, but also on the very vexed problem of the manner in which new species first come into being. It is beyond the scope of this work to enter into such controversial matters in any detail, but since the term species has been used fairly frequently, some sort of explanation of its meaning seems necessary. Of the various definitions which have been advanced, that given by Dr. Tate Regan to the British Association during their meeting at Southampton in 1925 seems to come nearest to the truth, and is one which would probably meet with the approval of a large number of systematic zoologists. "A species," he says, "is a community or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name." By the term community is meant a collection of individuals such as occurs in nature, with similar habits, which live together in a certain area and breed freely with one another. It is assumed that all the individuals composing a species are mutually fertile and produce offspring more or less like themselves, and if this can be proved to be not the case it may generally be taken for granted that two or more species have been confounded with one another. It has been held by some authorities that sterility, in the sense of incapacity to produce fertile offspring when crossed with another form, is a definite test of true species as opposed to mere varieties, but it not infrequently happens that crosses between two forms which no systematist would hesitate to regard as other than distinct species produce fertile hybrids (*cf.* p. 339). Other attempts to draw up stricter definitions of a species have been equally abortive, and it seems certain that in a large number of cases the individual judgment of the scientific mind will always enter into the matter. This is inevitable, not only in the matter of species, but also in the definition of larger units, such as genera and families. In the main there may be said to be general agreement on these points, but it sometimes happens that a group of individuals regarded by one worker as a true species will be looked upon by another as a mere race or variety of another species; similarly, two groups regarded as species of a single genus by one, will be placed in distinct genera by another. It is the practice of most systematists to unite two species, formerly considered to be distinct, if intermediate connecting links should subsequently come to light, and the definition of a species given by the late Professor Dendy is quite in accordance with the view that the destruction of the connecting branches has played a large part in the separation of those groups of individuals to which the term is applied. "A species," he writes, "is a group of individuals that closely resemble one another owing to their descent from common ancestors, which has become more or less sharply separated from all other co-existing species by the disappearance of intermediate forms."

It is one of the fundamental characteristics of living organisms that no two are ever exactly alike, and it follows that even within the limits of a species, and quite apart from differences due to age, sex, and so on, there will be a greater or lesser degree of individual variation. Ignorance of the wide range of variation exhibited by some species often leads systematists to describe as distinct species what are in reality nothing more than extreme variations of a single form, and it is only when a more complete series of specimens is studied and intermediate forms come to light that such errors can be rectified. In the case of the European Trout, to quote a characteristic example, specific names have been given to the Phinock or Eastern Sea Trout (*Salmo albus*), the Sewen or Western Sea Trout (*S. cambricus*), the Great Lake Trout (*S. ferox*), the Loch Leven Trout (*S. levenensis*), the Brook Trout (*S. fario*), the Gillaroo of Ireland (*S. stomachius*), and the Welsh Black-finned Trout (*S. nigripinnis*), among others, but in spite of the differences in size, form, colour, number of caecal appendages to the stomach, nature of the vomerine teeth, etc., a complete series of transitional forms has now been traced between the Brook Trout and the anadromous Sea Trout, and most modern authorities are agreed in regarding all the Trout found in the British Isles as belonging to a single very variable species. In the same way, most anthropologists regard all living races of mankind as representing one species of *Homo*, to which the name *Homo sapiens* is given, but supposing that all the races were to die out, with the exception of the European and the Bushman, these two types would undoubtedly be placed in distinct species.

A species, therefore, is not, and never can be, a fixed, immutable unit, and no systematist living is able to lay down any rule as to the amount of difference required to recognise a species. He must inevitably be guided by conveniences and by the circumstances of the particular case that he happens to be studying. As Dr. Regan puts it: "In practice it often happens that geographical forms, representing each other in different areas, are given only sub-specific rank, even when they are well defined, and that closely related forms, not easily distinguished, are given specific rank when they inhabit the same area but keep apart." Moreover, the value of a particular morphological character, whether it be the form of the fins, the structure of the scales, or the colour pattern, differs enormously in different families or orders, and a character which serves to distinguish two species of, say, Cyprinids, may be of sufficient importance to separate two genera of Cichlids. In spite of the huge collections preserved in some of the great national museums of the world, many of the species known to science have been described on the basis of one or two specimens, sometimes young, sometimes poorly preserved, and it is not until every species is represented by a complete series of examples illustrating its geographical range, variation, growth, seasonal changes, sexual differences, and so on (a highly Utopian and improbable state of affairs), that any sort of finality is to be expected. As it is, almost every new species discovered modifies in some way our conception of the relationship of the species already known, and it not infrequently happens that the discovery of one or two new forms leads to the complete reclassification of the genus, or even of the family to which it belongs.

Yet another unit of classification, the sub-species, may come between the individual and the species, and represents a community or group of related communities, whose distinguishing features are not of sufficient importance to entitle them to rank as a true species, but which, nevertheless, enable an expert to separate them from other nearly related communities. The different forms of Char (*Salvelinus*) found in the lakes of Switzerland, Scandinavia, and the British Isles, are probably to be looked upon as sub-species of the widely distributed Alpine Char (*S. alpinus*), which is a migratory fish in the Arctic Ocean. Here again, however, it must be remembered that some systematists would regard many of the lacustrine Char as distinct species, the only drawback to such a view being that once one starts giving specific names to such forms, there is no knowing where the matter will end. To turn to another example, recent research has shown that several of our important food-fishes, such as the Herring (*Clupea harengus*) and Plaice (*Pleuronectes platessa*) can each be split up by experts into a number of races, each with its own slight morphological peculiarities, area of distribution, and time and place of breeding. The differences between the races are sometimes so slight that the different forms can only be distinguished when a large number of examples are examined. Such races have not yet received sub-specific names, but they are of exactly the same nature as the lacustrine Char, and it may be concluded that in general the terms "race" and "sub-species" mean one and the same thing, the differences between them being only of degree.

It sometimes happens that certain individuals of a species differ from the normal or mean to a greater or lesser extent, but such differences are not found among a particular community, nor are they related in any definite way to the habits of the fish or to its environment. For example, among the individuals of a species characterised by its uniform coloration there may be some which exhibit a black spot on the head or a series of dark bars on the sides of the body. The name varieties may be given to such individuals, although this term has been used by some authors in a totally different sense. Well-known examples of varieties are the Gold-fish, Golden Carp, Mirror Carp, Leather Carp, Golden Trout, and so on.

So much for the lower units of classification. It is not sufficient, however, to group the individuals together into species, but the species must in their turn be arranged to form genera. Again, there can be no hard and fast rule as to the morphological differences necessary to distinguish one genus from another, it being entirely a matter of convenience and individual opinion; and it will sometimes happen that one worker will split up into a number of genera a group of species which another systematist would assign to a single genus.

The common Salmon and Trout are species belonging to the genus *Salmo*, and the species of Salmon and Trout found on the Pacific coast of North America are included within the same genus: the latter, however, form a group apart, distinguished from their European relatives by certain skeletal and other characters, and the mutual relationships of all the species are best expressed by regarding the Pacific forms as belonging to a distinct sub-genus, to which the name *Oncorhynchus* is applied. Thus, the Rainbow Trout of America is known by the scientific name of *Salmo* (*Oncorhynchus*) *irideus*, and the Atlantic Salmon as *Salmo* (*Salmo*) *salar*. Genera are, in their turn, grouped into families, separated from one another by morphological features of more fundamental importance, with sub-families as half-way groups where necessary. The Salmon and Trout (*Salmo*), the Char (*Salvelinus*), the White-fishes (*Coregonus*, *Leucichthys*, *Argyrosomus*), the Grayling (*Thymallus*), etc., constitute the family *Salmonidae*. Families are grouped into sub-orders and orders, orders into sub-classes and classes, classes into sub-kingdoms and kingdoms. There are only two kingdoms, animals and plants, but even here no sharp line of distinction can be

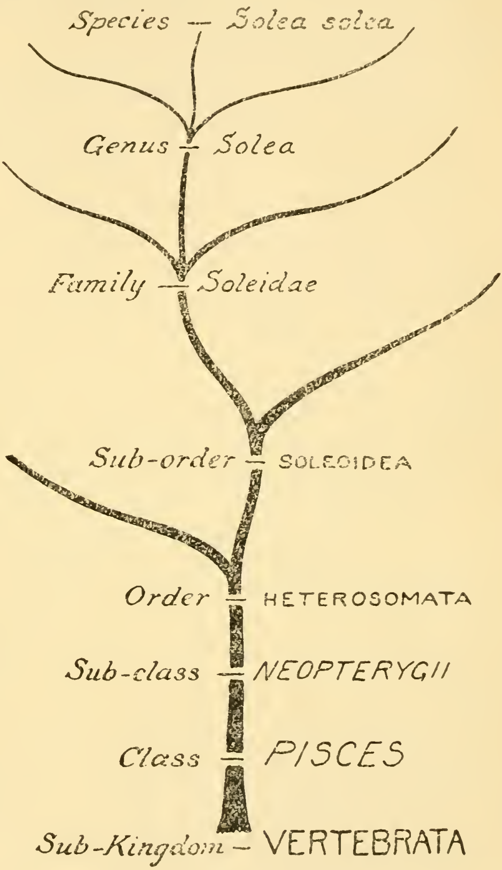


Fig. 133.

Diagram to show the systematic position of the Common Sole (*Solea solea*), illustrating the principles of classification.

drawn, for there are certain lowly forms of life which might equally well be described as animal or vegetable. The accompanying diagram (Fig. 133) illustrates these divisions, and represents a mere fragment of the taxonomic tree of living organisms which is intended to show the systematic position of a single fish, the Common Sole (*Solea solea*).

The question of nomenclature is an important one, and unfortunately there is still considerable diversity of opinion as to the correct scientific name to be applied even to our commonest food-fishes. It may well be asked why it should be necessary to give scientific names at all. The reason is that vernacular or common names, although convenient, are by no means precise, and are frequently used in a very loose manner. The same name may be given to two or more totally different fishes in different parts of the country or in various regions of the world; or, as is even more common, the same species may be known by quite different names in various localities. The name "whiting," for example, is not only applied to the well-known food-fish of the Cod family (*Gadus merlangus*), but also to various kinds of fresh-water fishes. Conversely, the following names, among others, are all used for the Sea Trout (*Salmo trutta*) in various parts of the British Isles, while the non-migratory members of this very variable species have received as many vernacular names again: Orange Fin, Black Tail, Phinock, Salmon Trout, Truff, Scurf, Sewen, Bull Trout, Grey Trout, and Round Tail. The names of Peal and Bull Trout are used in some parts of the country for the Trout (*S. trutta*), but in others to the Salmon. Another good reason for the use of scientific names is the fact that of the fifteen thousand odd species of fish known to-day probably less than half have a common name in any language. There are nearly a hundred species of Cichlids in Lake Tanganyika alone, but very few of them are distinguished by the natives under a particular name, and the same species will perhaps be given one name by one tribe and a totally different one by another. It is agreed, therefore, that, in order to obtain precision and to avoid any chance of confusion, it is necessary to give every species of fish a scientific name. In the words of Dr. Regan, the name of an animal "is a clue to all that is known or that has been recorded in literature about its structure, habits, economic importance or anything else; without the correct name we are in the dark and the conclusions we arrive at may be founded on erroneous grounds." It not infrequently happens that two scientific men have published conflicting statements about the habits or anatomy of a particular animal, but it has subsequently turned out that they were really dealing with different species, their specimens having been incorrectly named. In just the same way, it is of real importance for the economic entomologist to know the correct name of the insect pest which is ravaging the crops of cotton or tobacco. Closely related species of insects may have very different life-histories, and unless the correct name of the species is known it is impossible to be sure as to the right method of attack.

The first and one of the greatest of modern systematists was the Swedish naturalist Linnaeus, who was born in 1707 and died in 1778. He was the first to adopt the system of what is known as binominal nomenclature, that is to say, of referring to every species by two names, its generic as well as its trivial name. This method was consistently applied by him for the first time in the tenth edition of his famous *Systema Naturae*, published in 1758, and by common consent systematists throughout the world have agreed to regard this year as marking the commencement of the scientific naming of animals. No account of any names given before this year is taken, for, except by accident, these were never binominal. It has been already pointed out that the same species has often received two or more different names, and the question naturally arises as to how the correct scientific name of a species or genus is to be fixed, so that a particular animal shall be known by the same name throughout the world. A code of rules has been drawn up by an International Commission on nomenclature for the guidance of systematic workers, so as to secure as far as possible uniformity of method. Among other rules, this lays down that generic and trivial names should be given either in Latin or in Latinised Greek, and that, above all, strict attention must always be paid to the law of priority, the name first given taking precedence over any other that may be proposed at a subsequent date. Further, no generic name may be used twice among animals, and no trivial name twice in the same genus. Thus, if a fish and a bird have inadvertently been given the same generic name, that which was proposed first would stand and the other must receive a new designation. In theory these rules would seem to be quite straightforward, but in actual practice a certain amount of confusion has arisen with regard to the names of some animals, which is due to a number of reasons. Two different systematists, perhaps in ignorance of each other's work, or with an erroneous conception of the limits of a variable species, may have successively described the same fish and each given it a different name, or may have given distinct names to what are mere variations of the same species. In such cases that name which was first published takes precedence, even should the later one be eminently suitable and perhaps provide a better description of the fish in question; this becomes what is known as a synonym of the first name. It sometimes happens that the second or later name for a species or genus has been in use among zoologists throughout the world for generations, and it is only later discovered that another name has priority; the question then arises as to whether it is more fitting to apply the strict law of priority and to revive some long buried and little known name to supplant one which is familiar to all and has been in constant use. It is in such cases that the greatest divergence of opinion exists, some workers using one name, some the other. Other factors which tend to lead to confusion are the description of different fishes under the same name, or the inclusion of two or more distinct forms in a description which purports to be that of a single genus or species, but such debatable points cannot be considered here.

As a general rule, the Greek form is used for generic names, the Latin adjectives being more commonly used for the names of species. The most satisfactory generic names are those giving some sort of description of the main features of the group in question, or drawing attention to the morphological character or characters that separate the group from its nearest allies. *Ostracion* (a little box) for the Trunk-fishes, *Catostomus* (inferior mouth) for a genus of Suckers, and *Alepocephalus* (scaleless head) for a genus of Smooth-heads, are examples of such names. Others have been given in honour of some scientific man, such as *Copeina* or *Copeichthys* (literally, Cope's fish) after Dr. Cope, or *Valenciennellus* after the French ichthyologist, Valenciennes. Some workers have been less scientific in their methods, constructing names by drawing letters out of a hat, or, as in the case of Dr. Leach, by anagrams on his wife's name, Caroline (*e.g. Cirolana*, *Conilera*, *Nerocila*). The trivial name may be descriptive, such as *brachycephalus* (short-headed), *macrognathus* (large jawed), *maculatus* (spotted), *fasciatus* (barred), and so on; it may be in honour of a person, often the traveller who discovered the species, such as *livingstoni*, *shackeltoni*, *forbesi*, etc.; or it may refer to the place at which the fish was first found, such as *japonicus*, *hispanicus*, *nigeriensis*, *brasiliensis*, etc.

The code of rules lays it down that a name is nothing more than a name, and cannot be ignored because of its unclassical form or its unsuitability, or for any other reason except the existence of a prior name. Generally speaking, it is customary in books on systematic zoology to give, not only the full scientific name, but to add the name of the author who first described the species and gave it the name. Thus, "*Clupea harengus* Linnaeus" means that the common Atlantic Herring was first named and described by Linnaeus; "*Alosa finta* (Cuvier)" means that the trivial name *finta* was first given by Cuvier to the Twaite Shad, but he placed it in the Linnean genus *Clupea*, from which it was removed by a later authority and placed in the genus *Alosa*.

Of the four main classes constituting the "fishes," the Marsipobranchs and Placoderms have been dealt with in some detail in the previous chapter and need not be discussed further here. The latter are entirely extinct, and the living Marsipobranchs, the Cyclostomes, are divided into two families, the *Petromyzonidae* or Lampreys and the *Myxinidae* or Hag-fishes. The arrangement of the sub-classes, orders, sub-orders, etc., of the other two classes may be very briefly outlined, but this will consist of little more than a list of their scientific names: however, taken in conjunction with the accompanying "trees" (Figs. 134, 135), this will serve to give some idea of the manner in which modern authorities classify the Selachians and Bony Fishes.

Of the five main sub-classes into which the Selachians are divided, the first three (*Pleuropterygii*, *Acanthodii*, *Ichthyotomi*) contain only extinct forms and have been considered in the previous chapter (*cf.* pp. 351-352). The fourth, the *Euselachii*, is split up into two orders: in the first, the *Pleurotremata* or Sharks, the front margin of each pectoral fin is free, the external gill-clefts are on the sides of the head, and the eyes have free margins (Figs. 1; 14A; 23C; 32A, etc.); in the second, the *Hypotremata* or Rays, the front margin of the pectoral fin is joined to the side of the body or head, the gill-openings are on the lower surface of the head, and the upper edges of the eyes are not free (Figs. 8A; 14B; 107, etc.). The *Pleurotremata* are again sub-divided into three sub-orders, represented on the tree by the branches D, E, and F. The *Notidanoidea* are the most primitive of existing Sharks, and in these the gill-clefts number six or seven, the vertebral column is of simple form, and there is only one dorsal fin (Figs. 32C; 66A). The group includes the rare Frilled Shark (*Chlamydoselachus*) and the Comb-toothed Sharks (*Hexanchidae*). The *Galeoidea*, with five gill-clefts, and with two dorsals and one anal fin, the former not preceded by spines (Figs. 1; 23C; 32A; 34b), includes the Sand Shark (*Odontaspis*), and Elfin Shark (*Scapanorhynchus*), constituting the family *Odontaspidae*; the Mackerel Sharks (*Lamna*),

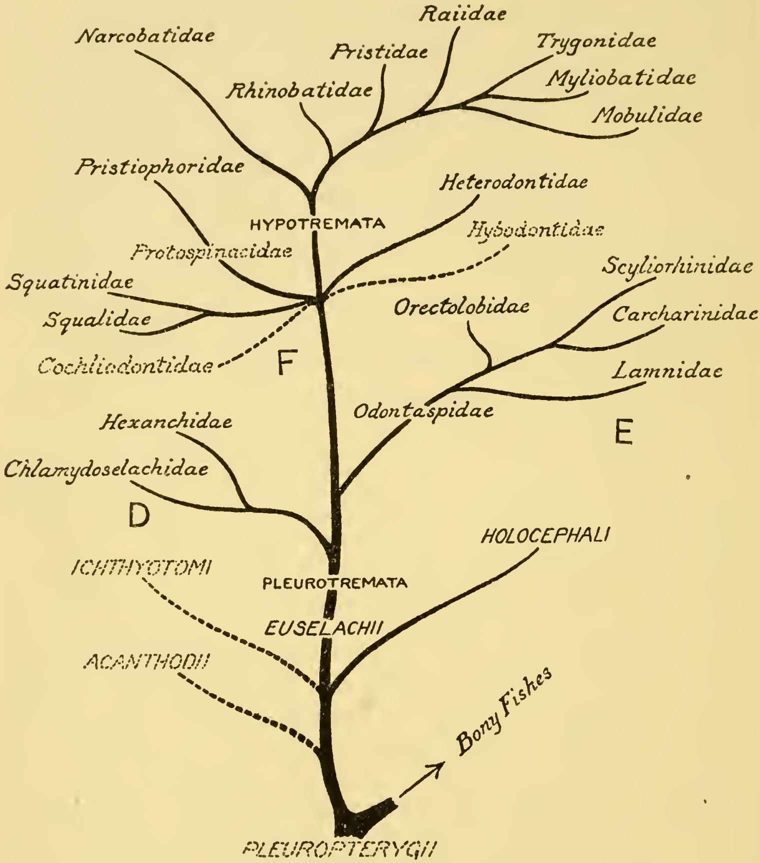


Fig. 134.—PHYLOGENETIC "TREE" OF THE CLASS SELACHII.

