INTRODUCTION

The term fish is applied to a variety of cold−blooded aquatic vertebrates of several evolutionary lines. It describes a life−form rather than a taxonomic group. As members of the phylum Chordata, fish share certain features with other vertebrates. These features are gill slits at some point in the life cycle, a notochord, or skeletal supporting rod, a dorsal hollow nerve cord, and a tail. Living fishes represent about five classes, which are as distinct from one another as are the four classes of familiar air−breathing animalsamphibians, reptiles, birds, and mammals. For example, the jawless fishes (agnathans) are the only fishes that have a suctorial, or filter−feeding, mouth, a feature which makes them dependent on an essentially parasitic way of life. They have either no fins or poorly developed ones. Extant examples of the agnathans are the lampreys and the hagfishes. As the name implies, the skeletons of fishes of the class Chondrichthyes (chondr, "cartilage," and ichthyes, "fish") are made entirely of cartilage. Modern fish of this class lack a swim bladder, and their scales and teeth are made up of the same placoid material. Sharks, skates, and rays are examples of cartilaginous fishes. The bony fishes are by far the largest class. Examples range from the tiny sea horse to the 450−kilogram (1,000−pound) blue marlin, from the flat soles and flounders to the boxy puffers and sunfishes. Unlike those of the cartilaginous fishes, the scales of bony fishes, when present, grow throughout life and are made up of thin, overlapping plates of bone. Bony fishes also have an operculum that covers the gill slits. The study of fishes, the science of ichthyology, is of broad importance. There are many reasons why fishes are of interest to humans; the most important is their relationship with and dependence on the environment. A more obvious reason for interest in fishes is their role as a moderate but important part of the world's food supply. This resource, once thought unlimited, is now realized to be finite and in delicate balance with the biological, chemical, and physical factors of the aquatic environment. Overfishing, pollution, and alteration of the environment are the chief enemies of proper fisheries management, both in fresh waters and in the ocean. (For a detailed discussion of the technology and economics of fisheries, see FISHING, COMMERCIAL.) Another practical reason for studying fishes is their use in disease control. As predators on mosquito larvae, they help curb malaria and other mosquito−borne diseases. Fishes are valuable laboratory animals in many aspects of medical and biological research. For example, the readiness of many fishes to acclimate to captivity has allowed biologists to study behaviour, physiology, and even ecology under relatively natural conditions. Fishes have been especially important in the study of animal behaviour where research on fishes has provided a broad base for the understanding of the more flexible behaviour of the higher vertebrates. There are aesthetic and recreational reasons for an interest in fishes. Millions of people keep live fishes in home aquariums for the simple pleasure of observing the beauty and behaviour of animals otherwise unfamiliar to them. To many, aquarium fishes provide a personal challenge, allowing them to test their ability to keep a small section of the natural environment in their homes. Sportfishing is another way of enjoying the natural environment, also indulged in by millions of people every year. Interest in aquarium fishes and sportfishing support multimillion−dollar industries throughout the world. As mentioned above, the fishes represent several classes of vertebrates rather than a single taxonomic group. This article presents a comparative study of all fish groups, including those that are now extinct, with emphasis on their structural diversity, natural history, and evolutionary relationships. The major classes of living fishesarranged in accordance with the complete Annotated classification (see outline)are treated individually. Special attention is devoted to the teleosts (infraclass Teleostei), or bony fishes, a group that includes most of the world's important sport and commercial fishes. (S.H.W./Ed.)

Structural diversity.

Fishes have been in existence for more than 450,000,000 years, during which time they have evolved repeatedly to fit into almost every conceivable type of aquatic habitat. In a sense, land vertebrates are simply highly modified fishes, for when fishes colonized the land habitat they became tetrapod (four−legged) land vertebrates. The popular conception of a fish as a slippery, streamlined aquatic animal that possesses fins and breathes by gills applies to many fishes, but far more fishes deviate from that conception than conform to it.

