PISCES

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Summary

Fishes are aquatic vertebrates that have gills and fins throughout their lives. They are the largest and most diverse vertebrate group and the only vertebrate food resource harvested directly from wild populations. Fishes display an astonishing diversity in geographical distribution, habitat, size, form, and biology, resulting from nearly 500 million years of evolution. The smallest fishes are gobies measuring 13 mm to 15 mm as adults. The largest is the whale shark that reaches a length of 12 m. Fishes live under extreme conditions of temperature, salinity, pressure, and light; in open, fast-flowing, or still water; on other fishes and on or inside invertebrates; and on or within the substrate. Evolving under ever-changing biotic and abiotic conditions, they have developed a multitude of shapes, numerous physiological adaptations, and a variety of life styles. There are about 25 000 extant fish species of which 10 000 species live in freshwater habitats and 15 000 in marine ones. They are classified in two major divisions, the Agnatha (jawless fishes) and the Gnathostomata (jawed fishes). The first group includes 1 order with 3 families and 41 species of lampreys. The jawed fishes are divided into three classes: the Chondrichthyes are the cartilaginous fishes, including the

Elasmobranchii with 9 orders and more than 800 species of sharks and rays, and the Holocephali with 1 order and about 30 species of chimeras; the Sarcopterygii are the lobe-finned fishes, including the order Coelacanthiformes with two species of coelacanths, and the order Dipnoiformes (lungfishes) with six species of lungfishes; and the Actinopterygii, the ray-finned fishes, including all the remaining taxa. The latter group includes 43 orders of which 39 are the Teleostei with more than 23 600 species. The order Perciformes is the largest and most diversified teleostean group containing about 150 families and more than 9 300 species.

1. Introduction

Fishes are by far the largest and most diverse vertebrate group. It is the only vertebrate food resource we harvest commercially directly from wild populations.
The number of known fish species is estimated at about 25 000, about half of all known vertebrates. It is impossible to give a finite number of species because of the dynamic nature of systematic research. Names change regularly, and about 200 new species descriptions are being added each year. Consequently, estimates of the eventual number of fishes vary between 28 500 species and 35 000 species. About 10 000 species live in freshwater habitats and 15 000 in marine ones (including about 500 species that migrate between freshwater and saltwater during their life). More than 8 000 species are contained in just eight (of about 470) families, including the freshwater Balitoridae (river loaches), Characidae (characins), Cichlidae (cichlids), Cyprinidae (minnows and carps), and Loricariidae (suckermouth, armored catfishes), and the marine Gobiidae (gobies), Labridae (wrasses), and Serranidae (sea basses).

Generally, species richness decreases with increasing latitude and water depth. Hence, the most diverse fish fauna is found in the tropical coral reefs. However, the geological history of an area (e.g., Antarctic continental shelf) and local conditions (e.g., east and west coasts of South Africa) can make a difference to species diversity in the same latitude and depth zones. Fishes display an astonishing diversity, unrivalled among vertebrates, in geographical distribution, habitat, size, form, and biology. This diversity is the result of nearly 500 million years of evolution through the interaction of species with biotic and abiotic conditions. The smallest fishes are found among gobies that reach an adult size of about 13 mm to 15 mm, such as the marine goby *Trimmatom nanus* and the freshwater goby *Pandaka pygmaea*. At the other end of the scale is the whale shark (*Rhincodon typus*), reaching a length of 12 m. Fishes live under extreme conditions of temperature, salinity, pressure, and light; in open, fast-flowing, or still water; on other fishes and on or inside invertebrates; on or within the substrate. To adapt to these conditions, fishes have developed a multitude of shapes, of which sea horses and pipefishes are just two of many examples, and colors, such as in the wrasses and the butterflyfishes among others, and a variety of life styles (e.g., grazers, filter feeders, ambush predators, active predators, pelagic and substrate spawners, mouthbrooders, and live-bearers).

2. The Biology of Fishes

To live in water, a medium that is much denser, is more viscous, contains dissolved salts, and holds much less oxygen than air, fishes had to evolve unique structures, physiological mechanisms, and behavioral patterns.