Sub-classes, orders and families are shown.

Porbeagles (*Isurus*), Man-eater Sharks (*Carcharodon*), Basking Shark (*Cetorhinus*), and Thresher Shark (*Alopias*), of the family *Lamnidae*; the large and varied family *Orectolobidae*, including the Carpet Sharks (*Orectolobus*), Tiger Sharks (*Stegostoma*), Nurse Sharks (*Ginglymostoma*) and Whale Shark (*Rhineodon*); the Dog-

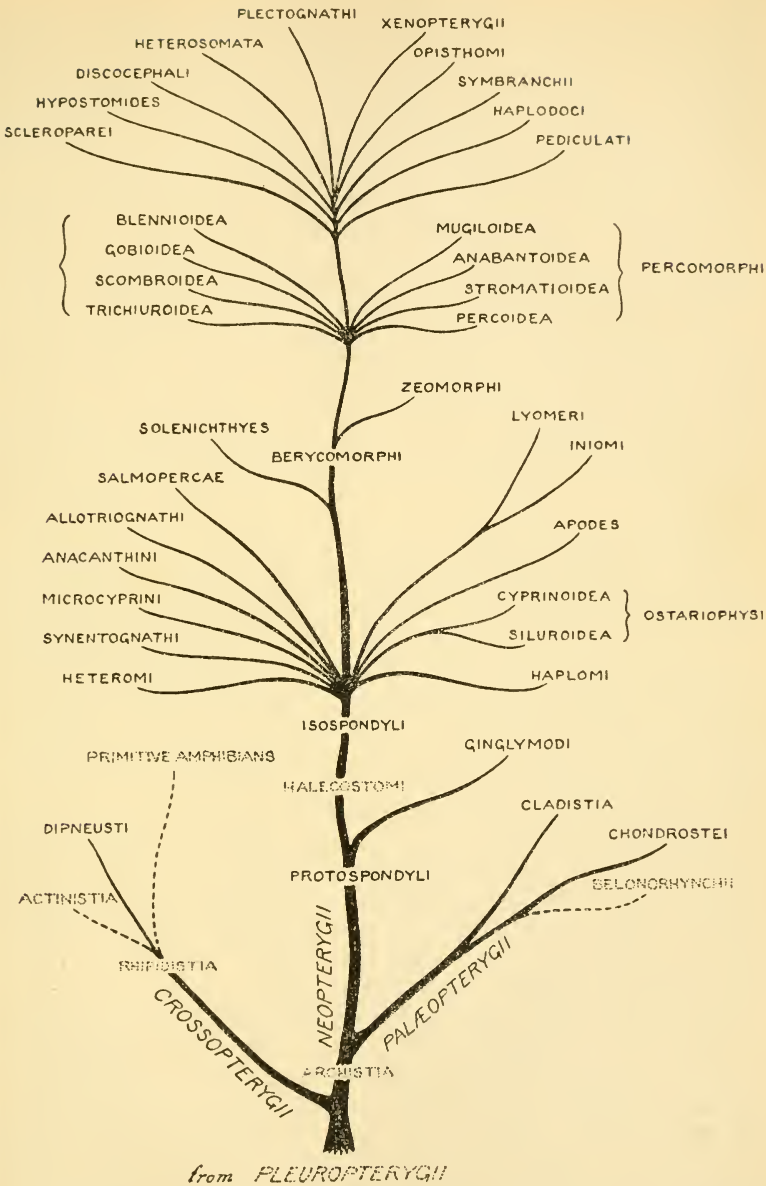


Fig. 135.—PHYLOGENETIC "TREE" OF THE CLASS PISCES (BONY FISHES).

Sub-classes, orders, and (in some cases) sub-orders are shown. One or two small orders have been omitted.

fishes or Rousettes of the family *Scyliorhinidae*; and the family *Carcharinidae*, including the Blue Sharks (*Carcharinus*, etc.), Topes (*Eugaleus*), Hounds (*Mustelus*) and Hammer-headed Sharks (*Sphyrna*). The last sub-order, the *Squaloidea*, includes four families which have sprung from the same common ancestral stock, and have subsequently evolved along divergent lines, as well as three more specialised families. In all the members of this sub-order, either the two dorsal fins are each preceded by a spine or the anal fin is absent (Figs. 53B; 60A). Two of the four families mentioned above (*Cochliodontidae*, *Hybodontidae*) are extinct; the other two are the Bull-headed Sharks (*Heterodontidae*) and the family *Squalidae*, including the Spiny Dog-fishes (*Squalus*), Bramble Shark (*Echinorhinus*), Greenland Shark (*Somniosus*) and a number of other forms. This family has given rise to the remarkable bottom-living Angel-fishes or Monk-fishes of the family *Squatinidae*, and the specialised Saw Sharks (*Pristiophoridae*) have probably been derived from the extinct *Protospinacidae*.

The Rays (*Hypotremata*) may be divided into two sub-orders, the first or *Narcobatoidea*, including only the Electric Rays or Torpedoes (*Narcobatidae*). Among the more primitive families of the *Batoidea*, the second sub-order, are the Guitar-fishes (*Rhinobatidae*) and Saw-fishes (*Pristidae*), which have retained the elongate form and muscular tail of the Sharks (Fig. 38), and the other families include the true Skates and Rays (*Raiidae*), Sting Rays (*Trygonidae*), Eagle Rays (*Myliobatidae*), and Devil-fishes (*Mobulidae*).

The last sub-class of Selachians, the *Holocephali*, includes the few existing Chimaeras and a host of extinct forms. The members of this group are readily recognised by having the primary upper jaw (palatoquadrate cartilage) fused with the cranium (Fig. 56A), and by the gill-clefts opening into a chamber with a single external aperture, a character in which they approach the Bony Fishes (Fig. 14C).

In the class of Bony Fishes (*Pisces*) the genera and species are so much more numerous and diverse that their arrangement becomes a matter of some difficulty, and there is considerable diversity of opinion as to the division into sub-classes and orders. The classification outlined here is mainly that of Dr. Regan, and in broad outline may be accepted as one which would receive the support of a large number of modern ichthyologists. Three sub-classes are recognised: *Palaeopterygii*, *Crossopterygii* and *Neopterygii*. The first two of these contain very few existing forms, and have been considered in some detail in the previous chapter. The third includes the vast majority of living Bony Fishes, and is further sub-divided into some thirty-one orders of varying size and importance. The Bow-fin (*Amia*) of North America is the sole existing survivor of the first of these orders, the *Protospondyli*; the second, or *Ginglymodi*, includes the fresh-water Gar Pikes (*Lepidosteidae*) of North America; and the third, or *Halecostomi*, contains the Herring-like *Pholidophoridae* already mentioned (*cf.* p. 362). The *Isospondyli*, the first of the orders of modern Bony Fishes, is an important group, including a vast assemblage of genera and species, all of which agree in having the air-bladder connected with the gullet by a pneumatic duct, and the pelvic fins abdominal in position. This is split up into seven sub-orders, of which the more important are the *Clupeoidea*, including the Ten-pounders (*Elopidae*), Lady-fishes (*Albulidae*), Herrings (*Clupeidae*), Smooth-heads (*Alepocephalidae*), Milk-fishes (*Chanidae*), etc.; the *Stomiatoidea*, oceanic fishes distinguished by the presence of luminous organs or photophores; and the *Salmonoidea*, including the Salmon, Trout, and their allies (*Salmonidae*), Argentines (*Argentinidae*), Smelts (*Osmeridae*), etc. The remaining sub-orders of importance are the *Osteoglossoidea*, *Notopteroidea*, *Mormyroidea*, and *Gonorhynchoidea*.

From the generalised *Isospondyli* have been derived a number of more specialised orders, represented on the tree (Fig. 135) by a group of radiating branches. These include the *Haplomi*, containing the Pikes (*Esox*), Mud-fishes (*Umbra*), and Black-fish (*Dallia*); the *Iniomi*, containing the Lizard-fishes (*Synodontidae*), Lantern-fishes or *Myctophidae*, and a number of other oceanic forms; the *Giganturoidea*, a very small order of specialised oceanic fishes; the *Lyomeri* or Gulpers, closely related to the *Iniomi*; the *Apodes*, containing all the Eels; and the *Heteromi*, a small group of fishes living at considerable depths in the oceans. The huge order, *Ostariophysi*, which includes the vast majority of the fresh-water fishes of the world, is closely related to the *Isospondyli*, differing only in the presence of the complicated Weberian mechanism (*cf.* p. 193). Two sub-orders of the *Ostariophysi* are recognised: the first, or *Cyprinoidea*, containing the Carps and allied forms (*Cyprinidae*), as well as the Characins (*Characinidae*, etc.), *Gymnotidae*, Suckers (*Catostomidae*), and Loaches (*Cobitidae*); and the second, or *Siluroidea*, all the families of Cat-fishes. Another fairly important order derived from the *Isospondyli* is the *Synentognathi*, a group which includes the Gar-fishes (*Belonidae*), Half-beaks (*Hemirhamphidae*) and the true

Flying-fishes (*Exocoetidae*) among others. The *Microcyprini* or Toothed Carps, generally known as Cyprinodonts, represent a large and varied order of small fishes, bearing a certain resemblance to the *Synentognathi*, as well as to the Trout Perches or Pirate Perches (*Percopsidae*), forming the order *Salmopercae*, which may be placed here. Two orders, whose exact position in the system is a little more obscure, although there can be little doubt that they have sprung from some rather generalised stock, are the *Solenichthyes* containing all the tube-mouthed fishes, such as the Trumpet-fishes (*Fistulariidae*), Shrimp-fishes (*Centriscidae*), Snipe-fishes (*Macrorhamphosidae*) and Pipe-fishes (*Syngnathidae*); and the *Anacanthini*, an important group including the Grenadiers (*Macruridae*) as well as the Cods and allied forms (*Gadidae*). Another interesting order to be placed here is the *Allotriognathi*, an assemblage of curious and diverse forms, which, nevertheless, all agree in possessing a protractile mouth, which has a peculiar structure and is actuated by a mechanism different to that of all other fishes (*cf.* p. 117). This group includes the large oceanic Opah (*Lampris*), the Deal-fishes and Ribbon-fishes (*Trachypteridae*), and the remarkable deep-sea *Stylophorus*.

All the fishes of the orders so far mentioned are provided with soft-rayed fins, but with the *Berycomorphi* or Berycoid fishes a brief survey of the spiny-rayed orders may be commenced. In these the rays of the anterior parts of the dorsal and anal fins are modified into (generally) stiff, pointed spines, and the pelvic fins are placed well forward, and the outermost ray of each is spinous. The Berycoids are usually regarded as the most primitive of Acanthopterygian fishes, but although a profusion of forms existed in the Cretaceous period, comparatively few are found living to-day. Allied to these fishes are the members of the order *Zeomorphi*, including the John Dories (*Zeidae*) and Boar-fishes (*Caproidae*) among others. Further up the main stem is the huge order of Perch-like fishes (*Percomorphi*), which is allied to the Berycoids and may be divided into some fifteen sub-orders. The sub-order *Percoidea* includes all the more typical families of the group: Sea Perches (*Serranidae*), Sun-fishes (*Centrarchidae*), Perches (*Percidae*), Snappers (*Lutianidae*), Grunts (*Haemulidae*), Drums (*Sciaenidae*), Horse Mackerels, etc. (*Carangidae*), Sea Breams (*Sparidae*), Red Mullets (*Mullidae*), Wrasses (*Labridae*), etc. Of the remaining sub-orders the more important include the *Teuthidoidea*, containing the Surgeon-fishes (*Teuthidae*); the *Trichiuroidea*, with the Hair Tails and Cutlass-fishes (*Trichiuridae*), etc.; the *Scombroidea*, with the Mackerels, Tunnies, and their allies (*Scombridae*), and the Sword-fishes (*Xiphiidae*), Spear-fishes and Sail-fishes (*Istiophoridae*); the *Gobioidea*, with the Gobies (*Gobiidae*) and allied forms; the *Blennioidea*, with the Wolf-fishes (*Anarrhichadidae*), Blennies (*Blenniidae*), Kelp-fishes (*Clinidae*), Brotulids (*Brotulidae*), and other forms; the *Stromateoidea*, with the Butter-fishes, Rudder-fishes, and Square-tails (*Stromateidae*); the *Anabantoidea*, including all the Labyrinthic-fishes; and the *Mugiloidea*, with the Grey Mullets (*Mugilidae*), and the Barracudas (*Sphyraenidae*).

The Mail-cheeked Fishes, forming the order *Scleroparei*, represent a large and varied assemblage of fishes, the more generalised of which are closely related to some of the Perch-like forms, but differ in having a bony "stay" or posteriorly directed process running from a bone below the eye towards the operculum. The Rock Perches or Scorpion-fishes (*Scorpaenidae*), Poison-fishes (*Synanceidae*), Gurnards (*Triglidae*), Greenlings (*Hexagrammidae*), Sculpins and Bull-heads (*Cottidae*), Flat-heads (*Platycephalidae*), Lump Suckers (*Cyclopteridae*), and Flying Gurnards (*Dactylopteridae*), all belong to this order, and probably also the Sticklebacks (*Gasterosteidae*). A small order, the *Hypostomides*, including the grotesque Dragon-fishes (*Pegasidae*), may be placed here, although their true systematic position is uncertain. The Remoras, or *Discocephali*, have been derived from the *Percomorphi*, differing in having the first dorsal fin transformed into a sucking disc (*cf.* p. 69); and the Flat-fishes, or *Heterosomata*, have been derived from the same stock (*cf.* p. 68). Three main groups of Flat-fishes may be recognised, the *Psettodoidea*, including the primitive genus *Psettodes*, the *Pleuronectoidea*, with the Halibut (*Hippoglossus*), Plaice (*Pleuronectes*), Turbot (*Rhombus*), etc., and the *Soleoidea*, with the Soles (*Soleidae*) and Tongue Soles (*Cynoglossidae*). The *Plectognathi*, another order allied to the *Percomorphi*, contains the Three-spined-fishes (*Triacanthidae*), File-fishes and Trigger-fishes (*Balistidae*), Trunk-fishes (*Ostraciontidae*), Puffers or Globe-fishes (*Tetrodontidae*), Porcupine-fishes (*Diodontidae*), and Sun-fishes (*Molidae*). The small order *Malacichthyes*, includes only one or two rare fishes whose systematic position is doubtful, and the Cling-fishes, forming the order *Xenopterygii*, are clearly modified Percoids. The *Haplodoci* represent a small order containing the Toad-fishes (*Batrachoididae*), etc., and this is closely related to the *Pediculati*, an order which includes the Angler-fishes (*Lophiidae*), Frog-fishes (*Antennariidae*), Bat-fishes (*Ogcocephalidae*), and the various families of oceanic Ceratioids, all differing from their Perch-like ancestors in having the first ray of the dorsal fin placed on the head and modified into a line and bait. Finally, there are the fresh-water Spiny Eels (*Opisthomi*), a small order containing fishes probably allied to the *Percomorphi*; and the eel-like *Symbranchii*, which may be descended from some Blennioid stock.

CHAPTER XIX

FISHES AND MANKIND

Fish as food. Composition of flesh. Value of fresh-water fishes. Different kinds of edible fishes. Commercial value of deep-sea fisheries. Fishing industry of Great Britain. Fishing methods: trawling, seining, drifting, lining. Preservation of fresh fish. Fish curing, etc. By-products of fishes: oils, meals, fertilisers, glue, isinglass, leather, etc.

As a staple article of food, fish must have found favour with man at a very early stage of his history, and there can be very few races living to-day who do not include this valuable protein food in their ordinary diet. Whether eaten raw, as in Japan and the Hawaiian Islands, cooked, salted, smoked, or preserved in one way or another, the popularity of fish-flesh is world-wide. Apart from certain species whose flesh is watery, dry, and tasteless, full of small bones, or heavily charged with rank oils, the flesh of fishes is generally white and flaky, and has an agreeable flavour. In the ease with which its contained proteins and fats are digested by the human body, it compares very favourably with beef or other meats, and it has been shown that man is able to digest completely as much as 93·2 per cent. of the protein content of tinned Salmon, and 93·1 per cent. of that of fresh Mackerel, and can make use of 93·7 per cent. and 95·2 per cent. respectively of the fatty content of the same fishes.

The muscular tissue or flesh of a fish is made up of 60 per cent. to 82 per cent. water, about 13 per cent. to 20 per cent. proteins, and a greater or lesser amount of fat. The following table illustrates the percentages of these substances in the flesh of some of our commoner food-fishes, and the figures in the fourth column represent the "energy value" or "fuel value" expressed in calories. Calories are nothing more than measurements of heat, and provide a simple means of comparing one article of food with another in terms of its energy value, which may be briefly defined as "the number of calories of heat equivalent to the energy which it is assumed the body would be able to obtain from one pound of given food material, provided the nutrients of the latter are fully digested."