For example, the body is elongate in many forms and greatly shortened in others; the body is flattened in some (principally in bottom−dwelling fishes) and laterally compressed in many others; the fins may be elaborately extended, forming intricate shapes, or they may be reduced or even lost; and the positions of the mouth, eyes, nostrils, and gill openings vary widely. Air breathers have appeared in several evolutionary lines. Many fishes are cryptically coloured and shaped, closely matching their respective environments; others are among the most brilliantly coloured of all organisms, with a wide range of hues, often of striking intensity, on a single individual. The brilliance of pigments may be enhanced by the surface structure of the fish, so that it almost seems to glow. A number of unrelated fishes have actual light−producing organs. Many fishes are able to alter their coloration, some for the purpose of camouflage, others for the enhancement of behavioral signals. Fishes range in adult length from less than 10 millimetres (2/5 inches) to more than 20 metres (60 feet) and in weight from about 1.5 grams (less than 1/16 ounce) to many thousands of kilograms. Some live in shallow thermal springs at temperatures slightly above 42° C (100° F), others in cold Arctic seas a few degrees below 0° C (32° F) or in cold deep waters more than 10,000 metres (3,500 feet) beneath the ocean surface. The structural and, especially, the physiological adaptations for life at such extremes are relatively poorly known and provide the scientifically curious with great incentive for study.

Distribution and abundance.

Almost all natural bodies of water bear fish life, the exceptions being very hot thermal ponds and extremely salt−alkaline lakes such as the Dead Sea and Great Salt Lake in Utah. The present distribution of fishes is a result of the geological history and development of the Earth as well as the ability of fishes to undergo evolutionary change and to adapt to the available habitats. Fishes may be seen to be distributed according to habitat and according to geographical area. Major habitat differences are marine and fresh waters. For the most part the fishes in them, even in adjacent areas, are different, but some, such as the salmon, migrate from one to the other. The freshwater habitat may be seen to be of many kinds. Fishes found in mountain torrents, Arctic lakes, tropical lakes, temperate streams, and tropical rivers will all differ from each other both in obvious gross structure and in physiological attributes. Even in closely adjacent habitats where, for example, a tropical mountain torrent enters a lowland stream, the fish fauna will differ. Marine habitats can be divided into deep ocean floors (benthic), midwater oceanic (bathypelagic), surface oceanic (pelagic), rocky coast, sandy coast, muddy shores, bays, estuaries, and others. Also, for example, rocky coastal shores in tropical and temperate regions will have a different fish fauna, even when such habitats occur along the same coastline. Although much is known about the present geographical distribution of fishes, far less is known about how that distribution came about. Many parts of the fish fauna of the fresh waters of North America and Eurasia are related and undoubtedly have a common origin. The faunas of Africa and South America are related, extremely old, and probably an expression of the drifting apart of the two continents. The fauna of southern Asia is related to that of central Asia and some of it appears to have entered Africa. The extremely large shore fish faunas of the Indian and tropical Pacific oceans comprise a related complex, but the tropical shore fauna of the Atlantic, although containing Indo−Pacific components, is relatively limited and probably younger. The Arctic and Antarctic marine faunas are quite different from each other. The shore fauna of the North Pacific is quite distinct, and that of the North Atlantic more limited and probably younger. Pelagic oceanic fishes, especially those in deep waters, are similar the world over, showing little geographical isolation in terms of family groups. The deep oceanic habitat is very much the same throughout the world, but species differences do exist, showing geographical areas determined by oceanic currents.

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Locomotion.

Many fishes have a streamlined body and swim freely in the open water. Fish locomotion is closely correlated with habitat and ecological niche (the general position of the animal to its environment). Many fishes in both marine and fresh waters swim at the surface and have mouths adapted to feed best (and sometimes only) at the surface. Often such fishes are long and slender, able to dart at surface insects or at other surface fishes and in turn to dart away from predators; needlefishes, halfbeaks, and topminnows are good examples. Oceanic flying fishes escape their predators by gathering speed above the water surface, with the lower lobe of the tail providing thrust in the water. They then glide hundreds of yards on enlarged, winglike pectoral and pelvic fins. South American freshwater flying fishes escape their enemies by jumping and propelling their strongly keeled bodies out of the water with their pectoral fins, which function as flapping wings. So−called midwater swimmers, the most common type of fish, are of many kinds and live in many habitats. The powerful fusiform tunas and the trouts, for example, are adapted for strong, fast swimming, the first to capture prey speedily in the open ocean, the second to cope with the swift currents of streams and rivers. The trout body form is well adapted to many habitats. Fishes that live in relatively quiet waters such as bays or lake shores or slow rivers usually are not strong, fast swimmers but are capable of short, quick bursts of speed to escape a predator. Many of these fishes have their sides flattened, examples being the sunfish and the freshwater angelfish of aquarists. Fish associated with the bottom or substrate usually are slow swimmers. Open−water plankton−feeding fishes almost always remain fusiform and capable of rapid, strong movement (for example, sardines and herrings of the open ocean and also many small minnows of streams and lakes). Bottom−living fishes are of many kinds and have undergone many types of modification of their body shape and swimming habits. Rays, which evolved from strong swimming, midwater sharks, usually stay close to the bottom and move by undulating their large pectoral fins. Flounders live in a similar habitat and move over the bottom by undulating the entire body. Many bottom fishes dart from place to place, resting on the bottom between movements, a motion common in gobies. One goby relative, the mudskipper, has taken to living at the edge of pools along the shore of muddy mangrove swamps. It escapes its enemies by flipping rapidly over the mud, out of the water. Some catfishes, synbranchid eels, the so−called climbing perch, and a few other fishes venture out over damp ground to find more promising waters than those that they left. They move by wriggling their bodies, sometimes using strong pectoral fins; most have accessory air−breathing organs. Many bottom−dwelling fishes live in mud holes or rocky crevices. Marine eels and gobies commonly are found in such habitats and usually seldom venture far beyond their cavelike homes. Some bottom dwellers, such as the clingfishes (Gobiesocidae), have developed powerful adhesive disks that enable them to remain in place on the substrate in areas such as rocky coasts where the action of the waves is great.

