THE STUDY OF FOSSIL FISHES.[1]

THE discovery of general principles in the study of fossils is much hampered by the imperfection of the geological record. As every geologist is aware, we are dependent for our knowledge of the life of past ages on a few isolated episodes which have been locally preserved. There is no continuous history of the life of long periods in the rocks of any region that has hitherto been well explored. Cessations in the deposit of sediment, the recurrence of unfavourable conditions, and extensive migrations, among other causes, have all contributed to this result. An increasing acquaintance with scattered episodes in the secular development of life, however, tends to reveal its main outlines; and if we are unable to discover the actual facts we can at least arrive at an approximation to them which serves all immediate purposes. If we can determine the "fashion," so to speak, which prevailed during each successive period in the geological history of a race of animals, we are able to distinguish between those changes in anatomical structure which led to stagnation or extinction, and those which were necessary for evolution to a higher plane. An acquaintance with the precise links between one grade and the next is not of supreme importance.

In the case of fossil fishes, some general principles are already discoverable, and they may be treated as an illustration of the results which palæontology is now attaining.

The earliest remains of fish-like animals satisfactory enough for discussion are those from the Upper Silurian rocks, both of Europe and North America. They suggest that long before the latter part of the Silurian period fishes had already become a flourishing and varied race, but could not be preserved among fossils because they had not acquired a hard skeleton. The Upper Silurian fossils show how this skeleton first began, and, if we may assume that the order in which the different kinds of hard parts successively predominate is the order in which they evolved, it is easy to perceive how they gradually arose. Fortunately all the phenomena can be traced in one compact group of lowly fish-like animals, the Ostracodermi or Ostracophori, which are so readily distinguished from the fishes proper that there is no risk of confounding with them members of any other line of descent. The hard skeletal parts were confined exclusively to the skin, and in most of the earliest members of the group they were merely scattered tubercles of limy matter like the shagreen of modern sharks (Fig. 1). The tubercles fused together into armour plates in two different ways. Sometimes (as in the Cephalaspidæ) a few regularly spaced tubercles grew larger than the others, and each of these became a centre of attraction round which the immediately surrounding tubercles coalesced to form polygonal plates. These coalesced again in accordance with the shape and motions of the underlying soft parts. More rarely (as in the Asterolepidæ) fusion of the tubercles occurred first along the sensory canals, thus eventually producing overlapping armour plates which were symmetrically arranged like those of Pterichthys.

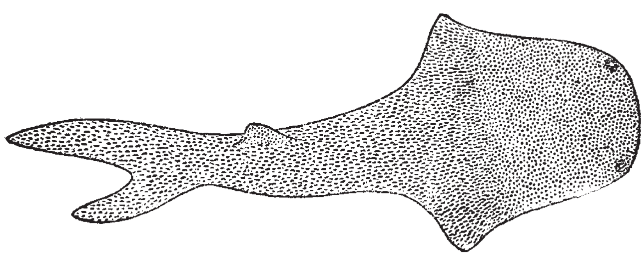

FIG. 1.—*Thelodus scoticus*, Traquair; head seen from above, the tail twisted to show dorsal fin and heterocercal tail mainly in side-view, about one-half nat. size.—Upper Silurian; Lanarkshire. To illustrate the most primitive skeleton of separate skin tubercles. [After Traquair.]

No link is known between the Ostracoderms and the typical fishes which have a lower jaw and paired fins; and it is evident that the latter had already appeared in Silurian times before they possessed a skeleton hard enough to be preserved among fossils. The Silurian and earliest Devonian Acanthodians (Fig. 2), however, cannot be far from the beginning of these typical fishes, and they seem to show how paired fins began. These very old Acanthodians are known because they are completely covered by small, hard skin-granules like those of the oldest fossilised Ostracoderms. Not only did the armour begin here in the same way as in the Ostracoderms, but there was also an occasional fusion of the skin-granules into plates where stiffness was possible or necessary. A few rows of the granules fused together at the front edge of the median fins above and below the body, thus forming cut-waters or "spines"; and as a double series of exactly similar "spines" occurs along the lower border of the abdomen where the two pairs of fins are found in later fishes, it is reasonable to infer that these are likewise the stiffened front edges of fins. In other words, paired fins were not originally restricted to two pairs, but formed a double series along the entire length of the abdomen. The later Acanthodians (Fig. 2, C, D) had only the ordinary two pairs