Name.	*Water.*	*Protein.*	*Fats.*	*Fuel value per lb.*
Herring . .	72·5	19·5	7·1	660
Salmon . .	61·4	17·5	17·8	1080
Cod . . .	82·6	16·5	·4	325
Haddock . .	81·7	17·2	·3	335
Mackerel . .	73·4	18·7	7·1	645
Halibut . .	75·4	18·6	5·2	565
Loin of beef .	61·3	19·0	19·1	1155
Leg of mutton .	67·4	19·8	12·4	890
Chicken . .	63·7	19·3	16·3	1045

It will be observed that the fat content varies considerably, and this is true, not only of different kinds of fishes, but of individuals of the same species taken at different seasons and in various conditions. Herring, Salmon, and Mackerel are to be looked upon as fatty fishes at all seasons, but Mackerel caught in the late autumn or winter are usually much fatter than those caught in spring or summer, and the percentage of fat in a spawning or spent Herring is considerably less than that in a fish taken at any other time. This variation in the fat content is shown in the next table. Such fishes as the Cod, Haddock, Plaice, and Sole are to be regarded as lean fishes at all seasons.

Name.	*Protein.*	*Fats.*	*Fuel value per lb.*
Herring—			
Shetland Matties . .	21·10	16·68	1095
Small immature autumn .	18·65	14·25	951
Spawning . . .	18·91	2·02	430
Spent	18·05	·68	360
Eel—			
Fat autumn . . .	13·40	32·90	1635
Lean average . .	17·60	7·90	660
Mackerel—			
Fat autumn . . .	18·21	16·30	1025
Average . . .	18·77	8·21	695

In addition, the flesh of a fish contains phosphorus, a substance which is believed to be of some importance in nutrition, as well as relatively large amounts of those precious substances known as vitamins, now considered to be indispensable to an adequate and properly balanced diet. The vitamins present in the bodies of fatty fishes and in the livers of almost all fishes, are derived directly from the plankton, that host of minute organisms which directly or indirectly provides the source of food for all fish.

Although in many countries, and more particularly in those situated in the tropics, fresh-water fishes provide a valuable source of food supply, it is the marine fishes that form the bulk of the food of mankind. In America, however, the fisheries of the Great Lakes are of considerable economic importance, the more valuable kinds of fish including the White-fish (Ciscoes and Lake Herrings), Pike, Perch, and Carp; and the river fisheries may be of some local importance. As far as the British Isles are concerned, apart from the Salmon and Eel, which are not exclusively fresh-water, the fishes of the lakes and rivers are quite unimportant as a source of food supply. The fresh-water area of England and Wales is only about three hundred and forty square miles, and the annual production of fish has been estimated as two thousand tons, a very small figure when compared with the seven hundred thousand odd tons yielded by the sea-fisheries. The total stocks of Trout and coarse fish of all kinds in England and Wales are believed to be in the neighbourhood of eight thousand tons, so that, in the words of the report published by the Departmental Committee set up by the President of the Board of Agriculture and Fisheries during the War, "the expenditure of public money on the development of our inland fisheries for Trout and coarse fish only in order to increase the food supply can hardly be justified."

There exists a regular market for fresh-water fishes in London and other large cities, but this amounts to only a few hundred tons each year. It is maintained chiefly by the importation of fishes from Holland, where, as in other parts of the continent of Europe, the cultivation of Carp and other coarse fishes for the table is a flourishing and well-organised industry. The supplies marketed in this country are bought largely by the foreign population and the Jewish community, and there seems to be a deep-rooted prejudice among our own people to the use of these fresh-water fishes as food. The chief objection lies in the muddy or weedy flavour which often permeates the whole flesh, but experiments have shown that this is readily overcome by special methods of cooking. As far as nutritive value and digestibility are concerned, they do not differ over-much from marine fishes, as illustrated by the following table, and the popularity of the latter must be entirely a matter of custom and palatability.

Name.	*Water.*	*Protein.*	*Fats.*	*Fuel Value per lb.*
Carp . . .	78·9	15·79	4·77	495
Bream . .	78·7	16·19	4·09	473
Pike . . .	79·5	18·76	·66	377
Perch . . .	78·8	18·45	1·40	402
Trout . .	80·5	17·96	·74	365

The number of different kinds of fishes eaten in some countries is comparatively small. In Great Britain, for example, the number of species that may be regarded as fairly common in the sea is about one hundred and sixty, yet the official returns and annual reports of the Ministry of Agriculture and Fisheries for England and Wales enumerate only thirty-four edible kinds, including Whitebait. This last is not a single species, as is sometimes supposed, but is composed of young Herrings or Sprats, and may occasionally include young Gobies, Sand Eels, Blennies, and other species. The fish trade classifies these thirty-four fishes into two main categories, round and flat, the last including the Skates and Rays as well as the true Flat-fishes. A fair amount of what is known as unclassified fish is also landed, and, with the fishing-vessels making extensive voyages, comparatively rare species make their way into the markets from time to time. The average housewife is probably familiar with less than half of the thirty-four fishes enumerated by the trade, and within recent years strenuous attempts have been made to overcome a deep-rooted conservatism or even actual prejudice, and to educate the British public to make use of several excellent food-fishes to which they were previously unaccustomed. The case of the much-despised Dog-fish is a particularly interesting one, for the modern industry concerned with this fish in England, Canada, and the United States, arose almost entirely as the result of an attempt to exterminate what was a serious pest to the existing fisheries. It was found almost impossible to do away with these fishes, or even to reduce their numbers to any appreciable extent, and it was finally found preferable to convert what was previously a useless and actually injurious creature into a valuable asset. The first step towards overcoming popular prejudice to the Dog-fish as food was to give it a more pleasing name, and it was marketed in England as "Flake," in Canada and the United States as "Gray-fish," and in Germany as "See-Aal" (Sea Eel). Chemical analysis of the flesh has shown that it is highly nutritious and easily digested, but so far its consumption has been limited largely to the poorer classes of the community, large quantities being used by the establishments supplying fried-fish dinners. In this country Dog-fish is eaten fresh, but abroad there are considerable tinning and preserving industries. Another fish which

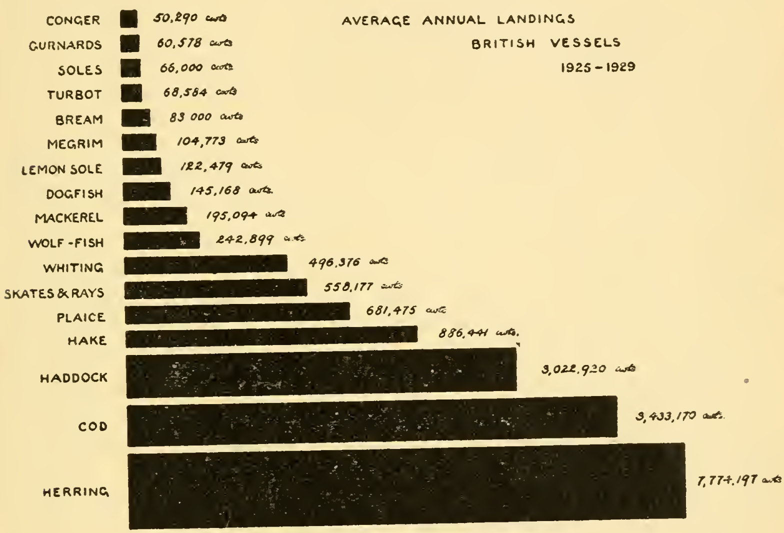


Fig. 136.

Diagram illustrating the relative importance of different kinds of British Food-fishes.

has come in for a good deal of unfair unpopularity is the Cat-fish or Wolf-fish (*Anarrhichas*), chiefly on account of its tough skin and ugly head. Here, again, it has been found convenient to market this perfectly wholesome fish under a more pleasing name, and, deprived of its head and skin, it is sold as "Rock Salmon," or, in Scotland, "Rock Turbot."

The sea fisheries of the world may be roughly divided into deep-sea and inshore fisheries, the former being very much more valuable. The deep-sea fisheries of the continental shelves and the banks of the great oceans lie almost entirely within the limit of a depth of two hundred fathoms, and the majority within one hundred fathoms. The principal fisheries of the world lie in the North Temperate Zone, for the most part between the latitudes of 40° and 70° N., regions in which there are great areas of water less than two hundred fathoms in depth, forming the grounds inhabited by the valuable demersal or bottom-living fishes on which the trawling industries depend. As an example of this concentration of the fisheries in northern seas it may be mentioned that those of Great Britain, France, Spain, Norway, Russia, Canada, the United States, and Japan together represent no less than 70 per cent. of the total yield of the fisheries of the world, and the total catch of these countries represents approximately 12,000,000,000 lbs. A visit to any fish market in the tropics will reveal the fact that in warmer seas the number of edible species of fish is far greater than in northern latitudes, but there are, as a rule, fewer great concentrations of individuals of any one species, and, at the same time, the areas of water of a depth of less than two hundred fathoms are of far less extent. In certain provinces of India attempts have been made in recent years to develop the sea fisheries, and these are actively exploited in Ceylon and Malaya, but it is the inland fisheries which are of greatest economic importance in these countries. Some idea of the huge numbers of individuals of certain species in northern climes may be gained by considering such a fish as the Herring, perhaps the most important of all food-fishes. It has been estimated that a single shoal of Herrings may contain anything up to 3,000,000,000 individuals, and there must be scores of these shoals scattered through the Atlantic and North Sea. To take yet another example, about 300,000,000 or 400,000,000 Cod are believed to be caught annually in the Atlantic alone, but this must be but a minute fraction of the total number of Cod in existence at a given time.

It is wellnigh impossible to quote any figures to give an adequate conception of the magnitude of all the great sea fisheries of the world, for it is only in certain countries that exact statistics are collected and published. An American authority has estimated the total value of the catches of marine and fresh-water fishes throughout the world, including fishery products, to be about $800,000,000 per annum, say about £160,000,000, but this is probably far too conservative, and the actual figure may be very much greater. The fisheries of Japan are the most valuable, and their total value is believed to be at least £30,500,000 per annum, while the industry employs no less than 2,000,000 men, as compared with some 80,000 in the British Isles. In 1925 the output in the British Isles was valued at £20,250,000, more than half the total value of those of all other northern European nations put together. France came next, with a total of £7,000,000, followed by Norway with £4,850,000, and Spain with £4,000,000, while outside Europe the total output of the United States was valued at £19,000,000, that of Canada at over £5,000,000, and that of Newfoundland and Labrador at more than £2,000,000. The latest figures for England and Wales alone, that is, for the year 1929, show that the total quantity of wet fish of British taking landed during the year was 14,287,000 cwts., valued at £14,444,000, showing an increase of 6 per cent. in quantity and 10 per cent. in value over that of the previous year. The growth of the British sea fisheries during the twenty-five years preceding the war was amazing, the total yield being more than doubled in this period. It was not until 1885 that the Board of Trade first made an attempt to collect adequate statistics in a scientific manner of the fish caught by British fishermen and landed at British ports. The total in 1888, the first year for which figures covering the whole of the British Isles are available, was given as 575,000 tons, valued at £5,471,000, but by 1913 it had reached the huge figure of 1,233,000 tons, valued at £14,693,000 when landed, and about £50,000,000 when it reached the consumers. On the outbreak of war our fisheries made up nearly one-half of the total for all the countries of north-west Europe, and nearly three-quarters of the North Sea fisheries alone. The enormous pre-war increase was due almost entirely to the replacement of the old sailing-vessels by highly specialised steam trawlers and drifters with large supplies of ice. Instead of being able to venture only a short distance from their home port, these modern vessels can go very much farther afield, and now range over the whole of the continental shelf from Iceland, Bear Island, and the White Sea in the north to Morocco in the south, remaining at sea for as long as two or three weeks. During the war itself deep-sea fishing was greatly reduced in the North Sea and other home waters, but to-day the yield has more than surpassed that of 1914, and at the same time the consumption of fish by the population of Great Britain is steadily increasing every year, being at the present time about forty lbs. per head each year.

Quite apart from their economic value, the sea fisheries in historical times have played an important part in the destinies of nations. Mr. Maurice has pointed out that fishing was probably the earliest form of hunting, and since men were almost certainly hunters before they were cultivators, it follows that fishing is the oldest industry in the world. Even in Tudor times our fishermen were at work, not only in the North Sea and other home waters, but also off the coasts of Lapland and Iceland, and from this time onwards the part played by the fisheries in the development of sea trade, in giving an impetus to the building of ships, and so on, was a very important one. The actual number of fishermen employed in Great Britain to-day is only about sixty thousand, but it must be remembered that thousands of hands are engaged in the subsidiary industries of fish-canning, curing, salting, herring-pickling, the preparation of fish meals and fertilisers, oils of all kinds, and the like. When to these are added the many men and women employed in the transport of fish from the markets to the retail shops, and to the fried-fish shops (handling about 40 per cent. of the total quantity consumed), and those engaged in shipyards, net factories, motor works, etc., it will be realised that a failure of the industry would be a serious calamity with far-reaching effects. It has been estimated that no less than four tons of coal and one ton of ice are required to catch a single ton of trawl fish, so that the industries concerned with these commodities would also suffer severely in such a contingency. As a further example of the importance of the sea-fisheries to the lives of nations, it may be mentioned that in their pursuit of the Cod the French fishermen were led further and further out into the Atlantic Ocean, and in due course this resulted in the discovery of Canada; and it is by no means unusual for the location of an important town or port to be settled with reference to its relation to the fishing industry. According to Dr. Björnsön, wherever a shoal of Herrings touches the coast of Norway, there a village springs up, and the same is true in Scotland, Newfoundland, Japan, Alaska, and Siberia.

With the possible exception of Japan, the deep-sea fishing industry of Great Britain is the most highly organised in the whole world. It possesses about 2000 steam fishing vessels, as compared with 465 in Germany, 456 in France, 366 in Norway, and 228 in Holland. The kind of vessel used is dependent, of course, on the sort of fish it is required to catch, but three main types may be recognised: the trawler and liner, used for catching demersal or bottom-living fish, and the drifter for pelagic fish.

To give some idea of the relative value of these different vessels, it may be pointed out that in 1926 the amount of demersal fish caught by British fishermen and landed at British ports was 10,961,000 cwts., valued at £13,541,000; the amount of pelagic fish, consisting chiefly of Herrings, landed in the same year was 8,000,000 cwts., valued at £3,503,000. The old sailing trawlers with their picturesque brown sails are rapidly being replaced by more efficient steam vessels, but sailing "smacks" and "cutters" may still be seen in some numbers at such ports as Brixham, Plymouth, Ramsgate, Great Yarmouth, and Lowestoft. The smacks are capable of making voyages of five or six days' duration, and generally fish in water less than forty fathoms in depth, while the cutters work in still shallower water, and rarely stay away from port for more than twenty-four hours. The steam trawlers of Great Britain number about 1560, of which more than 1200 fish from the ports of England and Wales. They are of three main types, and vary in length from 115 to 170 feet, and with a gross tonnage of 215 to 324. The fish-hold may be capable of accommodating as much as 50 to 60 tons of fish, but in the last year or two even larger vessels have been built, capable of storing much greater supplies, and provided with apparatus for extracting cod-liver oil on board. The drifters are somewhat smaller vessels, measuring about 86 feet in length, and with a tonnage of about 95.

The literature concerning the numerous and diverse methods of catching fish is voluminous, and it is no part of this work to do more than to touch briefly on some of the more interesting methods in use to-day. Leaving out of account such curious practices of oriental countries as fishing with a tame otter, with the Remora or Sucking-fish, and with a cormorant (a method used in Japan for catching the Ayu, a kind of dwarf Salmon), fishes may be said to be caught in four ways: by spears, by traps, by nets, and by baited hooks. The spear was almost certainly the earliest weapon to be employed, and is still in use to-day in certain parts of the world. This was soon followed by some kind of primitive trap, which may have partaken of the nature of a simple wicker-work cage or basket, suitably baited and designed to entrap roving fish. From this was evolved the more efficient fish-weir or dam, a snare which worked on the principle of allowing fishes to enter on the flood-tide and retaining them on the ebb. Such weirs are still in use on parts of the coast of Great Britain and in many other countries, and led on to the development of more elaborate structures composed of wattle fencing, and from these, by a process of gradual evolution, to fixed nets. Baited hooks must also have been used at a very early stage in man's history, the first probably being somewhat similar to the thorn hooks still

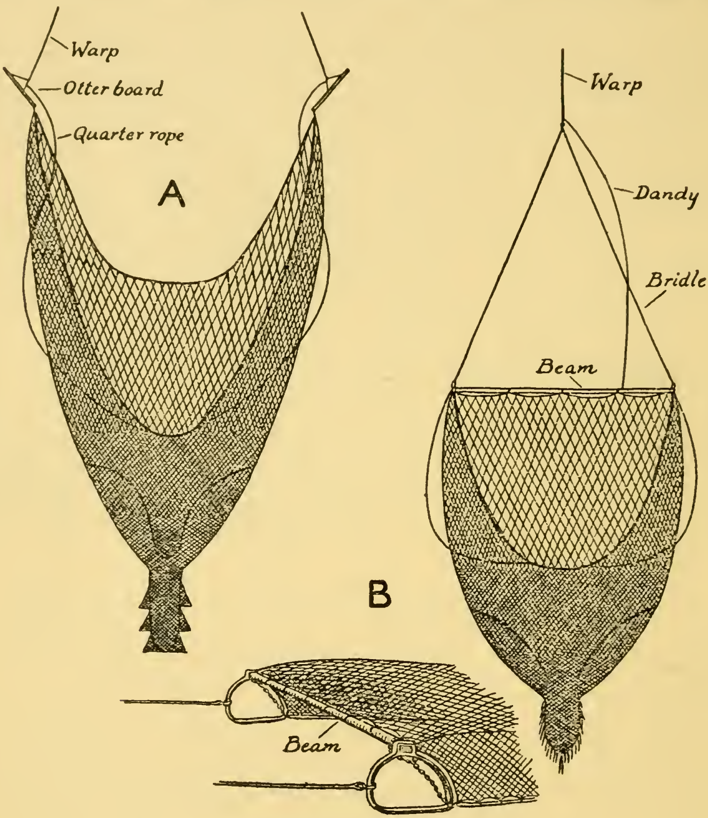


Fig. 137.—TRAWLS.

