Evolution and systematics

Modern vertebrates are classified into two major groups, the Gnathostomes (jawed vertebrates) and the Agnathans (jawless vertebrates). The Agnathans are classified into two groups, myxinoïds (hagfishes) and petromyzonïds (lampreys). The Gnathostomes constitute all the other living vertebrates, including the bony and cartilaginous fishes and the tetrapods. The hagfishes are considered the most primitive vertebrates known, living or extinct.

Hagfishes are members of the family Myxinidae, which is the only surviving family of the class Petromyzoniformes. The species are divided into two primary genera: Eptatretus and Myxine. The genus Eptatretus (found in the Pacific Ocean) has 37 species; the genus Myxine (found in the Atlantic Ocean) has approximately 18 species.

Hagfishes are the products of a long evolutionary history and can be considered as primitive, specialized, and degenerate. The hagfish lineage extends over 530 million years and is clearly monophyletic in its origin. Hagfishes are the oldest lineage of vertebrates and are thus very important to evolutionary studies. However, hagfishes are not well represented in the fossil record due to their lack of bony structures. The fossil record consists of a single fossil representing one species of one genus, Myxinolepis sivicki. The discovery of this fossilized hagfish, in sediments deposited roughly 330 million years ago, put the significance of the hagfishes into new light. The hagfishes are an important link between invertebrates and vertebrates, and thus are of interest to evolutionary biologists in regard to both their anatomy and physiology, because they may retain characteristics of ancestral extinct species that are common to their closest relatives, the primitive fossil fishes.

Physical characteristics

All hagfish species have a cartilaginous skeleton with no vertebrae, true fin rays, paired fins, or scales. Hagfishes lack jaws, but have two laterally biting dental plates with keratinous cusps. The mouth is an oval slit, with four fleshy barbels, and a strong tooth on the tongue. The single nostril is surrounded by another four sensory barbels that allow the hagfish to acutely scent food. The eyes of the Pacific hagfishes (Eptatretus stoutii) exist as degenerative eyespots covered with thick skin. Atlantic hagfishes (Myxine glutinosa) have more degenerative eyespots than Pacific hagfishes. Atlantic hagfishes range in size between 17.7–23.6 in (45–60 cm), but not exceeding 30.7 in (78 cm), in length. Pacific hagfishes are slightly smaller, not exceeding 25.6 in (65 cm) in length. Hagfishes have six to 10 pairs of internal gill pouches, which may open separately to the exterior or unite to form a single exterior opening on each side of the animal, depending on the species. In Pacific hagfishes, short efferent ducts lead to 10–14 external gill openings; in Atlantic hagfishes the efferent ducts discharge through a common external opening. Color ranges from reddish brown to grayish pink.

One interesting feature of the hagfishes that is unique among other fishes or vertebrates is the production of copious quantities of slime. Hagfishes have approximately 150 to 200 slime glands along the side of the body. When a hagfish is attacked or handled, it will secrete small amounts of slime. When the slime comes in contact with the surrounding seawater, the mucous component of the slime expands greatly as it is hydrated with the water, increasing its volume several fold. In order for the hagfish to rid itself of the slime, it literally ties itself in a knot and scrapes itself clean by moving the knot down the body. The slime is used as a defense mechanism and may be involved in reproduction.
Distribution
Hagfishes have been reported from the Atlantic, Pacific, Indian, Arctic, and Antarctic Oceans, and from the Bering, Mediterranean, and Caribbean Seas. Hagfishes do not occur in the Red Sea or the Gulf of Thailand. Atlantic hagfishes are found on both sides of the North Atlantic and in Arctic Seas in deep water of 3,937–11,811 ft (100–300 m) on soft muddy bottoms. Their distribution is varied and patchy, being confined to areas with a suitable bottom. Pacific hagfishes are found along the Pacific coast of North America, from southern California to southeast Alaska. They are found on diverse substrates from muddy bottoms to sand/gravel and boulder/sand substrates.

Habitat
Hagfishes mostly inhabit deep marine environments that are relatively free of circadian or seasonal changes. Temperature and salinity are thought to be two of the most important factors to influence hagfish distribution. The fishes are most often found in waters that are cooler than 71.6°F (22°C) and have salinities between 32–34 parts per thousand. Although they are most commonly found at the bottom of the ocean—the deepest reported hagfish sighting was 196,850 ft (5,000 m)—some species have been reported in depths as shallow as 394 ft (10 m). Pacific hagfishes occupy a wider range of substrate types than Atlantic hagfishes. Pacific hagfishes occur on substrates ranging from soft muddy bottoms to boulder/sand substrates, and are often found in a coiled position nestled among the rocks. Atlantic hagfishes are most often found on soft muddy substrates in which they form burrows. Atlantic hagfishes burrow by first orienting the body in a vertical position above the substrate and then swimming head first into the substrate. Once the anterior half is below the surface of the mud, the anterior portion pulls the posterior portion below the surface.

Hagfishes are an important part of the benthic marine environment. They are a substantial proportion of the benthic biomass; are critical for substrate turnover and the clean-up and processing of carrion falls; they prey on benthic inverte-
brates as well as provide prey for marine mammals and large predatory invertebrates.