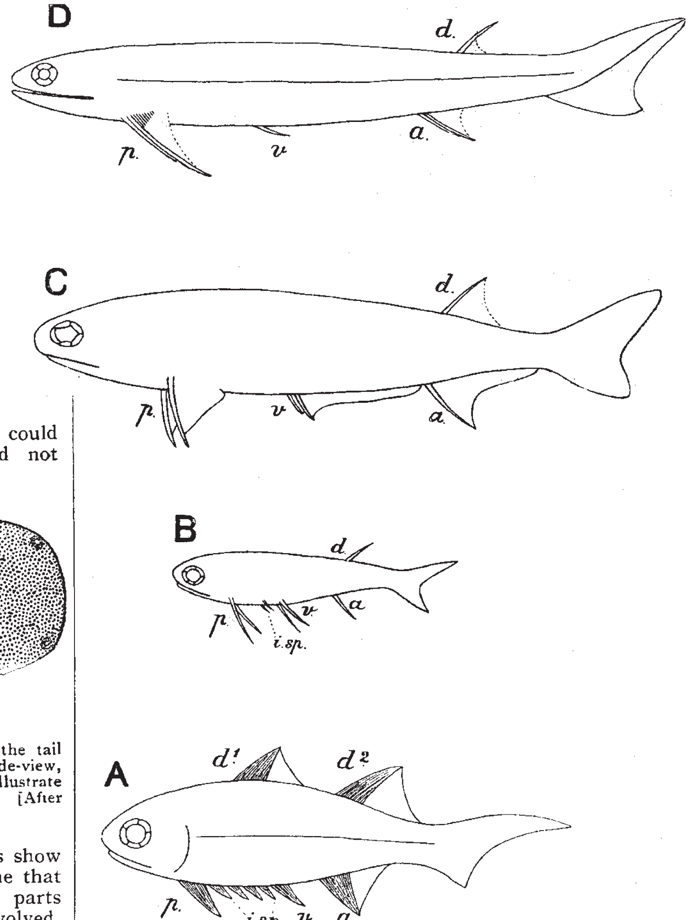

FIG. 2.—Outlines of Acanthodian Fishes, illustrating their gradual elongation in shape and loss of "intermediate spines," as they are traced upwards in geological formations. A, *Climatius scutiger*, Egerton; Lower Old Red Sandstone, Forfarshire. B, *Mesacanthus mitchelli* (Egerton); *ibid.* C, *Acanthodes sulcatus*, Agassiz; Lower Carboniferous, Edinburgh. D, *Acanthodes gracilis*, Roemer; Lower Permian, Bohemia. [Figs. B, C after Traquair, D after Fritsch.] *a.*, anal fin; *d.*, dorsal fin; *i. sp.*, pairs of spines between paired fins ("intermediate spines"); *p.*, pair of pectoral fins; *v.*, pair of pelvic fins.

[1] Abridged from the Presidential Address to the Geologists' Association, February 2, 1906. (Proc. Geol. Assoc., vol. xix., pp. 266–282, figs. 1–15.)

of fins; but as these were unsuited for further elaboration, the primitive fishes of this grade did not advance further. They became long-bodied or almost eel-shaped before their final extinction.

Fishes only began to make real progress when their fin-flaps were stiffened by internal rods of cartilage in addition to the hard skin-structures. Such fins were essentially paddles, and could be used for crawling in the mud as well as for ordinary swimming in water. It is therefore interesting to observe that during the Middle and Upper Devonian periods, when four-legged lung-breathers must have been just beginning to appear on the land, nearly all the highest fishes had their fins in the shape of paddles (Fig. 3, A). It seems as if at that time there was a general tendency for the fashionable and most advanced fishes to become crawlers rather than swimmers; and there cannot be much doubt that the known Crossopterygii, or "fringe-finned ganoids," as these fishes are commonly termed, are the unsuccessful survivors of the race which originally produced the earliest crawling lung-breathers or Labyrinthodonts. The Dipnoi, or paddle-finned fishes, which breathe both by gills and by a modified air-bladder (almost a lung), were also especially abundant at the same period. In fact, in having the fundamental part of the upper jaw fused with the skull instead of loosely suspended from it, the Dipnoi agree more closely with the land animals than do the Crossopterygii; but before this feature had been acquired, the roof-bones of the skull had subdivided into smaller plates, such as could not have changed into the skull-bones of an ordinary Labyrinthodont, while the teeth had curiously clustered into plates, so that they could never have produced the Labyrinthodont dentition. The few survivors both of Crossopterygians and Dipnoans at the present day exhibit the usual long-bodied or eel-shaped contour of decrepit derelicts.