A. Otter Trawl, viewed from above; B. Beam Trawl, viewed from above, and side view of front portion. (After Davis.)

employed in parts of Wales and in the Thames estuary. Finally, instead of waiting for the fish to enter the snare, attempts were made to bring the net to the fish, and the first trawls or seines worked from boats or from the shore were invented.

Four principal methods are used by the commercial fisheries of the present day, namely, trawling, seining, drifting, and lining, each method involving the use of a particular kind of gear and designed to catch particular kinds of fish. In 1926 the quantity of wet fish of British taking landed in Great Britain by each method of fishing was: trawl, 9,481,000 cwts; drift, 7,853,000 cwts.; lines, 993,000 cwts.; and Danish Seine 353,000 cwts. The trawlers, seiners, and liners take chiefly demersal fish such as the Cod, Haddock, Hake, Halibut, Plaice, and Sole, known to the trade as "white fish," while the drifters capture pelagic fish like the Herring, Pilchard, and Mackerel.

The trawl (Figs. 137, 138) is a net of flattened conical shape, sometimes as much as one hundred feet in length, with a wide mouth at one end and tapering at the other to the "purse" or "cod-end." This great bag is dragged slowly along the sea

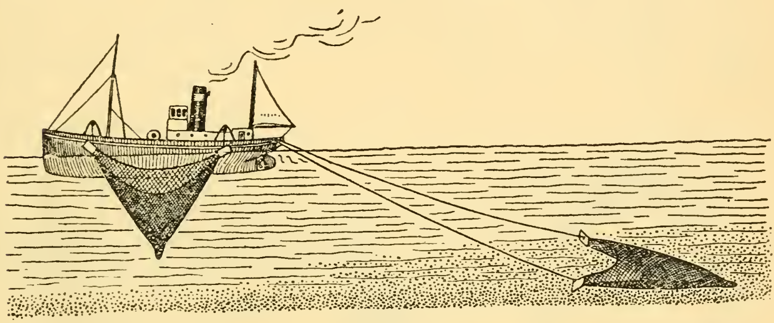


Fig. 138.

Steam Trawler fishing with Otter Trawl, and with net hauled.

bottom by means of strong "warps" attached to a powerful steam winch on the ship, and the fish, once they are in the net, are prevented from swimming out again by special valve-like devices. The "foot-rope," forming the lower edge of the mouth of the net, may play an important part in stirring up the fish, particularly those like the Flat-fishes, which lie buried in the sand. In the "beam trawl" (Fig. 137B), now used only by sailing vessels, the upper edge of the mouth-opening is formed by a stout wooden beam, anything from forty to fifty feet in length, at either end of which are D-shaped iron runners, the "shoes" or "trawl-heads," to which the towing warps are attached. The "otter trawl" (Fig. 137A) has no such frame round the mouth of the net, which is here kept open by two large "doors" or "otters," constructed of heavy, iron-bound wood, from eight to nine feet in length and four or five feet high.

As the net is towed slowly along the sea-floor, the resistance of the water causes the two doors to pull away from one another, each door with its attached warp acting after the manner of a boy's kite. This trawl has a great advantage over that of the beam variety in that the size of the opening is not limited by the size of the frame, and the mouth of a modern otter trawl may be anything up to one hundred feet in width. At the same time the beam keeps the mouth of the net open even if the vessel loses way, whereas if a boat towing an otter trawl comes to a stop, the boards tend to fall down flat and may not always come into position again when the vessel begins to move once more. An important modification of the otter trawl largely adopted in recent years is known as the "Vigneron-Dahl Trawl." In this net the wings are longer than in the ordinary trawl, giving a greater mouth opening or "fishing spread," and the ground warps being in close contact with the sea-floor tend to scare the fish inwards towards the track of the net.

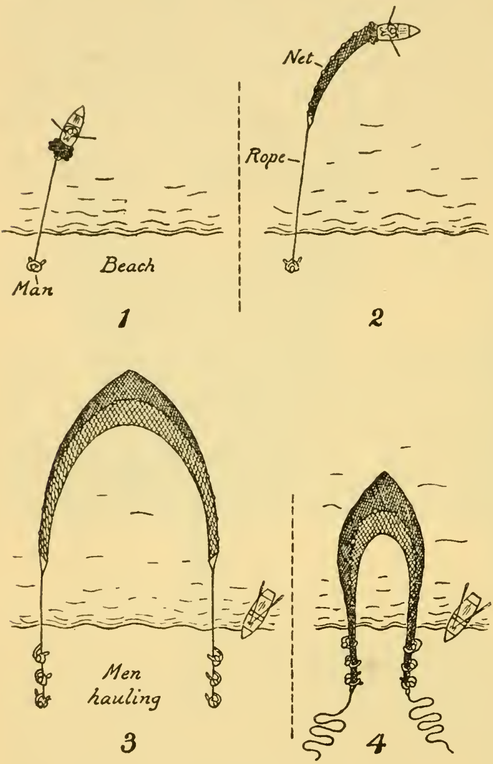


Fig. 139.
Diagram to illustrate the principle of working a Seine Net from the shore (seen in plan).

Several types of seine net are in use in various countries, but cannot be described in detail here. Briefly, seining consists in surrounding a shoal of fish with a long net, suitably buoyed, and gradually drawing this closer until the imprisoned fish can be readily removed. The net is usually paid out by a boat sailing or rowed round the shoal in a circle or half-circle, and this is finally hauled into the boat by the use of a special winch or is towed ashore (Fig. 139). In the days when the Pilchard industry flourished on the Cornish coast, deep seine nets were used to surround the shoals, which were paid out by rowing-boats and drawn slowly to the shore. The shoals were sighted by men known as "huers" or "balkers," who raised the cry of "Hev-ah, hev-ah!" when the fish were seen, and who received about three pounds a month and a share of the fish caught. The Purse Seine is a net extensively used in America for catching the valuable Menhaden.

The Danish Seine or "Snurrevaad" is another important type of net, the use of which has been much developed by

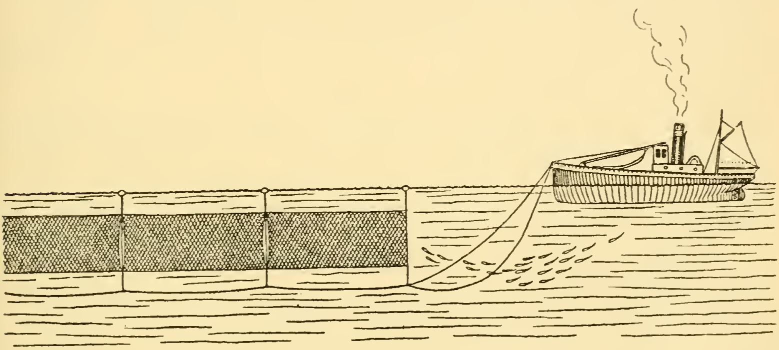


Fig. 140.—STEAM DRIFTER FISHING.

British fisheries in recent years. In many respects it lies midway between the trawl and the seine. Over a mile of warp is attached to each wing of the net, which may have a span of one hundred and sixty feet or more, and a large bag of some fifty to sixty feet in length. It is not hauled ashore, but is worked from a boat in offshore waters.

Drift nets are worked on a very different principle to the trawls and seines, and are not actually approached to the fish. At the same time, they differ from fixed nets and traps in that they are attached either to a slowly drifting ship (hence the name) or to a floating buoy, and move with the ship or buoy under the influence of the tide and wind (Fig. 140). The types of fish caught with the drift nets are those which spend their time swimming in the layers of water above the sea-floor, keeping, as a rule, fairly deep down during the day, but approaching the surface at night. Each drift net is a simple stretch of strong cotton netting, about fifty or sixty yards in length and about fourteen yards deep, the upper edge of which is buoyed with corks or "pellets" and the lower edge usually weighted slightly with lead. As night approaches the drifters start to shoot their nets with the tide, "fleets" of as many as eighty-five nets being used at one time from a single vessel, so that a complete wall of netting, perhaps three miles in length, is hanging vertically in the water, either at the surface or a few fathoms down. The ship then drifts for several hours with the tide, with one end of the wall of netting attached. The mesh of the net is so constructed that the fish is able to push its head through but not its body: once the gill-covers are through it is impossible for the fish to release its head, and in the dark vast numbers of fish swim into the nets and are strangled. At dawn the nets are hauled in to the ship and the catch shaken out of their meshes.

Lining is a method of fishing used to catch such demersal fish as the Cod and Halibut, the Cod fisheries carried on in this way on the Newfoundland banks being world famous. The old hand-line is now of little commercial importance and has been superseded by the long line, which may be more than four thousand yards in length, with hooks attached at regular intervals to short "snoods" about two feet long. On a large steam liner the number of hooks on a single line may be anything from one thousand to five thousand five hundred. The bait varies considerably, including whelks, mussels, squid, and herrings. The lines may be shot in the morning or afternoon, and, unlike the hand lines, are left quite unattended for several hours before being hauled in.

The flesh of fishes, as might be expected, is a highly perishable commodity, and very soon after death begins to undergo certain changes, at first not undesirable, but which, if allowed to continue, render it unfit for human consumption. The following table may be of interest to many, and shows some of the more important features distinguishing a fresh fish from one that is stale or putrid.

Fresh	Stale
1. The flesh is firm and elastic, exhibiting a condition known as "rigor mortis."	1. "Rigor mortis" has passed off.

Fresh	Stale
2. The flesh in the region just below the backbone is pale in colour.	2. The flesh below the backbone shows a reddish discoloration.
3. There is no trace of any unpleasant smell.	3. The flesh smells tainted or putrid.
4. The flesh can be removed from the backbone only with some difficulty, and pieces adhere to the bone.	4. The flesh can be removed from the backbone cleanly and easily.
5. The walls of the abdomen are firm and elastic.	5. The walls of the abdomen are soft and pulpy.
6. The gills are reddish or pinkish, with characteristic hues.	6. The gills are greyish and slimy.
7. The eyes are full and prominent, the pupils being clear and bright.	7. The eyes are sunken and greyish.

A few of the larger fishing vessels, making more or less extensive voyages, cure their catches in some way on board, but the majority carry supplies of ice sufficient to ensure that the fish first caught are landed in a saleable condition. The freshness of the supplies reaching the consumers is further ensured by the presence at the inland markets of inspectors, whose duty it is to examine any doubtful consignments, and to condemn those considered to be unfit for human consumption.

The bulk of the fish landed at the ports is consumed in a fresh condition, but the preservation of fish by freezing or curing is an important industry. Freezing is, as a general rule, only used to preserve the fish for short periods until they can be placed on the markets in a fresh state, but there are various types of plant now in use for more efficient refrigeration. Indeed, with the improvements in the freezing methods made in recent years, and with the general speeding up of modern transport facilities, cold-stored fish is more and more tending to compete with cured fish, and in time to come may largely replace it. In the early days of civilisation the heavy curing of many kinds of fish was almost essential, but the tendency nowadays is for the harder cures to be replaced either by fresh fish or by lightly cured preparations.

Four principal methods of curing fish are in use, namely, salting or pickling in brine, smoking, drying, and canning, the former being perhaps the method in most general use throughout the world. The dry salting of Cod is an important industry both in Europe and America. Sometimes the whole process is carried out ashore, but more generally the fish are decapitated, split, cleaned and salted almost as soon as they are caught, and after being washed are stacked in the fish-hold with heavy layers of salt between them. After being landed, the fish are removed to "cod farms," where the curing is completed by drying, and they are finally packed in barrels for export. Salt Cod, known as "klip-fish," are split and spread out on rocks to dry, whereas "stock-fish" are hung up to dry without being split in any way. Salt Cod has played an important part in the economy of European nations for several centuries, and formed the Lenten fare of Catholic Europe in the Middle Ages. To-day the principal markets for this commodity are in Catholic countries such as Spain, Portugal, and Italy in Europe, the West Indies, and Argentina, Brazil, and Uruguay in South America. In 1929 415,742 cwts. of salted Cod of British taking were exported from the United Kingdom, valued at £940,789, and of this total Spain received 50,474 cwts., Portugal 29,736 cwts., and Brazil no less than 205,506 cwts.

Brine salting or pickling is a method used mainly for Herrings, and is an important industry. The annual Scottish catch of Herrings is in the neighbourhood of 300,000,000 lbs., of which about 70 per cent. is cured in one way or another. The following table for the years 1920 and 1921 gives an idea as to how the catches are dealt with:—

	1920	1921
Consumed fresh . .	70,028,800 lbs.	61,105,200 lbs.
Gutted and salted .	552,828 barrels.	457,552 barrels.
Ungutted and salted .	20,735 ,,	9,326 ,,
Kippered . . .	253,483 ,,	174,494 ,,
Bloaters and "reds" .	14,700 ,,	10,036 ,,
Canned . . .	38,245 ,,	4,958 ,,

It is of some interest to note the marked shrinkage undergone by the pickled Herring industry since the recent war. The industry depends almost entirely on the export trade, and with the markets disorganised in many of the European countries consuming pickled Herrings in large quantities, and more especially those of Soviet Russia, which before the war absorbed about 40 per cent. of our total export, it has suffered very severely. The average pre-war export of pickled Herrings in Great Britain was about 400,000 tons, and to-day this has fallen to about 290,000 tons. This is in marked contrast to the previous increase, which may be illustrated from the figures of the Scottish cure, which grew from 89,934 barrels in 1811 to 1,886,596 barrels in 1913.

The Dutch, French, and German fishermen cure their catches of Herrings aboard the vessels, but in Great Britain the whole process is carried out ashore. In Scotland alone some thirty to forty thousand hands are employed in one capacity or another connected with this industry, and nearly 25 per cent. of these consist of women and girls whose sole duty it is to gut the catches brought in by the drifters. Owing to the different seasons at which the shoals approach various parts of the coasts of the British Isles to spawn, the drift fisheries tend to move gradually southwards during the year, commencing on the west coast of Scotland in the Hebrides in May, moving to the Orkneys and Shetlands in June, reaching Shields during the same month, Scarborough and Grimsby in July, Great Yarmouth and Lowestoft in early October, and then moving on to such places as Plymouth, where Herrings may be taken until the following January. As the fishery moves south, many of the drifters move round from port to port, and the great army of Scottish fisher-girls follows the fleet on land. During the holiday season the pickling plots of Yarmouth and Lowestoft are quite deserted, and only the growing stacks of wooden boxes forecast the coming autumn activities, when these towns are invaded by the girls, whose dexterity in wielding a sharp knife to split and clean the fish almost at a single stroke is amazing to behold. All day long they are employed in gutting the fish, while others are concerned with the pickling and packing for export. The process of pickling itself is quite simple: the fish are gutted by removing the gills and intestines (but not the milt or roe), and are then packed in water-tight barrels with layers of salt, in which they make their own pickling and are adequately cured.

The smoking of fish consists of a combination of salting and drying, and it is upon the degree to which either of these processes is used that the characteristic flavour depends. Smoking is employed largely for Herrings, but Whiting, Cod, Ling, Saithe, Haddock, Cat-fish, and Mackerel are also preserved in this manner. The primitive savage smoked his fish by hanging them over open camp fires, just as many native races do to-day, but as the commercial fishing industry grew up, more efficient methods were required, and in a modern smoke-house thousands of fish can be cured at one time. The type of wood used for the fires is of special importance, hard woods such as oak, hickory, and mahogany being preferred, as these contain less oils and resins which might impart a taste to the fish. The smoke is produced, not by burning the wood itself, but by burning sawdust, which smoulders gently and gives off dense clouds of smoke.

The three principal types of smoked Herring are Red Herring, Bloater, and Kipper. Red Herrings and Bloaters are both cured without splitting, only being cut open sufficiently for cleaning. The Red Herring is much more strongly salted, being buried in salt for at least five days and then smoked for ten days, whereas the Bloater is less heavily salted, and is smoked only long enough to dry the fish but not to cure it. The Red Herring can, therefore, be exported for considerable distances, but the Bloater, like the Kipper, is a perishable product, and cannot be kept for more than a few days at ordinary temperatures. A Kipper is a Herring which has been split down the back from head to tail, immersed in brine for a period varying from fifteen to sixty minutes, slightly dried, and finally smoked for several hours. In recent years many Kippers have been cured by immersion in chemical mixtures, but these are much inferior in taste, and may even prove injurious as food.

The smoking of Haddock dates back to the middle of the eighteenth century, and originated at Findon in Scotland, the smoked fish being known as Findon Haddocks, a name which was later abbreviated to Findon Haddies, and finally to Finnan Haddies. The fresh fish is decapitated and split down the back, gutted, and an extra cut made part of the way down the back from the right-hand side in order to facilitate the curing of the thick muscles of the back. It is then washed, salted for a short time in strong brine, dried, and then spread open on sticks to be smoked for a period of five or six hours over a fire burning a mixture of peat and sawdust.

Drying is a method of curing which is used to any appreciable extent mainly in tropical countries, where the heat of the sun's rays is sufficiently powerful, although the dehydration of fish in a scientific manner has been recently introduced with some success into Germany. It is the favourite method of preservation in India, Malay, the Philippines, China, and Japan, where dried fish is a staple article of food among people of all classes. Generally the fish are simply cut open, gutted, and laid in the sun to dry, but sometimes they are first salted to some extent. The well-known "Bombay Duck," that indispensable adjunct to an Indian curry, consists of the dried and salted bodies of the Bummalow (*Harpodon*), a fish which is particularly abundant in the estuaries of Bengal and Burma.

Canning is a comparatively modern method of preservation, and has many obvious advantages over the others. In America it has become a very important industry, particularly the canning of Pacific Salmon, carried on from Alaska to California. The total value of the tinned Salmon produced by North America is about fifty-six million dollars, and that of Sardines, an industry centred mainly on the coast of California on the Pacific, and the coast of Maine on the Atlantic side, about fifteen million dollars. In Europe, Herrings, Sprats, Sardines, Anchovies, Mackerel, and Tunnies are all tinned, the Sardine industry of France, Spain, and Portugal being of great commercial importance to these nations. The Sardine is not, as is often supposed, a distinct species of fish, but the young stage of the Pilchard. The method of curing consists in removing the head and viscera by hand, sprinkling lightly with salt, immersing for a short time in brine, washing, drying, and then frying for about two minutes in olive oil. The fish are then packed in olive oil in tins, which are finally hermetically sealed, other ingredients such as oil of lemon, cloves, bay, truffles, or pickles being sometimes used to give added flavour. A similar trade is carried on to a large extent in Norway, but here the fish used is the Sprat (Brisling) or the young of the Herring.