Reproduction.The methods of reproduction in fishes are varied but most fishes lay a large number of small eggs, fertilized and scattered outside of the body. The eggs usually remain suspended in the open water in pelagic fishes. Many shore and freshwater fishes lay eggs on the bottom or among plants. Some have adhesive eggs. The mortality of the young and especially of the eggs is very high, and often only a few individuals grow to maturity out of hundreds, thousands, and in some cases, millions of eggs laid. Males produce sperm, usually as a milky white substance called milt, in two (sometimes one) testes within the body cavity. In bony fishes a sperm duct leads from each testis to a urogenital opening behind the vent or anus. In sharks and rays and in cyclostomes the duct leads to a cloaca. Sometimes the pelvic fins are modified to help transmit the milt to the eggs at the female's vent or on the substrate where the female has placed them. Sometimes accessory organs are used to fertilize females internally; for example, the claspers of many sharks and rays. In the females the eggs are formed in two ovaries (sometimes only one) and pass through the ovaries to the urogenital opening and to the outside. In some fishes the eggs are fertilized internally but shed before development takes place. Members of about a dozen families each of bony fishes (teleosts) and sharks bear live young. Many skates and rays bear live young. In some bony fishes the eggs simply develop within the female, the young emerging when the eggs hatch (ovoviviparous). Others develop within the ovary and are nourished by ovarian tissues after hatching (viviparous). There are also other methods utilized by fishes to nourish young within the female. In all live−bearers young are born at a relatively large size and are few in number. In one family of primarily marine fishes, the surfperches from the Pacific coast of North America, the U.S.S.R., and Japan, the males of at least one species appear to be born sexually mature, although not fully grown. Some fishes are hermaphroditic, an individual producing both sperm and eggs, usually at different stages of its life. Self−fertilization, however, is probably rare. Successful reproduction and in many cases defense of the eggs and young is assured by rather stereotyped but often elaborate courtship and parental behaviour, either by the male, the female, or both. Some fishes prepare nests by hollowing out depressions in the sand bottom (cichlids, for example), build nests with plant materials and sticky threads excreted by the kidneys (sticklebacks), or blow a cluster of mucus−covered bubbles at the water surface (gouramis). The eggs are laid in these structures. Some cichlids and catfishes incubate eggs in their mouths. Some fishes, such as salmon, undergo long migrations from the ocean and up large rivers to spawn in gravel beds where they themselves hatched (anadromous fishes). Others undertake shorter migrations from lakes into streams, or in other ways enter for spawning habitats that they do not ordinarily occupy.

The digestive system.