2.1. Respiration

The main respiratory organs of fishes are the gills. To maximize the efficiency of oxygen extraction from the water, the gill structure provides a large surface area over which water flowing through the gills can exchange gases with the blood hemoglobin, whose oxygen affinity is pH dependent. To facilitate exchange of carbon dioxide with oxygen, blood flows in an opposite direction to the water flow. This countercurrent principle is also used in other places in the body where efficient and fast gas exchange is needed, e.g., the swimbladder. Synchronized movement of the mouth floor and opercles creates a pressure gradient between the mouth and the gill chamber and ensures continuous unidirectional water flow through the gills.

The solubility of oxygen in water decreases with increasing temperature and salinity. Fishes living in low-oxygen habitats, such as tropical rivers, and in rivers and lakes prone to drought, evolved additional ways to meet their oxygen requirements, most significantly air-breathing. In its simplest form air-breathing takes place through highly vascularized areas in the mouth and the gill chamber (e.g., mudskippers, knifefishes), in the physostomous swimbladder (e.g., bowfins, gars, tarpons), and in the stomach and intestine (e.g., catfishes). More advanced systems include suprabranchial organs (e.g., catfishes, swampeels, gouramis) and lungs (sarcopterygian lungfishes).

Gas exchange through the skin takes place in all fishes. It is particularly important in early life history stages in which the gills are not fully developed. Antarctic icefishes living in well-oxygenated waters rely on “skin breathing” for a different reason. To avoid freezing in the subzero temperature of the water around the Antarctic continent, these fishes produce antifreeze proteins found in their body fluids. To reduce the viscosity of the blood in such low temperatures, they lost most of their red-blood cells.

2.2. Osmoregulation

In addition to maintaining the chemical balance of their internal environment, fishes have to bear the additional cost of osmoregulation between the body fluids and the external environment. Marine bony fishes lose water through their skin because the concentration of solutes in their body fluids is about 2.5 times lower than seawater. To compensate for the loss they must drink seawater and rid their body of the extra salt. The monovalent ions (Na^+ and Cl^-) are absorbed in the gut and transported to the gills where they are excreted. Divalent ions (Mg^{++} and SO_4^{--}) are secreted via the kidneys that produce a small amount of concentrated urine. Elasmobranchs manage their water balance by allowing urea, produced in the liver, to remain in body fluids to bring the concentration of the latter to a level similar as that of the seawater. Their body fluids also contain trimethylamine oxide (TMAO) which reduces the toxicity of urea. Excess urea is removed by the kidney and by diffusion through the gills. Elasmobranchs gain salts from their food (monovalent and divalent ions) and from diffusion through the gills (monovalent ions). The excess monovalent ions are removed from the blood in the rectal gland, and divalent ions by the kidney which produces dilute urine.

Fishes living in freshwater have a higher concentration of solutes in their body fluids than the water does. They have to flush water entering through the gills and skin, and control electrolyte balance in the body fluids. Both functions are carried out by the kidneys which produce a high volume of dilute urine. Salts are gained from food by active intake in the gut, and there is active absorption of monovalent ions from the water by the gills. Only a few elasmobranchs adapted to freshwater habitats, and their blood contains much less urea compared with their marine relatives.

While most fishes can tolerate only small changes in salinity (stenohaline), estuarine species can withstand a wide range of salinities (euryhaline) and move freely from the sea to hyposaline and/or hypersaline habitats (e.g., the silverside *Atherina boyeri*, the Mozambique tilapia *Oreochromis mossambicus*).

2.3. Buoyancy

Much of the body mass of fishes is made of bones and muscles, both denser than water. To counteract sinking, fishes can generate dynamic lift through swimming, and/or become neutrally buoyant (i.e. generate static lift). Both types of buoyancy compensation are employed, at least to a small extent, by all groups of fishes.

Elasmobranchs do not have a swimbladder. In sharks dynamic lift is generated by the lower lobe of the heterocercal caudal fin, the low pectoral fins, and the snout, but they have to keep swimming to maintain their vertical position in the water column. Rays have a depressed body and do not use their tails for swimming. Instead they use their enlarged pectoral fins to “fly” through the water. The large surface area of these fishes produces significant drag forces (friction and pressure drag) that slow down sinking. Forward and upward thrusts are generated by waves that pass through the pectoral fins. In addition, elasmobranchs have a large liver with a high content of oil that produces static lift.