In some countries fish are pickled in vinegar or cured in one or two other unusual ways, while among the other food products which are derived from the flesh of fish may be mentioned fish sausages, rissoles, anchovy paste, the Delicatessen of Germany, fish cake of Japan, and caviare. This last is manufactured principally from the roes of the Sturgeons, the great caviare industries being carried on round the Black Sea and Caspian Sea, where these fishes are numerous. At one of the fishing stations in this region it has been estimated that as many as fifteen thousand Sturgeons have been caught in a single day. In Great Britain the Sturgeon is a "Royal Fish," for by an unrepealed law of Edward II it is enacted that "the King shall have the wreck of the sea throughout the realm, whales and great sturgeons . . . except in certain places privileged by the King." In parts of the Orient, notably in China and the Philippine Islands, there is a considerable trade in shark fins, which are used for making soup. After being cut from the body, the fins are well salted or dusted with lime, and then dried in the sun. The Japanese prepare a tasty dish from the flesh of Sharks and Dog-fishes, which is known by the name of "shark-flesh paste."

In addition to providing man with food, most fishes yield a number of by-products, which may be of some commercial importance. Chief among these are the oils of various grades, ranging from the crude oils used in certain manufacturing processes to the medicinal cod-liver oil, so valuable in the treatment of wasting diseases. In fishes like the Herring, Sardine, Menhaden, Salmon, and Mackerel, the bulk of the oil is found in the body, and furnishes what is known to the trade as "fish-oil," a product used to a large extent in the manufacture of paints. In the Cod and many other fishes, the oil is contained mainly in the liver, and yields a product which in the crude state is used by the tanning industry, being particularly valuable in the manufacture of "chamois" leather, for tempering steel, and in the preparation of lower-grade soaps, while, after refining, it provides the well-known medicinal oil. Norway alone produces nearly one and a half million gallons of cod-liver oil annually, Iceland about half a million gallons, while considerable quantities are produced by Canada, Newfoundland, the United States, Great Britain, and Japan.

Fish meals and fish fertilisers are products of some economic importance, and succeed in using up all the waste parts of the fish. The former is used to feed poultry, pigs, and cattle, and is particularly reliable for chickens and young animals, as it contains protein in a readily digestible form, as well as a high percentage of calcium phosphate. It is of interest to note that the Greek historian Herodotus, writing in about the fourth century B.C., mentions a tribe living in pile-dwellings round Lake Prasias that "feed their horses and other beasts on fish, which abound in the lake in such a degree that a man has only to open his trap-door, and let down a basket by a rope into the water, and then wait a very short time, when he draws it up quite full of fish" (Rawlinson's translation).

Fish glue is a product obtained mainly from such fishes as the Cod, Haddock, Pollack, and Hake. Most of it is derived from the skin of the fish, but waste glue and fish-head glue are also manufactured. Isinglass is a pure gelatinous substance obtained from the inner lining of the air-bladder of certain fishes, and is principally used for the clarification of wines and beer, for making jellies, etc., and in the preparation of certain cements. It is made in various parts of the world from the air-bladders, or "sounds," as they are known to the trade, of such diverse fishes as the Sturgeons, Carps, Cat-fishes, Cod, Ling, Hake, Squeteagues, Drums, and Thread Fins. The Russian isinglass, marketed as "leaf," "pipe," and "cake," is perhaps best known and of the finest quality, being manufactured entirely from the sounds of various species of Sturgeon.

The skins of some fishes, and particularly those of the Sharks and Rays, are sometimes of use to mankind. With the bony dermal denticles *in situ*, the crude skins of Sharks and Dog-fishes are used by carpenters and cabinet-makers for smoothing and polishing, as well as by metal-workers; suitably prepared and dyed skins provide the shagreen used for covering car cases, jewel boxes, sword scabbards, and for ornamental work of all kinds. After being specially tanned, and having had the dermal denticles removed, the skins of most Sharks and Rays provide a strong and highly durable leather, and with the increasing demand for this commodity in recent years the shark-leather industry is fast becoming a satisfactory commercial proposition. Recently, experiments have been made with the skins of some of the Bony Fishes, the Wolf-fish (known to the trade as "Sea Leopard"), Cod, Bream, Corvina, and Sole being most popular, but, although these are in some demand for fancy work, they lack the durability of shark leather. In certain of the Islands of the South Seas the natives make use of the dried and spiny skins of the Globe-fishes or Porcupine-fishes for war helmets, and in Japan it is a common practice to make lanterns out of the inflated and dried skins of Puffers, by cutting out the back and suspending the fish by a wire. A candle being placed inside, the light shines as brightly through the stretched skin of the fish as through a piece of oiled paper.

Finally, the silvery scales of the Bleak (*Alburnus*), a Cyprinid fish found all over Europe north of the Pyrenees and Alps, are used extensively in the manufacture of artificial pearls, especially in France, where the industry dates from the middle of the seventeenth century. A pigment is obtained by scraping the scales, which is coated on the inside of hollow glass beads, and these are then filled with wax.

CHAPTER XX

FISHES AND MANKIND (*continued*)

Harvest of the sea. Dangers of over-fishing and possible remedies. Fishery investigations. Methods of research. Pisciculture. Artificial propagation. Introduction of fishes into new countries. Angling. Improvement of Salmon and Trout fishing. Pollution and hydro-electric schemes. Fish diseases: Furunculosis, *Saprolegnia*, Salmon Disease. Fish parasites: Sea Lice, Gill Maggots, Worms. Monstrosities. Varieties of Goldfish. Fishes used in controlling disease. Aquaria. Fishes in museums.

Speaking in 1883 the late Professor Huxley said: "I believe that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries are inexhaustible; that is to say that nothing we do seriously affects the numbers of fish." In those days of trawling and lining from sailing vessels this statement was probably true enough, but with the advent of steam-trawling, and with the enormous growth in the volume of fishing that followed, coupled with a great increase in the destructiveness of fishing gear, conditions were altogether changed, and apprehensions have arisen as to whether the operations of mankind are not depleting the stocks of fishes in the sea. Many authors have described this great international asset as the "harvest of the sea," but it must be remembered that the harvest gathered by the fisherman is one that he has never sown, and that, although he may take large quantities of fish from the sea, he does nothing towards increasing or conserving the supply. As Dr. Jenkins has pointed out, the present generation is the trustee for future generations in the matter of preserving our species of fish and of maintaining a reasonable supply of the same, and it is, therefore, of great importance that this problem should receive the attention of scientific men before irreparable damage is done to the stocks. Much has been written concerning the application of various branches of science to the fishing industry, and in the following pages a brief account of some of the problems awaiting solution and of the methods employed by fishery investigators may be given.

Even after many years of research, it is far from easy for science to give a definite opinion on the all-important question as to whether or no modern intensive fishery operations are affecting the composition of the stock of edible fish in the sea. Speaking generally, however, it may be said that, as far as the pelagic species are concerned, fears of over-fishing are groundless, and that the stocks of such fishes as the Herring may actually be increasing. The case of some of the demersal fishes, inhabiting comparatively restricted areas of fairly shallow water, presents a different problem, and it may be that in places like the North Sea a greater weight of fish is being removed each year than can be fully replaced by the natural processes of reproduction and growth. It must be borne in mind that the area of the North Sea is little more than 130,000 square miles, and that more than one million tons of fish are taken from it every year. Further, the area covered by the nets of British trawlers alone has been estimated at about 110,000 square miles, and one authority has pointed out that every square foot of the Plaice grounds of the North Sea is trawled over on the average two or three times every year.

The Plaice is, of course, one of our most important demersal species, and apprehensions as to the stability of the stocks were first entertained in the latter years of the last century, following the introduction and spread of steam trawling, but the pressure on the home grounds was relieved for a time by the spread of trawling to more distant regions, and the matter did not become acute until recent times. The late war provided a very interesting scientific experiment on a large scale, and one which was watched with some interest by scientific investigators. During the period 1914-1918 the North Sea was virtually closed to trawlers, and as a result the Plaice grounds were almost completely rested. Immediately afterwards trawling was resumed, and the catches of Plaice during the first year after the war were very much greater than those recorded in 1913, but included large numbers of old and poorly nourished fish, due to the overcrowding of the grounds. In succeeding years the weight of fish became progressively less and less, and the figure to-day is just about the same as that of 1913. At the same time, however, the average size of the fish is distinctly smaller than in the year immediately after the war, suggesting that the fish are being caught before they have a chance to grow to a reasonable size. It would seem, therefore, that there are some grounds for alarm as far as the Plaice of the North Sea are concerned, but in view of the legislative measures that have been taken, the dangers of over-fishing are not now believed to be so very serious. The fact remains, however, that twenty-five per cent. of the catchable Plaice, that is to say, of fish big enough to be retained by the meshes of the nets, are taken out of the sea every year, and the situation requires to be carefully watched if the stocks of this valuable species are to be preserved for future generations.

Apart from the laws designed to conserve the existing stocks of fish—the prohibiting of the capture of young fish, closing of certain grounds, establishment of close seasons, and so on—the only possible means of sustaining or increasing the stocks of demersal fish in a region such as the North Sea lies in the artificial rearing of young fish or in the transplantation of young or mature fishes from other localities. The hatching of the eggs of Plaice and other Flat-fishes in special tanks, the rearing of the larvae through the critical period of their lives, and their subsequent liberation in the sea, has been carried out in hatcheries established at the Bay of Nigg in Scotland, Port Erin in the Isle of Man, and Piel on the Lancashire coast. Large numbers of fry have been released, but the chances of increasing to any appreciable extent the existing stocks of fish by such artificial methods are at present very remote. After all, what are the few millions of fry liberated every year to the many millions already in the sea? Transplantation, as a method of replenishing depleted stocks, has been tried in the North Sea with some success, but the obstacles to be overcome before it would be practicable to carry this out on a scale sufficiently large to have any definite effect on the resources of the North Sea are at present rather great. Small Plaice were caught off the coast of Holland, marked with discs, and half of them liberated on the spot, the remainder being taken alive in special tanks and released on the famous Plaice ground on the Dogger Bank. When the marked fish were subsequently recaptured, it was found that those on the Dogger Bank, a locality known to be particularly rich in a certain kind of shell-fish to which the Plaice is partial, had grown very much faster than those on the Dutch coast, where the food supply is less abundant.

It was the pressing need for a scientific investigation of the alleged decline in the numbers of fish, due to over-fishing, coupled with the increased interest taken in the science of oceanography, which had received a marked stimulus from the *Challenger* expedition in 1872 to 1876, that led to the establishment of fishery research towards the close of the nineteenth century. The Fishery Board for Scotland led the way in the 'eighties, but with the foundation of the now famous Marine Biological Association at Plymouth in 1884, similar investigations were soon undertaken in England. The greatest advance took place in 1899, when, realising the international character of the great sea-fisheries, the King of Sweden invited representatives of all the interested maritime powers to a conference at Stockholm "to elaborate a plan for the joint exploration in the interests of the sea fisheries of the hydrographical and biological conditions of the Arctic Ocean and the North and Baltic Seas." The response was general, and as a result of this conference and another similar gathering held in Christiania in 1901, the "International Council for the Exploration of the Sea" came into being, with permanent headquarters at Copenhagen and a central laboratory at Oslo. Included in the Council are representatives of all the countries of Northern Europe, with important fishing interests (with the exception of Soviet Russia), as well as those of Spain, Portugal, and Italy. Its object is to see that the natural resources of the sea are exploited in a rational manner, and to this end to co-operate the researches of the various countries involved, each being allotted a certain area of the sea for special investigation, in addition to carrying out general work on a more extensive scale with the approval of the Council. The central bureau publishes a number of monographs, papers, and notes of all kinds, mostly of a technical nature and written in various languages, dealing with the fish and fishery investigations, and in addition each country publishes its own reports, often of a voluminous nature, of investigations undertaken by its own specialists in the different branches of fishery research. In this way a great deal of overlapping is avoided, and a vast amount of valuable information has been placed on permanent record.

In Scotland the investigations are carried on under the auspices of the Fishery Board for Scotland, with a laboratory at Aberdeen and a vessel of the trawler type, the *Explorer*, for research at sea. In addition, there is another laboratory at Millport at the mouth of the Clyde. Up to the year 1910 the English share of the international investigations was undertaken largely by the Marine Biological Association, which, in addition to their laboratory and research vessel at Plymouth, maintained another station at Lowestoft, with another vessel, the *Huxley*, for marine work. In 1910 the complete control was taken over by the Ministry (then Board) of Agriculture and Fisheries, with its headquarters in London. After the war a fisheries laboratory with an augmented staff was established in one of the big houses on the Esplanade at Lowestoft, and a powerful vessel, the *George Bligh*, was also acquired and converted for research purposes. The very important work in marine biology and hydrography which is required to supplement that of the Fishery Department was continued at Plymouth and other marine laboratories in England, these being subsidised out of public funds for this purpose. The more important of these laboratories are situated at Port Erin, and at Cullercoats on the coast of Northumberland, and are attached to the Universities of Liverpool and Durham respectively.

Considerations of space will not allow even a brief account of the many and varied branches of fishery research, and it must suffice to indicate a few of the more important problems that present themselves and the methods adopted for their solution. Mention has been made of the comparatively recent science of oceanography, and it is clear that no hard and fast line can be drawn between this and fishery research. Practically all the work carried out by the oceanographer, whether of a biological or hydrographical nature, will be found to have some bearing, direct or indirect, on the lives of the food-fishes. Even when in its infancy the practical value of marine biological work to the welfare of the fisheries was amply demonstrated when a controversy arose in the latter part of the last century as to the possible harmful effects of the introduction of steam trawling. It was suggested that the heavy trawl dragged over the sea-floor would destroy large quantities of fish eggs, but on the matter being referred to the scientific advisers, they were able to say at once that such fears were without foundation. The development of the more important food-fishes had already been studied, and it was pointed out that, with the sole exception of the Herring, whose eggs are deposited in adhesive masses on grounds generally so rough that trawling would be almost impossible, the eggs of all our food-fishes are of the pelagic, drifting kind.

To obtain a complete and intimate knowledge of the life-history and habits of each species is one of the most important branches of research. This involves a study of the spawning habits, the location of the spawning grounds, the recognition of the eggs and larvae and a knowledge of their development, the rate at which the fish grow, and the relation between this growth-rate and the available food supply, as well as an investigation of the migrations of the shoals of adult and young fish, and so on. Further, in order to study the life-history of a particular fish, it is necessary to study its environment, and fishery research must include the study of the plankton food of the pelagic fishes, as well as the bottom-living invertebrates forming the food of the demersal fishes. This in turn involves the study of the minute vegetable and inorganic constituents of the diet of the plankton and the invertebrates of the sea bottom, and the lines of research must be further broadened out to include a study of the physical nature of the sea-floor, the movements of the tides, the currents, the temperature and salinity of the water; in fact, the general physics and chemistry of the sea. In addition to the biological and hydrographical investigations, the collection of statistics forms another important branch of inquiry. Records of the quantities and sizes of the different species landed at various ports by vessels employing different kinds of fishing gear must be accurately kept over long periods, and numerous measurements of individual fishes made at sea, for it is only by methods of this nature that it is possible to obtain some idea of the stocks of fish in the sea and the reasons for the fluctuations in their composition.

While at sea the fishery investigator is kept constantly employed in measuring fish, obtaining otoliths and scales from selected specimens in order that their age may be ascertained, marking fish with metal discs for the purpose of studying their movements, collecting samples of the sea bottom and of the surface plankton, making observations of the temperature and salinity, and of the chemical constituents of the water at various depths, collecting eggs and larvae, and releasing special drift bottles, which, when subsequently recovered, serve to measure the movements of the water under the influence of tides and currents. Back in the laboratory, the water samples are analysed, the physical and chemical data tabulated, the plankton and bottom samples studied with the lens and microscope, the scales and otoliths read, and the thousand and one tasks connected with fishery research are constantly being carried out. Each specialist working on his own particular subject contributes his quota to the solution of the general problems involved. "What, then, are these general problems?" writes Dr. Russell in an account of the work of the laboratory at Lowestoft. "Apart from the general acquisition of knowledge, which has a remarkable way of turning out in the long run to be of practical use, the main problems whose solution we seek may be said to be two—the rational and economical exploitation of the fisheries, and the prognostication of good and bad years." As far as the second of these problems is concerned, science has for some time been able to form a pretty good idea of the probable success or failure of a particular fishery during the next year or two, and a stage has now been reached when actual and accurate prophecy is possible. That stocks of fish do vary considerably from year to year, quite independent of the amount of fishing, has been known for some time, and it will clearly be of the greatest practical importance to the industry when the factors that govern these fluctuations are thoroughly understood. Finally, there is room for a good deal of research on the types of gear used in fishing, and on such subsidiary branches of the industry as the handling of fish, refrigeration, preservation, packing, etc.

The maintenance or improvement of the stocks of certain species of edible fish by some form of pisciculture is a very ancient practice, and it is known that in classical times the Greeks and Romans made a habit of cultivating fishes in captivity for the table, and of stocking their lakes and ponds with ova or young fish obtained from other localities. Two main types of modern pisciculture may be recognised: (1) the rearing of fishes in confinement until they are large enough to be eaten, and (2) the stocking of waters with eggs or fry obtained from fishes breeding in captivity. The ancient Romans certainly carried on the first method, and were in the habit of admitting young fishes from the sea into special enclosures or *vivaria* by means of sluices, and then fattening them up for the table. Exactly similar cultivation of marine fishes is carried out at the present day in the lagoons of the Adriatic and the salt marshes of various parts of France. The number of different kinds of fish which can be reared from the egg to maturity in captivity is very small indeed, the best-known examples among fresh-water forms being the familiar Goldfish, and the little Top Minnows or Cyprinodonts so popular with aquarium lovers. The Carp, Crucian Carp, Tench, Orfe, Ide, Bream, Roach, Dace, Trout, Pike, Eel, and Perch are all cultivated to a greater or lesser extent by fish culturists of Europe, but only the Carp lends itself to domestication to an extent which makes it a commercial proposition. This is the principal fish used in pond culture throughout the world, and in Central and Southern Europe, as well as in China and other oriental countries, Carp culture forms a flourishing industry: it has been introduced with some success into the United States, but has long died out in England. The fish farms in Germany are often of considerable size, some of them being six or seven thousand acres in extent. The Carp is a very hardy fish, can be bred and reared to maturity under all kinds of conditions, requires no costly food, consuming refuse and other natural products which are otherwise useless, grows rapidly, and, if properly cooked, has a delicate flavour. Rapid growth to a marketable size is essential to a profitable industry, and modern growers have succeeded in producing races that grow to an average weight of two and a half pounds at the end of their third summer, and in some tropical countries the rapid growth is even more striking.