The digestive system, in a functional sense, starts at the mouth, with the teeth used to capture prey or collect plant foods. Mouth shape and tooth structure vary greatly in fishes, depending on the kind of food normally eaten. Most fishes are predacious, feeding on small invertebrates or other fishes and have simple conical teeth on the jaws, on at least some of the bones of the roof of the mouth, and on special gill arch structures just in front of the esophagus. The latter are throat teeth. Most predacious fishes swallow their prey whole, and the teeth are used for grasping and holding prey, for orienting prey to be swallowed (head first) and for working the prey toward the esophagus. There are a variety of tooth types in fishes. Some, such as sharks and the piranhas, have cutting teeth for biting chunks out of their victims. A shark's tooth, although superficially like that of a piranha, appears in many respects to be a modified scale, while that of the piranha is like that of other bony fishes, consisting of dentine and enamel. Parrotfishes have beaklike mouths with short incisor−like teeth for breaking off coral and have heavy pavement−like throat teeth for crushing the coral. Some catfishes have small brushlike teeth, arranged in rows on the jaws, for scraping plant and animal growth from rocks. Many fishes (e.g., the Cyprinidae or minnows) have no jaw teeth at all but have very strong throat teeth. Some fishes gather planktonic food by straining it from their gill cavities with numerous elongate stiff rods (gill rakers), anchored by one end to the gill bars. The food collected on these rods is passed to the throat where it is swallowed. Most fishes have only short gill rakers that help keep food particles from escaping out the mouth cavity into the gill chamber. Once reaching the throat, food enters a short, often greatly distensible esophagus, a simple tube with a muscular wall leading into a stomach. The stomach varies greatly in fishes, depending upon the diet. In most predacious fishes it is a simple straight or curved tube or pouch with a muscular wall and a glandular lining. Food is largely digested here and leaves the stomach in liquid form. Between the stomach and the intestine, ducts enter the digestive tube from the liver and pancreas. The liver is a large, clearly defined organ. The pancreas may be imbedded in it, diffused through it, or broken into small parts spread along some of the intestine. The junction between the stomach and the intestine is marked by a muscular valve. Pyloric ceca (blind sacs) occur in some fishes at this junction and have a digestive or an absorptive function, or both. The intestine itself is quite variable in length depending upon the diet. It is short in predacious forms, sometimes no longer than the body cavity, but long in herbivorous forms, being coiled and several times longer than the entire length of the fish in some species of South American catfishes. The intestine is primarily an organ for absorbing nutrients into the bloodstream. The larger its internal surface, the greater its absorptive efficiency, and a spiral valve is one method of increasing its absorption surface. Sharks, rays, chimaeras, lungfishes, surviving chondrosteans, holosteans, and even a few of the more primitive teleosts have a spiral valve or at least traces of it in the intestine. Most modern teleosts have increased the area of the intestinal walls by having numerous folds and villi (fingerlike projections) somewhat like those in man. Undigested substances are passed to the exterior through the anus in most teleost fishes. In lungfishes, sharks, and rays it is first passed through the cloaca, a common cavity receiving the intestinal opening and the ducts from the uro−genital system.

The respiratory system.

Oxygen and carbon dioxide dissolve in water and most fishes exchange dissolved oxygen and carbon dioxide in water by means of the gills. The gills lie behind and to the side of the mouth cavity and consist of fleshy filaments supported by the gill arches and filled with blood vessels, which give gills a bright red colour. Water taken in continuously through the mouth passes backward between the gill bars and over the gill filaments, where the exchange of gases takes place. The gills are protected by a gill cover in teleosts and many other fishes, but by flaps of skin in sharks, rays, and some of the older fossil fish groups. The blood capillaries in the gill filaments are close to the gill surface to take up oxygen from the water and to give up excess carbon dioxide to the water. Most modern fishes have a hydrostatic (ballast) organ, called the swim bladder, that lies in the body cavity just below the kidney and above the stomach and intestine. It originated as a diverticulum of the digestive canal. In advanced teleosts, especially the acanthopterygians, the bladder has lost its connection with the digestive tract, a condition called physoclistic. The connection has been retained (physostomous) by many relatively primitive teleosts. In several unrelated lines of fishes the bladder has become specialized as a lung or, at least, as a highly vascularized accessory breathing organ. Some fishes with such accessory organs are obligate air breathers and will drown if denied access to the surface, even in well−oxygenated water. Fishes with a hydrostatic form of swim bladder can control their depth by regulating the amount of gas in the bladder. The gas, mostly oxygen, is secreted into the bladder by special glands, rendering the fish more buoyant; it is absorbed into the bloodstream by another special organ, reducingthe overallbuoyancy and allowing the fish to sink. Some deep−sea fishes may have oil in the bladder, rather than gas. Other deep−sea and some bottom−living forms have much reduced swim bladders or have lost the organ entirely. The swim bladder of fishes follows the same developmental pattern as the lungs of land vertebrates. There is no doubt that the two structures have the same historical origin in primitive fishes. More or less intermediate forms still survive among the more primitive types of fishes such as the lungfishes Lepidosiren and Protopterus.

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The nervous system and sensory organs.