The next grade of fishes, the Chondrostei (Fig. 3, B), which specially characterised the Carboniferous and Permian periods, had fins in which the internal cartilages formed only an effective basal support, while the greater part of their expanse was stiffened by flexible skin-fibres, which had become "fin-rays." Some of these fishes degenerated into eel-shaped creatures in the Triassic, Rhætic, and Liassic periods, while others grew to unwieldy proportions and eventually passed into the modern sturgeons.

Thus far there had been scarcely any ossification of the internal skeleton of the head and trunk in fishes; but by the dawn of the Triassic period a large number of the Chondrostei had passed into the Protospondyli, and then the formation of a hard brain-case and vertebral column began. This only happened after the median fins had become absolutely complete, namely, after the upper lobe of the tail had shortened so that the tail-fin formed a flexible fan-shaped expansion at the blunt end of the body, while each separate ray in the other median fins was provided with its own definite support. The Protospondyli (Fig. 3, C) characterised the Triassic, Rhætic, and Jurassic periods, and exhibited endless variety; but their sole survivors at the present day are the long-bodied Lepidosteus and Amia of American fresh waters.

Associated with almost the earliest Protospondyli, there were a few precocious fishes which evidently completed their vertebral column at once. This race, including such genera as Pholidophorus and Leptolepis, seems to have temporarily exhausted itself in the effort, for it always occupied a secondary place in the fish-faunas until the beginning of the Cretaceous period, when it rapidly multiplied, became fashionable, and replaced the Protospondyli. Thus arose the modern fishes of the same grade as the herring and salmon, characterised, not only by a complete vertebral column, but also by a simplified lower jaw, which consists only of two pieces on each side (without the splenial bone which forms so conspicuous a feature of the earlier fishes). The Isospondyli, as they are termed, being thus provided with a completely bony internal skeleton as well as completed fins, admitted of many more variations than any of their forerunners. The typical fish-head now began, for the first time in its history, to exhibit essential changes. The supraoccipital bone often grew upwards to project on the roof, and thrust outwards the now well-ossified and enlarged ear-capsules (Chirocentridæ); while the premaxilla sometimes extended backwards to slip beneath the maxilla and exclude the latter from the margin