The second type of pisciculture, namely, the artificial propagation of fishes for stocking purposes, is carried on extensively in various parts of Europe and America. Trout lend themselves particularly well to this form of cultivation, and can be profitably hatched in special receptacles. In our own country great advances have been made in this industry with the marked growth which has taken place in the volume of angling, and every Trout stream of any value or note is restocked from time to time as a matter of course. In the United States the Brook Trout, Black Bass, and to a lesser extent some of the Sun-fishes, are cultivated in huge numbers, the Brook Trout also being reared to a fair size in ponds. By feeding these fishes on a diet of slaughter-house offal, in addition to the natural food in the ponds, they can be made to grow two or three times as fast as in the wild state. The actual process of artificial fertilisation is very simple, the ripe female fish generally being "stripped," the eggs being pressed from the body into a vessel into which a little of the milt of the male is introduced. When fertilised, the eggs are either distributed at once to the waters which have to be stocked, or they are placed in special receptacles provided with a suitable stream of water until the fry are hatched. These may be planted at once, but do not always flourish, and it is advisable to stock the waters either with unhatched eggs or with fry which have been reared for a period in the hatcheries until they are active and hardly.

The ease with which the natural development of the ova can be retarded by storing them in ice makes it possible to introduce certain species of fish into new countries or even into fresh continents. Trout were taken into New Zealand from England as early as the late 'sixties, and this country now boasts the finest Trout fishing in the world. American Trout of various kinds have been introduced into England from time to time, and our own Brown Trout introduced into the United States, but neither of these experiments can be described as an unqualified success. The only foreign species at all well known in Great Britain is the Rainbow Trout. This has been used extensively for stocking sporting waters, but, although it has sometimes bred for a few seasons, it has very rarely become permanently established under natural conditions. Comparatively recently, Trout have been introduced with great success into Tasmania, Ceylon, Kashmir, South Africa, Kenya Colony, etc., in every case for sporting ends, and during the last year or two it has been suggested that the American Black Bass should be planted in Lake Naivasha in Kenya. However much such introductions of foreign species may benefit the sportsman, they are to be wholly deprecated by the biologist, who wishes to study the indigenous fauna of a country under normal conditions, and it has been found necessary to enter a strong protest against these interferences with natural conditions. It is well known that the introduction of new elements into a fauna may upset the balance of nature and produce quite unexpected results, and the new species may even become a serious pest and defy all efforts to exterminate it. It is said that the Carp in North America and the Goldfish in Madagascar have spread and done considerable damage to the existing fisheries for other and better fish, and the Trout in New Zealand have affected the fisheries for Eels and Crayfish. In the Great Lake of Tasmania lives a most interesting crustacean of an archaic type, which is found nowhere else in the whole world: the introduction of Trout into the lake has played a considerable part in the decimation of this creature, which is now confined to a very limited area and is in serious danger of complete extinction.

As far as the British Isles are concerned, it has already been pointed out that, apart from migratory species such as the Eel and the Salmon, the fresh-water fishes are of very little value as a potential source of food supply, so that the artificial propagation of Trout is looked upon by many as of very slight economic importance. For the same reason, it may well be argued that the decline which is known to have taken place in the stock of fresh-water fish in England and Wales during the last hundred years is comparatively unimportant, and that the expenditure of any public money in maintaining or improving the stock is to be deprecated in view of the urgent need for national economy. Such reasoning is distinctly unfair, for it leaves out of account one very important aspect of the matter, and one which was emphasised very ably and forcibly by Mr. H. G. Maurice of the Ministry of Agriculture and Fisheries to a recent meeting of the Freshwater Biological Association of the British Empire, an association which, if sufficient support is forthcoming, it is hoped will fulfil the same function for fresh-water biology as does the Marine Biological Association at Plymouth for the biology of the sea. "I hope," said Mr. Maurice, "that there are in this room a considerable number of persons who represent what I will call the angling community. One of the principal reasons, and a very justifiable one, for taking care as well as we can of the fisheries of our streams is not their commercial but their recreative value. There is an enormous body of freshwater fishermen in this country, working class anglers, who find their recreation in fishing. The rivers ought to be their playground, and it is our business, if we possibly can, to maintain them as such." It is no part of the purpose of a book of this nature to deal with the various methods of angling, a subject which possesses a voluminous literature of its own; nor is it possible or even necessary to justify the sport as a means of what Professor Jordan has called "physical and moral regeneration." Angling for food must be accounted one of the earliest of human activities, and certainly dates back to the Stone Age. Its development as a sport or craft is, comparatively speaking, recent, but as such provides healthy recreation for a large percentage of the population of civilised countries. It has been estimated that in England and Wales alone probably some four hundred thousand persons make a regular hobby of angling, and in the county of Yorkshire, before the war, there were no less than forty thousand anglers belonging to recognised societies out of a total population of some four millions. In the Trent Fishery Board area, to mention one region well known for its fishing prospects, seventy-three thousand licences were taken out for angling in 1929. Unfortunately, the great increase that has taken place in the number of fishermen has led to a corresponding rise in the value of rivers and other stretches of water, particularly those famous for their game fishes, so that angling, at least for Salmon and Trout, is fast becoming a pastime for the rich alone. Enough has been said to emphasise the value of the sport to the general welfare of mankind, and this has been well summed up by the great Izaak Walton, the father of modern angling, in the following words: "No life, my honest scholar,—no life so happy and so pleasant as the life of a well-governed angler"; and again: "God never made a more calm, quiet, innocent recreation than angling." Furthermore, the keen angler, with an earnest desire to know something of the lives and habits of the fishes which he catches or of the insects that he uses as lures, may well be in a position to provide scientific men with valuable data regarding their habits, movements, food, and so on. Indeed, many of the interesting specimens of fish preserved in our national collection at South Kensington have found their way there through the good offices of members of the angling fraternity, and more than one fish hitherto unknown to science has been first of all discovered by a fisherman.

If the strictly fresh-water fishes are commercially unimportant, the same cannot be said of the migratory forms such as the Salmon, Sea Trout, and Eel, and it behoves us to make every effort to maintain or even increase the numbers of these fishes, which are believed to have declined markedly within recent years. It is held by some people that artificial hatching of Salmon will provide an easy and infallible remedy for any amount of over-fishing, but so far there is no definite evidence that the yield of any river has been maintained or improved by this method of cultivation. It seems far more likely that a careful regulation of the fisheries, coupled with a thorough knowledge of the life histories of the fishes concerned, will do more towards improving the stocks than any amount of hatching and stocking. To improve the fisheries it is necessary to regulate the netting, so as to allow of the passage of a reasonable number of adult fish to propagate their kind and to satisfy the angler; the journey of the fish to the spawning grounds in the upper waters must be facilitated as far as possible; and finally, the fish must be protected while engaged in spawning. As far as the netting is concerned, a good deal has already been carried out, and serious over-fishing practically stopped. The removal of obstructions of all kinds, whether natural or artificial, lying between the fish and the spawning beds, is of the greatest importance, and it is in this direction that action is urgently required on many rivers. Such natural obstacles as waterfalls may provide a complete barrier to the ascent of Salmon or Sea Trout, and those of the artificial kind, such as dams, dykes, and weirs, are even more numerous. The remedy lies in the provision of some type of Salmon pass, ladder or lift, to facilitate the passage of the fish over or round the obstacle, but the expense incurred has prevented this from being done in many cases, and it seems certain that stringent legislative measures will have to be taken if the stocks of fish are to be saved.

The most serious obstacle of all to the welfare of fresh-water fishes, and one which provides an all too effective barrier to the ascent of Salmon and Sea Trout, is the wholesale pollution of the rivers which has been going on practically unchecked for a long time. The development of certain industries has reduced the water in some of the rivers to a terrible state, and crude, untreated sewage, the poisonous effluents of steel and iron works that manufacture by-products, from sugar beet and artificial silk factories, chemical works, collieries, mines, and the like, are being poured into our rivers and streams in ever-increasing quantities to poison or asphyxiate vast numbers of fishes and other forms of animal life. Fortunately, the outlook is not hopeless, and a vast amount of research and inquiry is now being carried out as to the best methods of dealing with this menace. A great deal of unnecessary pollution is due solely to ignorance or indifference on the part of factory owners and local bodies, as there are comparatively few waste products that cannot be dealt with scientifically and their harmful effects minimised. "The country is waking up to the fact," writes Mr. Calderwood, "that growth in industry does not necessarily mean the fouling of our rivers, and manufacturers and others responsible for the present state of affairs are realising that public opinion is against them if they persist in their inattention to the needs of river purification. . . ." Another form of commercial undertaking that provides a new menace to the fisheries for Salmon and Trout is the development of hydro-electric schemes, which means the building of large dams, the alteration of water-courses, and changes in the volume of water, to say nothing of the damage done to the spawning grounds. The Salmon rivers of the Pacific coast of North America have been particularly affected by such undertakings for a number of years.

Among minor contributory causes to the decline in the stocks of fish, mention may be made of the depredations of otters and fish-eating birds, and of human poachers, but these are unimportant in comparison with those dealt with above.

The subject of fish diseases is worthy of some consideration, for there are certain contagious maladies that play havoc with the stocks of fresh-water fish and constitute a serious menace to fish culturists. Tumours and growths of various kinds have been described in some of our food-fishes, but by comparison with other animals, marine fishes seem to suffer from very few specific diseases: it is among the fresh-water forms, and more particularly among those living under artificial conditions, that predisposition to serious maladies is most marked. These maladies may be due to bacterial infection, to animal or vegetable parasites, to bad feeding, to pollution of the water, and to physical causes of all kinds.

Among the more serious epidemic diseases is that known as Furunculosis or "Ulcer Disease," and the damage caused by this malady to the stocks of Salmon and Sea Trout has reached alarming dimensions in recent years. It is due to a specific germ, *Bacillus salmonicida*, which invades the blood-stream and is thus distributed through every organ of the body. It is highly infectious, being spread by the contact of infected with healthy fish, or by the discharge of the germs from the body of a diseased fish into the water: there is also reason to believe that perfectly healthy fish may act as carriers without themselves developing the disease. So far, it has been possible to do very little in the matter of treatment, but the prompt notification of outbreaks, and the quick removal and burial of dead fish from infected waters, may do much towards preventing the spread of the disease. The "Salmon Disease," so-called because it is most prevalent in Salmon and Sea Trout, is likewise caused by a bacillus (*B. salmonis pestis*), and this invades the tissues of the fish, gaining entrance through an abrasion or ulceration of the skin, multiples rapidly, and forms areas of mortified flesh which form ideal soil for the growth of a deadly fungus (see below). In "Tail-rot" and "Fin-rot," particularly rife among Goldfish and other cultivated species, bacilli of one kind or another are again the causative factors. The tail or fins become gradually frayed and stringy, finally disintegrating and dropping off. Ichthyophthiriasis or "White-spot Disease" is another very common fish malady, the victim being covered with white specks, each of which represents a minute pit eaten through the scale pigment by a protozoan parasite. Such an attack is not necessarily fatal in itself, but the resulting sores are nearly always attacked by fungus spores which eventually kill the fish. The parasitic protozoa, known as *Myxosporidia* often cause epidemic diseases of a serious nature, the epidermis of the gills, the fins, and certain internal organs, developing creamy white, wart-like growths or tumours in which bacilli develop and multiply rapidly. When these tumours burst, the parasites are disseminated in the water, and the resulting ulcers are attacked by fungus.

The fungus mentioned above (*Saprolegnia ferax*) is not in itself a specific disease, but only makes its appearance on individuals weakened by other maladies, or those whose vitality has been lowered by unhealthy conditions, pollution, or by the effort of the reproductive act; it nearly always attacks fish with bruises, wounds, or abrased surfaces, on which the spores floating in the water are able to obtain a hold. Once established, the roots or rhizoid portions of the fungus penetrate into the living tissues of the victim, and commencing with a small infection on the site of an injury, it spreads like leprosy over the whole body, fins, eyes, gills, and other parts, until death supervenes. It attacks young and old fish alike, and the spores may lodge on dead or unfertilised ova, and from thence spread to healthy eggs. Examined under a powerful lens, the fungus may be observed to have the form of numerous fine filaments projecting from the surface of the skin, while to the naked eye the growth has the appearance of fine cotton-wool. It is particularly prevalent among fishes kept in small ponds and aquaria, but also attacks those living in a wild state. The most satisfactory remedy lies in dipping the infected individuals in salt water (one ounce of common or rock salt to a gallon of water) or into a mixture of permanganate of potash (Condy's Fluid) and water of a deep claret colour, wiping off the visible growth with a swab of cotton wool. Other remedies which have proved fairly successful include paraffin oil, kerosene, formalin, carbolic acid, copper sulphate, lime and boracic acid, but it depends largely on the condition of the fish whether it be killed or cured by such drastic treatment. It is not sufficient to remove the fungus from the fish themselves, but the receptacle, whether bowl or pond, must also be treated with one of the above-mentioned fungicides to avoid the danger of re-infection. In the case of aquaria or cement basins this can be done without difficulty, but where the fishes are living in natural ponds or large stretches of water the complaint is very much harder to eradicate. Complete disinfection of the whole pond, followed by a period of some weeks or months during which the water is allowed to lie fallow, provides the only hope of a permanent cure. The matter is really one of prevention rather than cure, for in nearly every case of a severe epidemic it can be shown that the general hygiene of the pond is at fault.

Nearly all fishes are infested to a greater or lesser extent by animal parasites of various kinds, some of them causing serious discomfort or injury, others apparently harmless. Two kinds may be recognised: (1) those that live on the external surface of the host (ectoparasites), and (2) those that live inside the host (endoparasites). The first category includes the Leeches and Crustaceans, the second the Protozoa and worms of various kinds. Leeches are frequently found attached to fresh-water fishes, but, although they suck the blood of their hosts, they do little harm unless present in large numbers. Among the crustacean parasites are included the Sea Lice and Gill Maggots. Fresh-run Salmon and Sea Trout are generally infested with Sea Lice (*Lepeophtheirus*), belonging to the group of Crustacea known as Copepods, but differing from their free-swimming relatives in having fewer segments and limbs, and in having their organs modified in various ways to fit them for their peculiar mode of life (Fig. 141). They become firmly attached to the body of the fish, living entirely on the nourishment obtained from its blood. They are unable to live for any length of time in fresh water, so that their presence is a sure indication that the fish has recently left the sea. Females are much more numerous than males, and are considerably larger, measuring about three-quarters of an inch in length. Other forms of parasitic Copepods occur in both marine and fresh-water fishes, and many of them are so much modified for a parasitic life

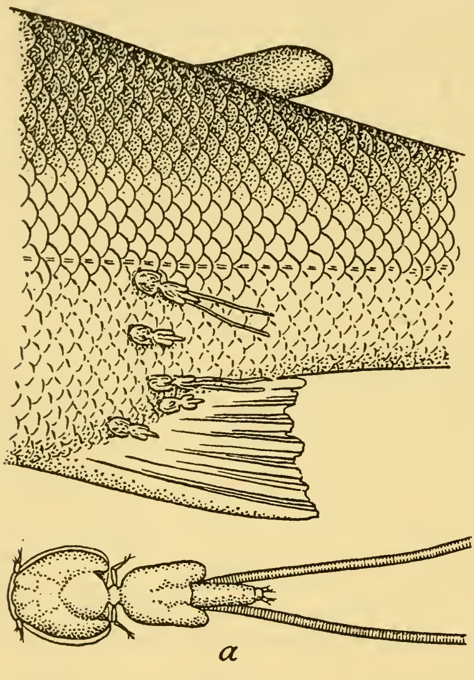
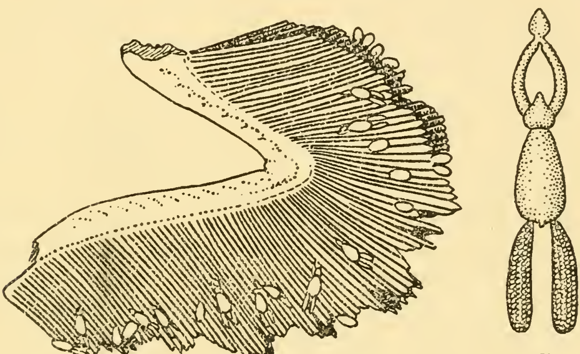


Fig. 141.
Sea Lice (*Lepeophtheirus salmonis*) on Salmon.
a. Single specimen, × 3.

that their crustacean affinities are scarcely recognisable, and it is only when their whole life history is known that their place in the system can be determined. Generally, the conspicuous egg-sacs draw attention to the presence of the parasite, whose head and anterior parts may be buried in the tissues of the host.

The so-called "maggots" (*Salmincola*) infesting the gills of Salmon and other fish are more remarkable, and are much less crustacean-like in appearance. One pair of limbs has been modified into long arms, uniting at the tip to form a sucker, by means of which the animal adheres to the gills. At the



a

Fig. 142.
Gill Maggots (*Salmincola salmonea*) on gills of Salmon.
a. Single specimen, ×3.

other end of the shapeless, fleshy body is a pair of long egg-sacs, each containing several series of eggs (Fig. 142). The males of this genus are little known, but are dwarfed, and sometimes to be found attached to the females, which grow to a length of a little more than a quarter of an inch.

Mention may also be made of the so-called Carp Louse (*Argulus*), another crustacean parasite resembling the Copepods, although its relationship to that group is now considered doubtful. This creature has a broad, flat, and very transparent body, about three-sixteenths of an inch in length, and attaches itself to different species of fresh-water fishes by means of a pair of large round suckers on the under side of the head. It is only a temporary parasite, and is frequently found swimming free in ponds and rivers. It sucks the blood of the fish, but does little harm except in the ponds of hatcheries, where the fish are crowded together.