Extant bony fishes evolved from an ancestor with a swimbladder, and taxa without it have secondarily lost the swimbladder as an adaptation for a changed life style (e.g., benthic fishes). In many deep-sea fishes the gas in the bladder is replaced with fat; taxa without swimbladders usually employ the strategy of increasing the amount of low density compounds in the body, such as weakly ossified skeleton, reduction or loss of scales and fins, water retention, and visceral and subdermal lipid deposits.

The swimbladder develops from a diverticulum of the gut. Primitive teleosts have a physostomous bladder in which the connection to the gut via the pneumatic duct remains open. In this type of bladder the passage of gas in and out of the bladder is through the mouth and the gut. In more advanced fishes the pneumatic duct is lost during development (physoclistous). Gas exchange in the physoclistous swimbladder is controlled by the gas gland and the oval. The gas gland is responsible for releasing gas from the blood into the bladder from a network of capillaries controlled by a pH and countercurrent system. The oval releases gas from the bladder into the blood by controlling the size of a thin-walled area exposed to contact with blood vessels. Gas is prevented from escaping the walls of the swimbladder by a layer of cells containing guanine crystals.

2.4. Prey Detection and Predator Avoidance

Prey detection and predator avoidance activities are both concerned with survival. The fish may use the same sensory systems to detect and locate potential predator and prey.

Visual Detection. The general structure of the fish's eye is similar to that of other vertebrates. Unlike higher vertebrates, however, fishes focus by moving the lens toward and away from the retina instead of by changing its curvature, and, with the exception of the elasmobranchs, they have a fixed-size iris. To achieve a wide field of view the lens is kept close to the cornea and, in teleosts, it bulges out of the cornea. The elasmobranch eye is highly adapted to the predator life style. It is permanently adapted to low light conditions because its retina contains only or mostly rod-like photoreceptors. The adjustable iris of these fishes is used to control the amount of light entering the eye. Teleosts cannot use their fixed iris to control the amount of light coming into the eye. Instead they control it by changing the position of the cones and the rods within the retina.

Predators are usually larger than their prey. To avoid being discovered prematurely, many predators attack their prey from below. This gives them the advantage of coming out of an area of low light intensity where they are not easily detected. On the other hand they see prey as a clear silhouette against the bright down-welling light. To avoid being detected from below (vertically or obliquely), many fishes use countershading. Seen from above under a dark background, the dorsal and dorsolateral parts of the fish are also dark or mottled; seen from below against a bright background, the fish ventrolateral and ventral parts are silvery and reflect light horizontally and somewhat downward. However, this does not prevent the fish from appearing as a silhouette from directly below. To diminish this effect, pelagic fishes such as sardines and anchovies have a narrow ventrum. A similar effect can be achieved with photophores emitting light downward.

Mechanical detection—the lateral line system. Vibrations in the water, such as fins strokes while swimming, produce pressure waves which bony fishes can detect using their lateral line system. This system is made of mechanoreceptor organs called neuromasts. The neuromasts are usually distributed inside sensory canals on the head and the body of the fish, but free neuromasts are present in many fishes, mostly on the head. The trunk part of the system is usually a single line of modified tubular scales that runs more or less along the middle of the body from behind the head to the caudal-fin base. In some taxa it is divided into two or three lines, or there is a single line that runs along the dorsal or the ventral part of the body. The canals of the head are simple or branched and may be partially or fully enclosed in bone. There is much variation among teleosts in the canal and pore patterns and they are frequently used in fish systematics.

When vibrations hit the neuromasts they send signals to the brain. By comparing the signals received from different parts of the body, the fish is able to determine the direction and distance from the source.

Chemical detection. Fishes are sensitive to chemical stimulation. In a dense medium such as water, chemicals do not disperse as quickly, and olfaction and taste can be an effective means for detecting food, especially where other senses cannot be used, i.e. in turbid water or in sand. The olfactory organ can be on the dorsal or ventral surface of the snout. In elasmobranchs it opens posteriorly to the mouth cavity and the generation of flow through the nostril is associated with respiration. In teleosts the olfactory organ is not connected to the mouth. Movement of water through the nostrils is generated passively by the movement of the fish through the water, or actively by ciliated cells or special sacs that act as pumps activated by breathing movements of the jaws.