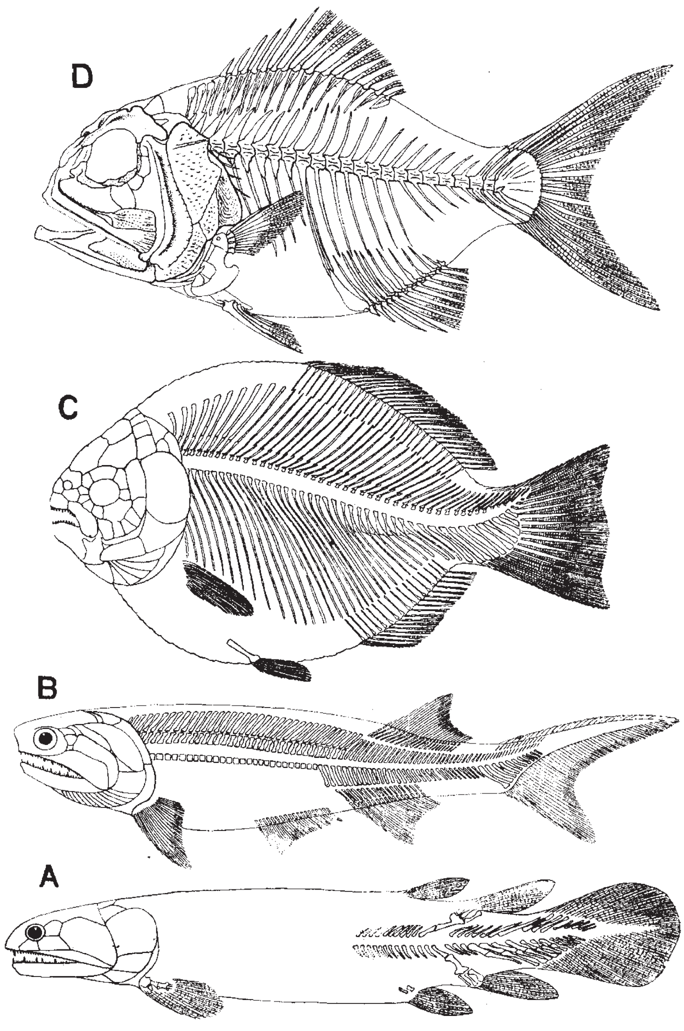

FIG. 3.—Diagram illustrating grades in the evolution of bony fishes.—A, Paddle-finned fish (Rhizodont Crossopterygian) characteristic of the Middle and Upper Old Red Sandstone periods, internal skeleton only partially shown in drawing; *tendency* towards shortening lobes of fins and simplifying their internal supports. B, Ray-finned fish (Palæoniscid) characteristic of the Carboniferous and Permian periods, showing the extended pelvic fin with numerous supports, the dorsal and anal fins with supports fewer than rays, and the caudal fin heterocercal; *tendency* towards shortening upper lobe of tail, and towards equality in number between rays and their supports in the other median fins. C, Ray-finned fish (Dapedius) characteristic of the Triassic and Jurassic periods, showing short-based pelvic fin with one large support, the dorsal and anal fins having a separate support for each ray, and the caudal fin almost homocercal; *tendency* towards acquisition of bony vertebræ and ossification of the cartilaginous skull. D, Modern ray-finned bony fish (Hoplopteryx) characteristic of the Upper Cretaceous and Tertiary periods, showing premaxilla below maxilla, completed internal skeleton, pelvic fins far forwards, and some spinous fin-rays; *tendency* towards extreme development of ear-capsules, supraoccipital bone, and premaxilla, besides a fixed number of spinous fin-rays and the forward position of the pelvic fins.

of the upper jaw (Enchodontidæ). The pelvic fins in a few fishes were now displaced forwards, so that their supports even touched the bones bearing the pectoral fins (Ctenothrissidæ). Still more interesting, the bones of the gill-cover began for the first time to develop spines (Enchodontidæ).

Among fishes, as among other animals, spines characterise only the latest representatives of the class. When the skeleton is well ossified, races which have reached or just passed their prime tend to acquire more skeletal matter than they actually need, and the surplus is then arranged as spines and bosses, usually in a symmetrical manner. In the case of fishes, some of the fin-rays become hardened, and spines arise chiefly on the cheeks and gill-covers. The Acanthopterygii ("spine-finned") are thus the highest and latest fishes of all, though they sometimes eventually descend from their high estate by degeneration. They exhibit all the peculiar changes in the skull, upper jaw, and pelvic fins noticed as first appearing in a variable manner in the Cretaceous Isospondyli. They also differ from all the earlier races of fishes in the common numerical fixity of their vertebræ and fin-rays. There are whole families in which the number of vertebræ never varies, and there are large genera in which all the species have the same definite number of spinous fin-rays.

The spiny-finned fishes began by Berycoids and possibly Scombroids in the Chalk, closely resembling, but not identical with, genera living at the present day. The so-called Beryx of the Chalk (Hoplopteryx, Fig. 3, D) is now proved to be very different from the existing genus bearing that name. By the Eocene period, however, nearly all the modern groups of Acanthopterygii had become completely separated and developed, and their sudden appearance is as mysterious as that of the early Eocene Mammalia.

The study of fossil fishes, as now pursued, is thus an attempt to solve the following fundamental problems:—

(1) The nature and order of the successive advances in anatomical structure which have suddenly infused new life into the class—the "expression points," as Cope termed them.

(2) The new possibilities of development which arose with each successive "expression point."

(3) The direction of the various abortive lines of advance and degeneration in each successively higher grade.

The results of such a study have an important bearing on the most fundamental questions concerning "living" matter as contrasted with "dead" matter; for, in my opinion, we are much more likely to approach some explanation of life by studying the secular development of whole races than by examining the vital processes of individuals or by comparing the members of a single contemporaneous fauna.

A. SMITH WOODWARD.

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