Internal parasitic worms of one kind or another often occur in most marine and fresh-water fishes, and include Trematodes or Flukes, Tape Worms, Round or Thread Worms, and Thorn-headed Worms. Flukes (*Trematoda*) are most common in river and lake fishes, some occurring in the adult form, either as ectoparasites on the gills or skin, or as endoparasites in the alimentary canal, while others in the pre-adult stage become encysted in the tissues or in the body cavity. Thus, sometimes the fish is the final host of the fluke, but in other cases it is only a temporary or intermediate host, and the development of the parasite is completed within some fish-eating vertebrate. Roach, Dace, Bream, and other coarse fish are sometimes found with the body covered with small black spots, and examined under a microscope each of these is seen to consist of a mass of pigment surrounding a larval Trematode. No harm appears to be done to the fish, and heavily spotted individuals are as healthy as those which are uninfected.

As with the Flukes, so with the Tape Worms (*Cestoda*), the fish is sometimes the final host, the worm passing the earlier stages of its development in some smaller animal preyed upon by the fish, and sometimes only the intermediate host. Two genera, of which one (*Ligula*) occurs in various fresh-water fishes, and the other (*Schistocephalus*) is very common in the Sticklebacks, grow to a very large size as larval forms in the body cavity of the fish, and become adult in the intestine of various fish-eating birds. In certain seasons nearly all the Sticklebacks living in a given locality have been found to be infected with this parasite, which fills the abdominal cavity to such a degree that the host appears unusually plump or is even swollen like a miniature balloon. In North America, Tape Worms forty centimetres in length, attributed to the genus *Ligula*, have been taken from Suckers (*Catostomidae*) only ten centimetres long, the weight of the parasite being more than one-quarter that of the fish. The worms lie quite free in the body cavity, and although they do not move about and have no suckers or hooks to cause definite injury, they do considerable damage by crowding the organs of the fish into unnatural positions, as well as by absorbing the serous fluid. It is of some interest to note that *Ligula* is considered a delicacy in Italy and the south of France, where it is known as "Maccaroni piatti" and "Ver blanc" respectively. A Tape Worm known as *Diphyllobothrium latum* passes the last larval stage of its development in fishes, the larvae occurring in large numbers in the viscera and muscles of the Pike and other fresh-water species, which become infected by swallowing the small "water-fleas" in which the earlier stages occur. Cooking destroys them, but in parts of Eastern and Central Europe, as well as in North America and Japan, the fish are eaten in a raw, smoked, or inadequately cooked state, and the worm continues its life-cycle in the intestine of its human host. The larvae (plerocercoids) may grow to a length of twenty to thirty feet, and are sometimes responsible for a severe type of anaemia. Man is not the only host, the same worm occurring in wild and domesticated carnivorous mammals.

Round Worms or Thread Worms (*Nematoda*) of various kinds occur in the adult form in almost all fishes, generally in the alimentary canal, while larval Nematodes may be found in the connective tissue, body cavity, or muscles. These parasites rarely do much harm unless very abundant. Small Nematodes are frequently to be seen encysted or free in the tissues surrounding the abdominal cavity of such food-fishes as the Cod, Hake and Haddock, and many people hesitate to eat the fish on this account. Such fears are quite groundless, however, for not only are the worms destroyed by cooking, but they are not of the type likely to flourish in a human host. Thorn-headed Worms (*Acanthocephala*) may occur in large numbers in the intestines of fishes, where they may sometimes cause intense irritation and gastric disturbance. The larval stages are passed in some smaller animal, forming part of the normal diet of the fish.

Monstrosities are comparatively rare in a state of nature, and cannot be considered in any detail. "Bulldog-nosed" or "Pug-headed" Trout, Pike, etc., in which the snout is abnormally shortened so that the lower jaw projects, are captured from time to time, and hump-backed or hog-backed specimens, with the vertebral column shortened, curved, or otherwise malformed, also occur among marine and fresh-water fishes. Such individuals do not appear to be necessarily unduly handicapped in the struggle for existence, often attaining to a fair age, and generally appearing well nourished. Abnormalities of the fins also occur in a wild state, extra fins being developed in unusual situations, or normal ones reduced in size or absent altogether, as well as variations in scaling, coloration, and so on. Among domesticated fishes monstrosities are much more common, and, in the case of the Goldfish (*Carassius*), abnormal types originally appearing as mutations or "sports" have been perpetuated by the Japanese breeders to become distinct races or varieties. The grotesque "Pop-eye," the "Veil-tail," and the remarkable "Lion-head" are familiar objects in aquaria (Fig. 143), and represent monstrosities that have bred true to

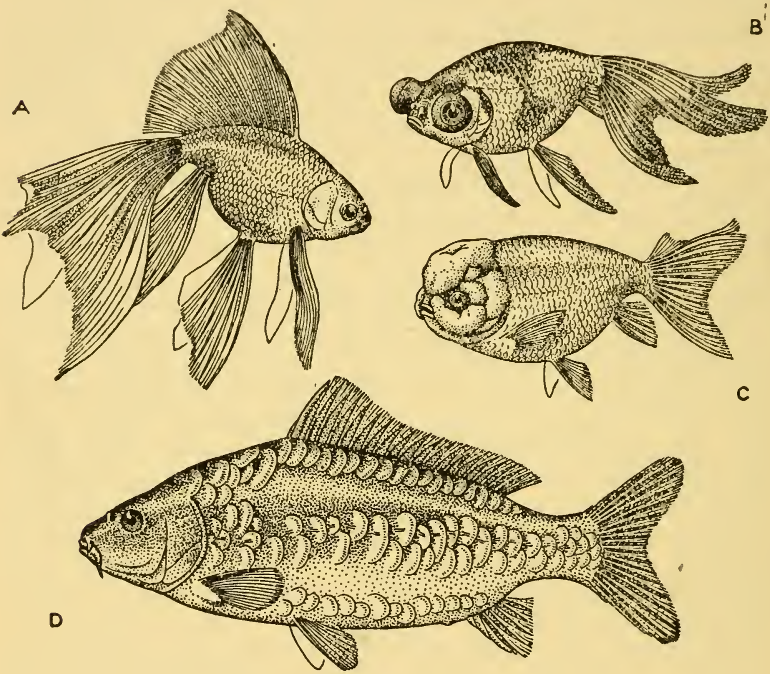


Fig. 143.—DOMESTICATED FISHES.

A. Veil-tailed variety of Goldfish (*Carassius auratus*); B. Pop-eyed variety; C. Lion-headed variety. All × about $\frac{1}{3}$; D. Mirror Carp, a cultivated variety of the Common Carp (*Cyprinus carpio*), × about $\frac{1}{6}$.

type. Double-headed fry, or young fishes abnormally united or incompletely divided, frequently occur in fish hatcheries, but very rarely live beyond the stage at which the yolk-sac is absorbed. These and other abnormalities of a like nature are generally congenital in origin, but some may be due to accidents to the young or adult fish. Fishes in general have little power to regenerate lost parts, beyond reproducing the tips of the fins and other superficial structures which may be injured or broken. Many fish that have had their tails bitten off will survive the injury, the wound will heal, and rudimentary fin-rays may be developed in the region of the scars.

There is another important relationship between fishes and mankind which has not yet been mentioned, namely, the use of certain species in the control of disease. During the last twenty years great advances have been made in the study of this subject, and it has been found that a number of fishes are valuable allies to man in his war against malaria, yellow fever, and other dread diseases of tropical countries. These maladies are spread through the agency of mosquitoes, and it has been shown that the most effective method of reducing the numbers of these insect pests is to destroy them while still in the larval stage. The absence of yellow fever in Barbados, although prevalent in the neighbouring islands, had long been noticed, and it was suggested that this might be due to the presence of a Top Minnow or Cyprinodont known as the "Millions" (*Lebistes*), so called because of its great abundance. This little fish (Fig. 144) inhabits the pools and marshes in which the mosquitoes habitually breed, and the theory was that the fish fed on the larvae in sufficient quantities to make the numbers of fever-bearing adult insects negligible. The theory has recently been put into actual practice with excellent results, and the introduction of the "Millions" into fever-stricken districts of tropical America has proved most efficacious in checking the scourge. Attempts were made to introduce the same species into Africa and Asia without much success, but it was soon found that these countries also possessed their larvicidal fishes, and it was only necessary to find out which species included mosquitoes in their normal diet, or could be persuaded to feed on them if required. These include not only Cyprinodonts but Carp, Gold-fish, Barbels, Eels, Cichlids, Gobies, and many other forms, and all have been used with some success in controlling human disease. In most cases the assistance of man is required in order to bring the fish to the breeding-grounds of the mosquitoes, but once established there they will carry out their duties "without further charge"!

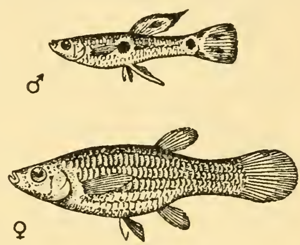


Fig. 144.
Male and female "Millions" (*Lebistes reticulatus*). Nat. size.

In considering the relations between fishes and mankind, the keeping of living examples in aquaria and the exhibition of dead specimens in museums will naturally come to mind. Where it is impossible to observe fishes in their natural surroundings, much may be learned of their habits by studying them in captivity, and aquarium-keeping undertaken in an intelligent manner will be found to provide a fascinating hobby at a comparatively small cost, and will prove a source of infinite amusement and instruction. Many rare and interesting tropical fishes are nowadays imported by dealers, especially in Germany, where many devotees are to be found. The formation and maintenance of marine and fresh-water aquaria is a subject too vast to be dealt with here, and, moreover, is one which has been treated by experts in books especially devoted to the matter. The subject of museum exhibitions is likewise worthy of a chapter to itself, but considerations of space will make it necessary to give only a few lines on the collection of fishes in the National Museum at South Kensington.

A visitor to the fish gallery at the Natural History Museum often goes away under the impression that the series of some two or three thousand coloured plaster casts and models, stuffed and painted skins, preparations in alcohol, skeletons, etc., represent the whole of the collection, and some have expressed disappointment at the absence of representatives of certain species from the cases. Actually, the exhibits represent a carefully selected series of specimens, displayed and labelled in such a manner as to interest visitors and to give a general impression of some of the more interesting members of the fish world, and arranged to illustrate their relationships one to the other. In addition, special cases are devoted to breeding, development, coloration, sexual differences, and so on, while others are designed to give an idea of the anatomy of the fish's body as described in these pages. But this is by no means the only collection in the museum, and there is a very much more important series of specimens which is not exhibited to the public. Some of these consist of dried skins, stuffed examples, and skeletons, but the vast bulk of them are preserved in alcohol in glass bottles. These bottles are clearly labelled with the correct name of the species, and are all catalogued and arranged in cupboards according to their natural relationships. This study collection contains more than one hundred and fifty thousand specimens, and although there are naturally a number of gaps still to be filled, it includes representatives of about eleven thousand out of some fifteen thousand species known to science. This vast series of fishes is available to recognised students, and scientific men from all over the world come to the museum to work on some of the specimens. Every year some thousand or more new examples are added to the existing collection, and it is one of the duties of the curator to see that these are correctly named and incorporated with the others. Many are obtained through the medium of large expeditions sent out to various regions of the world, but even more owe their existence in the museum to the good offices of explorers, travellers, and others resident in foreign countries, who have spent their spare time in amassing collections in little known parts of the world to enrich the National Museum.

CHAPTER XXI

MYTHS, LEGENDS, ETC.

Size: largest and smallest fishes. Longevity. Medicinal uses of Tench and other fishes. Myth of the "ship-holder." Monk-fish, Bishop-fish, Mermaid and Sea Serpent. Fishes from the clouds. The Miraculous Draught. Crucifix-fish.

Myths and legends concerning fishes are both numerous and diverse, but since it is impossible to include a fraction of them within the space of a single chapter, it must suffice to select a few of the more interesting for consideration here.

Legends concerning fish of abnormal size and weight are all too common, and incredible tales have appeared in print of monstrous specimens that have just escaped the fisherman's net or the angler's hook, to say nothing of those "fish stories" never actually published. Certain fishes do, of course, grow to a large size, and as far as the sea is concerned, pride of place must be given to the Whale Shark (*Rhineodon*), which attains to a total length of fifty feet or more and a weight of several tons (Fig. 145). The Basking Shark (*Cetorhinus*), with a length of some thirty-five to forty feet, comes a good second, with some of the Blue Sharks (*Carcharinidae*) not very far behind. Certain species of Flat-fishes (*Heterosomata*) grow to a comparatively large size, the classical example being the Adriatic Turbot (*Rhombus*) mentioned by Juvenal in his Fourth Satire. This particular fish is described as being so enormous that the fisherman promptly took it as a present to the Emperor Nero, who summoned his senators to view this monster, for which there was no dish of sufficient size. A touch of comedy is given to the scene by the description of the blind Catullus Messalinus, who was profuse in his wonder and admiration of the fish, although turning in the direction exactly opposite to that in which it lay! The Halibut (*Hippoglossus*) attains to an even greater bulk, specimens of seven or eight feet in length and weighing three hundred or four hundred pounds being by no means rare, and much larger examples have been recorded. Among strictly fresh-water fishes, the record for size is held by the Arapaima or Pirarucu (*Arapaima gigas*) of the rivers of

Brazil and the Guianas, with a length of about fifteen feet and a weight of four hundred pounds (fig. 100c).

At the other end of the scale is a tiny Goby (*Mistichthys luzonensis*) found only in one of the lakes of Luzon in the Philippine Islands, which enjoys the distinction of being the smallest of all known vertebrates, fully mature individuals measuring only half an inch in total length (fig. 146). This fish is very abundant, and in spite of its small size forms an important article of food. Some of the Gobies found in the coral-reef pools of Samoa and other islands of the Pacific are nearly as small, and certain Top Minnows or Cyprinodonts of the New World (*Poeciliinae*) are less than an inch long when fully grown.

There is a widespread and popular belief that certain species

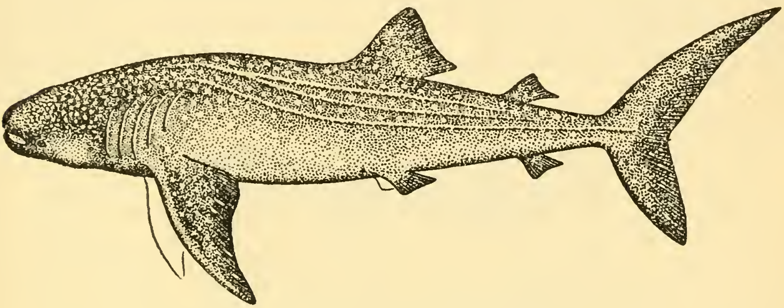


Fig. 145.—THE LARGEST FISH KNOWN.
Whale Shark (*Rhineodon typicus*), $\times$ about $\frac{1}{140}$. (After Gudger.)

of fish live to a vast age, and stories of Carp of one hundred or one hundred and fifty years of age, and of hoary Pike more than two hundred years old, occur in some of the works on natural history published during the eighteenth and nineteenth centuries. As Dr. Regan has pointed out, the statements concerning most of the very old Carp "rest on very unreliable evidence," and although there is good reason for believing that under artificial conditions this fish may attain to a good old age, it is doubtful whether it exceeds fifteen years in a wild state. Satisfactory proofs of the alleged great age of Pike are likewise difficult to find, but the same author remarks that "it is probable that fish of sixty or seventy pounds weight are at least as many years old." The story of the so-called "Emperor's Pike" makes amusing reading, and is one that was a great favourite with all writers on fishes since it was first printed by Gesner in 1558. The fish was said to have been captured in a lake in Württemburg in the year 1497, and was found to have a copper ring encircling the gill region bearing an inscription to the effect that the Pike had been placed in the lake by the Emperor Frederick II in the year 1230, no less than two hundred and sixty-seven years before its final capture. Unfortunately, the accounts given by other authors reveal a number of discrepancies, and they cannot agree as to which of the Fredericks was responsible for marking the fish, or as to the exact locality at which it was finally recaptured. Its length has been stated to be nineteen feet, and its weight five hundred and fifty pounds, and an oil painting of it is said to be preserved at the castle of Lautern in Swabia: what appears to be a contemporary copy of this painting is in the Natural History Museum at South Kensington. The actual skeleton of the monster is reputed to be preserved in the cathedral at Mannheim, but this was studied by a celebrated German

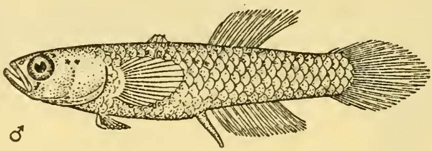


Fig. 146.—THE SMALLEST FISH KNOWN.
Mistichthys luzonensis, × 4. (After H. M. Smith.)

anatomist during the last century, who found that the vertebrae in the backbone were too numerous to belong to a single individual—in other words, that the skeleton had been lengthened to fit the story!

The shortest-lived fish would appear to be the Transparent or White Goby (*Latrunculus pellucidus*), the course of whose life is run in a single year. This is probably the only recorded example of an "annual vertebrate," although it has been stated that the little Ice-fish (*Salanx*) of China has a similarly short life.

A curious myth has arisen concerning the alleged healing powers of the Tench, and it has long been believed that sick or wounded fish were cured by the touch of this fish. It is true that other fishes have been observed to rub themselves against the Tench's body, but the idea that the slime acts as a kind of balsam is now generally discredited. According to Izaak Walton the Tench is the particular physician of the Pike, who "forbears to devour him though he be never so hungry." As a matter of actual fact, a small Tench is regarded by many anglers as an excellent bait for Pike in certain localities. Its healing powers were also supposed to extend to man: applied to the hands or feet of a sick person it cured him of fever, and jaundice, headache, toothache, and other complaints were treated in a similar manner. In ancient times fish played an important part in the pharmacopeia of the physician, and Mr. Radcliffe tells us that, in one book alone of Pliny, fish are recommended as remedies, internal or external, no less than (according to his reckoning) three hundred and forty-two times. Many of these curious remedies have been collected together by Mr. Radcliffe, and may be found in his book, *Fishing from the Earliest Times*. Among other medicinal uses of fish at the present time, mention may be made of cod-liver oil; the flesh of the Escolar or Castor-oil-fish (*Ruvettus*), which acts as a purgative; and the insulin obtainable from the pancreas of certain species. In certain parts of the world the otoliths or ear-stones of fishes are used as a prevention or cure of colic, as well as a talisman to avert the evil eye.