Taste buds are usually associated with the mouth, but in many teleosts they may also be found on other parts of the body that play a role in food detection such as barbells of catfishes, or the free pectoral-fin rays of sea robins. The taste bud is usually a cylindrical structure with the receptor cells arranged like segments of an orange.
Electroreception. Elasmobranchs and some teleosts possess electroreceptors, which are sensitive to weak electric fields, especially those generated by living organisms. Electroreceptors are divided into two functional types.

- Ampullary organs, which respond to low frequency (0.05 Hz to 8 Hz) stimuli with a long-lasting pulse and are found in most non-teleosts (e.g., the Ampullae of Lorenzini of cartilaginous fishes).
- Tuberous organs, which respond to high frequency stimuli with either a short-lasting or long-lasting pulse and are found only in several teleost groups (i.e. mormyrids, gymnarchids, gymnotids, and catfishes).

The basic structure and function of the two types of electroreception organs is similar. The vase-shaped organ is filled with a highly conductive jelly, and its wall is highly resistant to electricity. The receptor cells are located at the base of the organ. The tuberous organ is always associated with the production of electricity used for electrocommunication and active electrolocation.

Bioluminescence. Fishes are the only vertebrates capable of producing light. The light may be produced by the fish itself (e.g., lanternfishes) or by bioluminescent symbiotic bacteria living in its body (e.g., flashlight fishes). In the former case the light is a product of a chemical reaction involving proteins and enzymes such as luciferin and luciferase, respectively. The fish acquires the luciferin from its diet and synthesizes its own luciferase. The symbiotic system is common in coastal fishes whereas the chemical system is more widespread in oceanic ones.

Fishes use bioluminescence to detect or attract prey, to avoid predators, and for communication, although the first purpose is by far the most common. Advanced prey detection is found in some deep-water stomiids that have a preorbital photophore emitting red light invisible to their prey. Strategies of predator avoidance include producing a countershading effect by illuminating the ventral part of the fish, thereby reducing or eliminating its silhouette for predators attacking from below (lanternfishes), or blink-and-run behavior (flashlight fishes). To save energy and avoid attracting predators, bioluminescent fishes use their light intermittently.

2.5. Reproduction

In all elasmobranchs (sharks and rays) and holocephalans (chimaeras) fertilization is internal. Once the egg is fertilized it is encased in a tough capsule and when released into the water it sinks to the bottom. Some elasmobranch taxa have internal development that circumvents the need for egg protection in the external environment. Coelacanths also have internal fertilization and development, but it is not yet known how sperm is transferred into the female's reproductive system.

Ray-finned (actinopterygian) fishes evolved a variety of reproductive modes. Most are multiple spawners laying pelagic or demersal eggs that are fertilized and develop externally, and are not cared for. A few species spawn once and die (e.g., salmon). The sexes are separate in most fishes. In hermaphrodite taxa, both sexes may be expressed simultaneously or successively. In the former case, self-fertilization rarely occurs and the mating individuals take turns in acting as male and female. Successive hermaphrodites begin their life as one sex and later change to the other sex; the timing of the sex change may be controlled by social behavior. The terminal phase of successive hermaphrodites is frequently morphologically different than the initial stage (e.g., goldies, parrotfishes, wrasses), but sexual dimorphism is not restricted to hermaphrodites.

A small number of teleosts are live-bearers (e.g., clinids, goodeids, poeciliids, some scorpionfishes), but many care for their young in a variety of ways, including post-spawning nest guarding and egg ventilation, and mouth or pouch brooding. Parthenogenetic reproduction in fishes occurs only in certain poecilliid taxa.

Breeding in fishes may involve complex behavior including migration, schooling, territoriality, nest building, courtship, spawning, and parental care.

3. The Emergence of Fishes

Modern classifications of the animal kingdom are based on the methodology of phylogenetic systematics, or cladistics. This methodology determines evolutionary relationships from a comparison of the various forms or states that characters acquire through their evolution (see *Schools of Taxonomy*).