As in all vertebrates, the nervous system of fishes is the primary mechanism coordinating body activities, as well as integrating these activities in the appropriate manner with stimuli from the environment. The central nervous system, the brain, and spinal cord, are the primary integrating mechanisms. The peripheral nervous system, consisting of nerves that connect the brain and spinal cord to various body organs, carries sensory information from special receptor organs such as the eyes, internal ears, nares (sense of smell), taste glands, and others to the integrating centres of the brain and spinal cord. The peripheral nervous system also carries information via different nerve cells from the integrating centres of the brain and spinal cord. This coded information is carried to the various organs and body systems, such as the skeletal muscular system, for appropriate action in response to the original external or internal stimulus. Another branch of the nervous system, the autonomic system, helps to coordinate the activities of many glands and organs and is itself closely connected to the integrating centres of the brain. The brain of the fish is divided into several anatomical and functional parts, all closely interconnected but each serving as the primary centre of integrating particular kinds of responses and activities. Several of these centres or parts are primarily associated with one type of sensory perception such as sight, hearing, or smell (olfaction). Olfaction.The sense of smell is important in almost all fishes. Certain eels with tiny eyes depend mostly on smell for location of food. The olfactory, or nasal, organ of fishes is located on the dorsal surface of the snout. The lining of the nasal organ has special sensory cells that perceive chemicals dissolved in the water such as substances from food material and send sensory information to the brain by way of the first cranial nerve. Odour also serves as an alarm system. Many fishes, especially various species of freshwater minnows, react with alarm to the body fluids produced by an injured member of their own species. Taste.Many fishes have a well−developed sense of taste, and tiny pitlike taste buds or organs are located not only within their mouth cavities but also over their heads and parts of their body. The barbels ("whiskers") of catfishes, which often have poor vision, serve as supplementary taste organs, those around the mouth being actively used to search out food on the bottom. Some species of naturally blind cave fishes are especially well supplied with taste buds, these often covering most of their body's surface. Sight.Sight is extremely important in most fishes. The eye of a fish is basically like that of all other vertebrates, but the eyes of fishes are extremely varied in structure and adaptation. In general, fishes living in dark and dim water habitats have large eyes, unless they have specialized in some compensatory way so that another sense (such as smell) is dominant, in which case the eyes will often be reduced. Fishes living in brightly lighted shallow waters often will have relatively small but efficient eyes. Cyclostomes have somewhat less elaborate eyes than other fishes, with skin stretched over the eyeball perhaps making their vision somewhat less effective. Most fishes have a spherical lens and accommodate their vision to far or near subjects by moving the lens within the eyeball. A few sharks accommodate by changing the shape of the lens, as in land vertebrates. Those fishes that are heavily dependent upon the eyes have especially strong muscles for accommodation. Most fishes see well, despite the restrictions imposed by frequent turbidity of the water and by light refraction. Experimental evidence indicates that many shallow−water fishes, if not all, have colour vision and see some colours especially well, but some bottom−dwelling shore fishes live in areas where the water is sufficiently deep to filter out most if not all colours, and these fishes apparently never see colours. When tested in shallow water, they apparently are unable to respond to colour differences. Hearing.Sound perception and balance are intimately associated senses in a fish. The organs of hearing are entirely internal, located within the skull, on each side of the brain and somewhat behind the eyes. Sound waves, especially those of low frequencies, travel readily through water and impinge directly upon the bones and fluids of the head and body, to be transmitted to the hearing organs. Fishes readily respond to sound; for example, a trout conditioned to escape by the appoach of fishermen will take flight upon perceiving footsteps on a stream bank even if it cannot see the fisherman. Compared with humans, however, the range of sound frequencies heard by fishes is greatly restricted. It is thought that many fishes communicate with each other in a crude way by producing sounds in their swim bladders, in their throats by rasping their teeth, and in other ways. Other senses (touch, pain, and special senses).A fish or other vertebrate seldom has to rely on a single type of sensory information to determine the nature of the environment around it. A catfish uses taste and touch when examining a food object with its oral barbels. Like most other animals, fishes have many touch receptors over their body surface. Pain and temperature receptors also are present in fishes and presumably produce the same kind of information to a fish as to humans. Fishes react in a negative fashion to stimuli that would be painful to human beings, suggesting that they feel a sensation of pain. An important sensory system in fishes that is absent in other vertebrates (except some amphibians) is the lateral line system. This consists of a series of heavily innervated small canals located in the skin and bone around the eyes, along the lower jaw, over the head and down the midside of the body where it is associated with the scales. Intermittently along these canals are located tiny sensory organs (pit organs) that apparently detect changes in pressure. The system allows a fish to sense changes in water currents and pressure, thereby helping the fish to orient itself to the various changes that occur in the physical environment.

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