There is an extremely ancient legend concerning the Remora or Shark-sucker (*Echeneis*) to the effect that it is able to impede the progress of sailing vessels or even to stop them altogether. It occurs repeatedly in classical and mediaeval literature, and is illustrated on Greek and Roman vases and other pottery. Pliny tells us that the death of the Emperor Caligula was due to his great galley being held up by a Remora while the remainder of the fleet escaped. The earliest known published figure of this fish in the act of staying the progress of a ship is to be found in J. von Cube's *Hortus sanitatis*, a curious work published in 1479. The method of fishing for turtles with the Remora, witnessed by Christopher Columbus in 1494 and described by his son, Ferdinand Columbus, has been dealt with in a previous chapter (*cf.* p. 389). The scientific name of the fish, *Echeneis*, signifies "holding back," and the older writers consequently refer to it as the Reversus or "Ship-holder." The name Reversus was also applied to the Porcupine-fish (*Diodon*), a species which seems to have been confused with the Remora, one author, Aldrovandis, describing and figuring it as the spinous variety of the Reversus. It has been suggested that this name was applied to the Porcupine-fish on account of its curious antics when hooked.

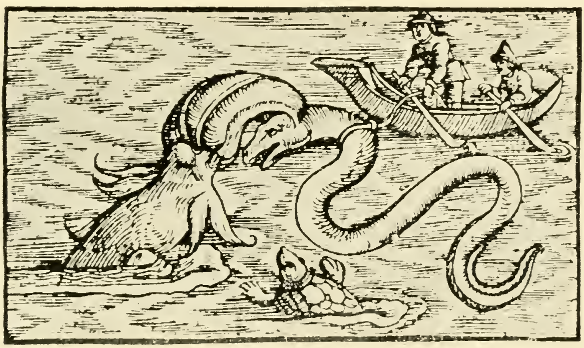
Among the grotesque and entirely mythical fishes described during the Middle Ages mention may be made of the "Monk-fish" and "Bishop-fish," both of which are illustrated in Rondelet's *Histoire Entière des Poissons*, published in 1558. Rondelet remarks that his picture of the "Monk-fish" was given to him by the very illustrious lady, Margaret de Valois, Queen of Navarre, who received it from a gentleman, who gave a similar one to the Emperor Charles V, then in Spain. This gentleman affirmed that he had actually seen the monster portrayed cast on to the shore in Norway during a violent storm!

The mermaid, half-maiden, half-fish, represents a particularly tenacious myth, which still persists among ignorant people at the present day. In certain cases Dugongs and Sea Lions, with their somewhat human heads and fish-like bodies, have been mistaken for mermaids, but the persistence of the belief is due largely to the dried specimens brought home by travellers in the Orient. On close examination these are found to consist of the head and shoulders of a monkey cleverly united by wires to the tail-end of a fish (often the Nile Perch). These are manufactured in some numbers by the Egyptians and Chinese, who sell them at a handsome profit to credulous tourists, together with documents purporting to be signed by witnesses of the capture of these creatures in the sea. It is said that the great Linnaeus was once forced to leave a town in Holland for questioning the genuineness of one of these mermaids, the property of some high official.

Another persistent myth, but one which may any day be transferred from the realm of legend to that of actual scientific fact, is that of the great Sea Serpent. There are, of course, the poisonous Sea Snakes of tropical seas, some of which grow to a length of ten or twelve feet, but these, although certainly "serpents," are not the Sea Serpents of legends. The great Sea Serpent, descriptions of which have appeared in almost every language of civilised peoples, has unfortunately not yet come under the observation of scientific men, and it is to be feared that very nearly all the records of its occurrence are to be put down to seamen's yarns, perhaps aided by strange tricks of memory, the power of suggestion, the effects of over-indulgence in alcohol, or to cases of mistaken identity. The Sea Serpents of Aristotle, Pliny, and other classical authors seem to have been nothing more than gigantic eels. The monster described as having the head of a horse with a flaming red mane is the Oar-fish or Ribbon-fish (*cf.* p. 65), a species which

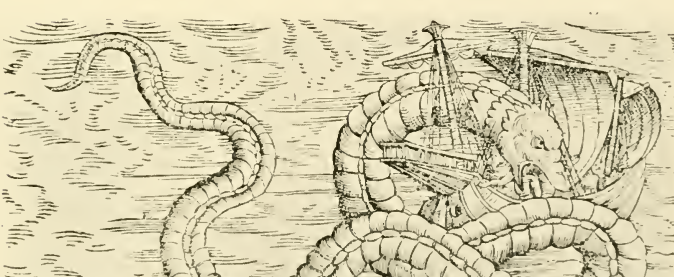
a.

A downpour of Fishes in Scandinavia. From Olaus Magnus' *Historia de Gentibus Septentrionalibus*, 1555.



b.

Fishing with the Remora. From Conrad Gesner's *Historiae Animalium*, Lib. iv., 1558.



c.

The great Sea Serpent. From Conrad Gesner's *Historiae Animalium*, Lib. iv., 1558. (After Olaus Magnus, 1555.)

Plate VII.

probably grows to more than fifty feet in length, and may sometimes be seen swimming with undulating movements at the surface of the sea. The famous Sea Serpent, measuring fifty-six feet in length, that was cast up on the shore of Orkney in 1808 was almost certainly this fish. Other reputed Sea Serpents are believed to be giant Squids or Cuttle-fishes, many of the oceanic species attaining to an immense size, and although normally living in the abyssal depths, they are known to come to the surface on occasions or to be stranded on the shore after a violent storm. Very little is known of these monsters of the deep, and some of the species have been described only from the semi-digested remains that have been taken from the stomachs of Sperm Whales. It will be recalled that many of the tales of the Sea Serpent describe it as battling with a whale, and the long and sinuous tentacles or arms of these molluscs, coupled with their habit of sometimes spouting water, account for the so-called "spouting head and writhing tail." Other objects that might conceivably be mistaken for a serpent by an untrained observer include a school of porpoises swimming in line, their curved bodies suggesting the sinuous coils of an eel-like body; two large Basking Sharks, swimming one behind the other, as is sometimes their habit; a fragment of wreckage, or even a long string of seaweed. Dr. Oudemans has published a most valuable book on the subject, in which nearly all the records are discussed at some length, and the available evidence carefully sifted. He concludes that, although many of the accounts may be disposed of in one of the ways mentioned above, there remain a number which display a certain amount of general agreement and appear to describe something for which none of these theories will really suffice. What this "something" may be can only be guessed, but Dr. Oudemans believes it to be a large mammal allied to the Seals and Sea Lions. Finally, mention may be made of a remarkable creature that was observed off the coast of Brazil in 1905 by two competent naturalists, and described in the *Proceedings of the Zoological Society of London*. "At first," they write, "all that could be seen was a dorsal fin about four feet long, sticking up about two feet from the water; this fin was of a brownish-black colour and much resembled a gigantic piece of ribbon seaweed. . . . Suddenly an eel-like neck about six feet long and of the thickness of a man's thigh, having a head shaped like that of a turtle, appeared in front of the fin." The creature soon disappeared from view, before it was possible for them to make out the shape or size of its body, and it is still doubtful whether it was mammal, reptile, or fish.

The following news item appeared in the *Northern Whig and Belfast Post* on 30th May 1928 and caused considerable interest:—

> "Dozens of tiny red fish were found on the roof of a bungalow on the farm of Mr. James McMaster, Drumhirk, near Comber, and on the ground in the vicinity yesterday morning, and the extraordinary occurrence caused considerable speculation. In the course of enquiries it was ascertained that just before the discovery of the fish there had been an exceptionally violent thunderstorm with heavy rain. There is no river in the neighbourhood, the nearest sheet of water being Strangford Lough, two miles distant, and the theory advanced by an expert was that the fish had been lifted from the sea in a waterspout."

Occurrences of this nature are rare, but by no means unknown, more than fifty accounts of these "rains of fishes" having been recorded from various parts of the world. The first mention of the phenomenon is to be found in the *Deipnosophistae* of Athanaeus, who lived at the end of the second and the beginning of the third century A.D. In an English translation, under the heading, "De pluvia piscium," occurs the following:—

> "I know also that it has rained fishes. At all events Phoenias, in the second book of his *Eresian Magistrates*, says that in the Chersonesos it once rained fishes uninterruptedly for three days, and Phylarchus, in his fourth book, says the people had often seen it raining fish."

Several explanations have been put forward to account for the sudden appearance of fishes from the clouds, but there seems to be little doubt that the suggestion of Eglini in 1771, that the falls are due to the action of heavy winds, whirlwinds and waterspouts, is the correct one. The "rains" have nearly always been described as being accompanied by violent thunderstorms and heavy rain, and moreover they are usually confined to restricted areas, and the fishes are found in a comparatively straight path over a wide stretch of country. It appears that the action of a waterspout passing over shallow coastal water, or of a tornado over shallow inland pools and lakes, may be sufficient to lift small fish to a considerable height, and to transport them and deposit them at some distance from the locality at which they were picked up. Waterspouts and tornadoes are physically similar phenomena, the former occurring over stretches of water or over the ocean, the latter over dry land. In some cases it is believed that the fishes are not only carried up into the rapidly rotating vortex of air that forms the body of the waterspout or tornado, but even right up into the thunderstorm cloud itself. There is a case on record in which a hailstone as large as a hen's egg was observed to fall during a heavy storm at Essen in 1896, containing a frozen Crucian Carp (*Carassius*) about forty millimetres in length, indicating that the fish must not only have entered the cloud but have been lifted to the very considerable height necessary for the formation of hail. Occasionally, the fish involved are of larger size, and at Jelalpur, in India, a specimen has been described as falling with others, which was about "one cubit in length and weighed more than six pounds." Falls in Europe have included Herrings, Sprats, Trout, Smelts, Pike, Minnows, Perch, Sand Eels, and Sticklebacks, and the small red fishes mentioned in the Irish account quoted above were probably of the latter species.

The Biblical story of the Miraculous Draught, to be found in the twenty-first chapter of the Gospel according to St. John, will be familiar to all, and an American ichthyologist, Mr. E. W. Gudger, has quite recently pointed out that this seemingly miraculous phenomenon is capable of a perfectly normal and rational explanation in the light of modern research on the habits of the fishes to be found in the Lake of Tiberias or Galilee. These fishes are chiefly of the family *Cichlidae*, and occur in huge numbers in the lake, habitually swimming at or near the surface of the water. Writing on the habits of the commonest species (*Tilapia galilaea*), Canon Tristram observes: "I have seen them in shoals of over an acre in extent, so closely packed that it seemed impossible for them to move, and with their dorsal fins above the water, giving at a distance the appearance of a tremendous shower pattering on one spot of the surface of the glassy lake. They are taken both in boats and from the shore by nets run deftly round, and enclosing what one may call a solid mass at one swoop, and very often the net breaks." Now the procedure of the lake fishermen at the present day, as described by Dr. Masterman in his account of the inland fisheries of Galilee, is as follows:—a man is stationed on the high ground on shore, whose duty it is to detect the presence of a shoal of Cichlids and to direct the movements of those in the boats, who proceed at once to the point indicated and surround the fish with a net. The bottom of the lake is said to be covered with large stones, and it is frequently necessary for one or more of the fishermen to leap overboard to free the net and to prevent it from breaking.

It is of interest to note that the habit of these Cichlids of congregating in shoals at the surface leaves them open to the attacks of the myriads of Crested Grebes that abound in this region. Where the fish are too large to be seized whole, the birds are in the habit of snatching at the most tasty morsel, the eyes, lifting out the eyeballs and the infra-orbital partition with a single stroke of their long, sharp beaks. This does not always cause the death of the victim, and many members of the shoals may be observed to be flourishing in a condition of absolute blindness.

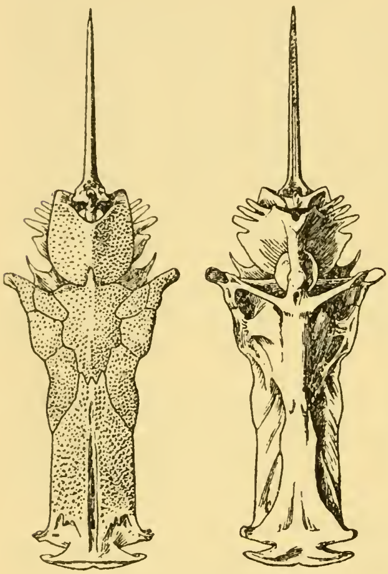


Fig. 147.—"CRUCIFIX-FISH." Upper and lower view of skull of Sea Cat-fish (*Arius proops*), × ⅓.

Of the species of *Tilapia* found in the Lake of Galilee, one is characterised by the presence of a dark spot on each side of the body, and this is locally reputed to represent the mark of St. Peter's thumb, made when he took a piece of money from the fish's mouth. The Cichlid competes for the honour of bearing this mark with the John Dory (*Zeus*), which likewise has a round black spot on the side. This fish is known in Germany as the "Peterfisch," and our own name, John Dory, is believed to be the equivalent of the Italian "Janitore," meaning a doorkeeper.

Travellers in South America and the West Indies often return with tales of the so-called "Crucifix-fish," which is said to be held in great esteem and even veneration by the natives of these parts, who look upon it as a kind of fetish or charm against danger or sickness. These are nothing more than the prepared skeletons of certain Cat-fishes of the genus *Arius*, that abound on the coasts and in the rivers of Central and South America. The name *Arius* is derived from a Greek word meaning martial, an allusion to the bony plate or shield that extends from the back of the skull to the powerful spine of the first dorsal fin. The skulls of many of these fishes exhibit on their lower surfaces a rough but readily recognisable resemblance to a crucifix (Fig. 147), while the small bones known as the Weberian ossicles (*cf.* p. 193) form a halo. The upper surface of the skull, with its rugose bones, has been described as resembling "a hooded monk with outstretched arms," or "the breastplate of a Roman solider"; the dorsal spine is said to represent the spear; and the otoliths, which rattle when the skull is shaken, are the "dice with which the soldiers cast lots for the garments of our Lord"! Another account published in 1789 states that "when the bones of the head are separated, each represents some one of the instruments of the passion of our Redeemer, forming the spear, cross, nails, etc." Such crucifix skulls may be seen frequently in the Orinoco district, and in the Guianas, and are familiar objects in the curio shops of the West Indies as well as in Georgetown, British Guiana, some of the specimens being fancifully painted and decorated.

Many other interesting matters more or less remotely connected with fishes must be omitted for considerations of space, or because they lie somewhat outside the scope of this work. These include the Fish Gods, of which Ebisu of Japan is perhaps best known; the reverencing of certain species by the ancient Egyptians; the preparation of fish mummies; and the part played by fishes in the myths and legends of various lands, or in pagan and Christian symbols. Many of these matters are dealt with in Mr. Radcliffe's valuable book, *Fishing from the Earliest Times*, the only work of its kind, and a monument of painstaking research.

LIST OF BOOKS

The following list does not pretend to provide an exhaustive bibliography of even the more important works on fishes and related subjects, but is rather in the nature of a list of easily obtainable books which it is believed should be of interest to those desiring further reading in relation to the scope of the present work. They represent, for the most part, those to which the author is most indebted in the preparation of this volume.

Allen, E. J. (edited by), *The Science of the Sea.* Second Edition. Oxford, 1928.

Boulenger, G. A., and Bridge, T. W., *Fishes.* Volume VII of the Cambridge Natural History. London, 1910.

Calderwood, W. L., *The Life of the Salmon.* London, 1907.

Calderwood, W. L., *Salmon and Sea Trout.* London, 1930.

Cunningham, J. T., *The Natural History of the Marketable Marine Fishes of the British Islands.* London, 1896.

Cunningham, J. T., *Fishes.* In "Animal Life. An Evolutionary Natural History." Edited by W. P. Pycraft. London, 1912.

Daniel, J. F., *The Elasmobranch Fishes.* California, 1928.

Day, F., *The Fishes of Great Britain and Ireland.* Two volumes. London, 1880-1884.

Day, F., *British and Irish Salmonidae.* London, 1887.

Dean, B., *Fishes Living and Fossil.* New York and London, 1895.

Fries, B., Ekström, C. U., and Sundevall, C., *A History of Scandinavian Fishes.* Second Edition. Revised and completed by F. A. Smitt. Stockholm and London, 1893.

Goodrich, E. S., *Cyclostomes and Fishes.* Part IX, fascicle 1, of "A Treatise on Zoology." Edited by Sir R. Lankester. London, 1909.

Günther, A. C. L. G., *An Introduction to the Study of Fishes.* Edinburgh, 1880.

Hutton, J. A., *The Life History of the Salmon.* Aberdeen, 1924.

Jenkins, J. T., *The Sea Fisheries.* London, 1920.

Jenkins, J. T., *The Fishes of the British Isles.* London, 1925.

Jordan, D. S., *A Guide to the Study of Fishes.* Two volumes. New York, 1905.

Jordan, D. S., *Fishes.* New York and London, 1925.

Jordan, D. S., and Evermann, B. W., *American Food and Game Fishes*. New York and London, 1902.

Kerr, J. G., *Text-book of Embryology*. II. *Vertebrata with the exception of Mammalia*. London, 1919.

Kyle, H. M., *Biology of Fishes*. London, 1926.

McIntosh, W. C., and Masterman, A. T., *The Life-Histories of the British Marine Food-Fishes*. London, 1897.

Malloch, P. D., *Life-History and Habits of the Salmon, Sea Trout, etc*. London, 1910.

Meek, A., *The Migrations of Fish*. London, 1916.

Murray, J., and Hjort, J., *The Depths of the Ocean*. London, 1912.

Radcliffe, W., *Fishing from the Earliest Times*. London, 1921.

Regan, C. T., *The Fresh-Water Fishes of the British Isles*. London, 1911.

Regan, C. T., Articles on Fishes, Selachians, etc., in the Fourteenth Edition of the *Encyclopaedia Britannica*. London and New York, 1929.

Russell, F. S., and Yonge, C. M., *The Seas*. London, 1928.

Tressler, D. K., *Marine Products of Commerce*. Washington, 1923.

Woodward, A. S., *Outlines of Vertebrate Palaeontology*. Cambridge, 1898.

INDEX

Words in italics are names of genera or species; figures in thick type refer to an illustration; f. = and in following page or pages. Specific names have not been included.

J. AND J. GRAY, PRINTERS, EDINBURGH