Fishes are commonly defined as aquatic vertebrates that have gills and fins throughout their life (fins may be secondarily lost in some taxa, e.g., certain eels). The term "fishes" commonly refers to three distinct groups of fishes that include extinct and extant forms, the jawless fishes, the cartilaginous fishes, and the bony fishes. Much of our knowledge of the evolutionary history of these lineages comes from studies of the extensive fossil record of fishes. But we know little about their ancestors. It is generally accepted that fishes have evolved from a primitive chordate group such as tunicates or lancelets (see *Tunicata and Cephalocordata*), but for a long time there was no conclusive evidence in favor of a particular group. The earliest fish fossils exhibit relatively complex mineralized bony tissue and structures implying that some links are missing between the early chordates and the fishes. Studies have shown that conodonts may be one of these missing links. These 4 cm long to 40 cm long animals are morphologically similar to living jawless fishes. Many of their characteristics, such as tail fins with ray-like supports, chevron-shaped muscle segments, cellular bone, mineralized endoskeleton with enamel on the toothed elements, retinal pigment, and eyeballs, suggest relationship to vertebrates.

3.1. Agnatha (Jawless Fishes)

There is a growing body of evidence to the effect that hagfishes (Myxiniformes), traditionally considered agnathans, are not vertebrates. Major vertebrate characters absent in hagfishes include two semicircular canals (they have only one), arcualia, enamel, and dentine. The absence of these characters makes the hagfishes the sister group of all the other agnathans and vertebrates. The Agnatha of old classifications, therefore, did not represent a monophyletic group. The evolution of agnathans gave rise to features that played an important role in the evolution of higher vertebrates. These included paired limbs; inner ear with two, possibly three, semicircular canals; external serial sensory organs; cellular bone; brain differentiation; and a muscle-driven suction feeding mechanism that was superior to the cilia-driven mechanism of invertebrates and earlier chordates. Seven orders of extinct agnathans are known from marine and freshwater deposits on all continents. The Arandaspiformes, Pteraspidiformes, Cephalaspidiformes, Galeaspidiformes, and Pituriaspidiformes had a bony shield over the head and anterior part of the body; in the Anapsiformes and the Thelodontiformes the body was covered by scales. They appeared in the Ordovician, 470 million years before present (MYBP), and became extinct in the Upper Devonian (360 MYBP), probably as a consequence of intense competition from rapidly diversifying and better adapted jawed fishes. They were mostly small fishes, usually less than 30 cm, but several taxa attained lengths of 1 m. The only agnathan order with living members is the Petromyzontiformes (lampreys). Their body is naked and without paired fins and they have one or two dorsal fins and a caudal fin supported by thin cartilaginous rays; oral sucker disk armed with teeth; a piston cartilage as a suction device; paired small olfactory lobes sharing a single median external opening; seven gill openings on each side; and eyes with a unique corneal muscle for visual accommodation. The Agnatha include 3 families and 41 species of anadromous or freshwater fishes (Figure 1) of the cold temperate waters of the world, attaining about 1 m in length.

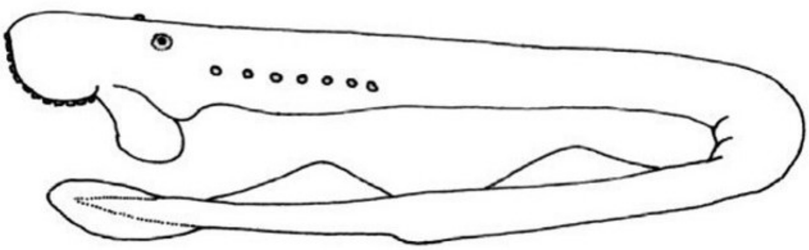

Figure 1. A living lamprey of the family Petromyzontidae

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Biographical Sketch

Ofer Gon was born in Israel in 1949 and studied oceanography and marine biology (M.Sc.) at the Hebrew University, Jerusalem. He was trained in marine fish systematics while working under J.E. Randall at the Bernice P. Bishop Museum, Honolulu, Hawaii (1979–1981), and he joined the then JLB Smith Institute of Ichthyology, Grahamstown, South Africa, in 1982. Research interests include tropical reef fishes, particularly the family Apogonidae, Antarctic fishes, and the history of ichthyology in South Africa.