Behavior
The Japanese hagfish (*Eptatretus burgeri*) is the only known species that undertakes an annual migration, which is thought to be associated with the reproductive cycle.

Feeding ecology and diet
Hagfishes are chiefly scavengers and feed on crustaceans, small marine worms, and vertebrate remains. Using its strong teeth, the hagfish pierces the fish's skin and bores into the body, eating the flesh and eventually only leaving the bone and skin. Gut analyses of Atlantic hagfishes have shown a diet consisting primarily of invertebrate organisms, including polychaetes, hermit crabs, and shrimps.

The Atlantic hagfish has few known predators. Small hagfish have been found in the stomachs of codfish, harbour porpoise, octopus, Peale's dolphin, and sea lions. Hagfish eggs have also been found in the stomachs of male hagfish.

Reproductive biology
The reproductive patterns of most hagfishes are unknown. Females produce a small number (20–30) of large yolked eggs 0.8–1 in (20–26 mm) long. The eggs are enclosed in a tough shell with threads at each end, which act as anchors in the mud. Males produce a small amount of sperm. As neither sex has a copulatory organ, the mode of fertilization is thought to be external.

Sex is often difficult to determine in hagfishes. Atlantic hagfishes have been considered functional hermaphrodites, with their single unpaired sex organ developing sperm in the posterior portion and eggs later in the anterior portion. Other investigations have shown that hagfishes are not hermaphrodites, but that the gonads undergo differentiation into male and female gonads. More recent studies suggest that Atlantic hagfishes could indeed function as hermaphrodites for part of their life cycle, reproducing as either male or female at other times.

The spawning behavior and frequency is unknown. The Japanese hagfish appears to have an annual reproductive cycle associated with its migration into deep waters. At least two species of hagfishes spawn throughout the year, for ripe Atlantic hagfish females and those nearing ripeness have been recorded during all seasons.

It has been noted that Pacific hagfish females in an aquarium ceased to feed when they approached sexual maturity, as do many other fishes. Hagfishes lay their eggs in clutches, strongly supporting evidence that hagfishes do not die after spawning. Although there are no documented answers to how hagfishes reproduce, considerable data have led to the following conclusions: reproduction takes place at a depth in excess of 164 ft (50 m), there is no marked season of sexual activity (except in the Japanese hagfish), and the eggs are fertilized externally and anchor themselves by their hooks not far from where they were extruded. The last fertilized hagfish eggs reported were obtained by Julia Worthington in 1903.

Conservation status
No species are listed on the IUCN Red List. During the past 40 years, hagfishes have constituted a valuable fishery off the coasts of Japan and Korea, for both meat and skins. A commercial fishery for hagfishes began in 1967 on the West Coast of the United States, and moved to the East Coast in early 1992 when catches on the West began to decline. There are currently few regulations on the commercial hagfish industry in the United States. Catches from the Gulf of Maine have increased steadily since the mid 1990s, as the Atlantic hagfishes were targeted by U.S. and Canadian fishermen to meet the South Korean demand for “eel” skin, used to manufacture leather goods. Since the fishery began along the New England coast there has been an apparent decline in the number of hagfishes caught in the nearshore fishery.

Significance to humans
Atlantic hagfishes are considered an important species in the Gulf of Maine because they play a significant role in the benthic ecosystem throughout the gulf; have both important direct and indirect effects on commercial fisheries in the gulf, consuming by-catch and providing food; and are targeted by U.S. and Canadian fishermen to meet the South Korean demand for “eel” skin. It is likely that all hagfishes have a crucial and significant role in the benthic ocean ecosystem, and the loss of hagfishes could have a major impact on nutrient recycling in the world’s oceans.
Atlantic hagfish
*Myxine glutinosa*

**FAMILY**
Myxinidae

**TAXONOMY**
*Myxine glutinosa* Linnaeus, 1785, Europe; Mediterranean to Murmansk.

**OTHER COMMON NAMES**
English: Slime eel.

**PHYSICAL CHARACTERISTICS**
Between 17.7–23.6 in (45–60 cm) in length, but not exceeding 30.7 in (78 cm). Jawless, single nasal opening, single pair of external gill openings, degenerative eyespots covered with thick skin. Grayish or reddish brown.

**DISTRIBUTION**
Widely distributed in European seas from Murmansk to Mediterranean Sea. Absent in eastern Mediterranean and Black Seas. Present in northwest Atlantic.

**HABITAT**
Deep waters of 328–984 ft (100–300 m) on soft muddy substrates in which they form burrows.

**BEHAVIOR**
Burrows by first orienting the body in a vertical position above the substrate and then swimming head first into the substrate. Once the anterior half is below surface of the mud, the posterior portion is pulled below the surface by the anterior, leaving only the nasal opening extruding above the mud.

**FEEDING ECOLOGY AND DIET**
Feeds on dead and dying fishes, crustaceans, and other small benthic organisms.

**REPRODUCTIVE BIOLOGY**
Females produce 20–30 large yolky eggs. Fertilization is thought to be external, but has never been observed. It is not known if there is a seasonal reproductive cycle.

**CONSERVATION STATUS**
Not listed as a threatened or endangered, but fishermen have reported reduced catches in recent years in the Gulf of Maine.

**SIGNIFICANCE TO HUMANS**
Hagfish skin is processed into various leather goods and marketed as "eel" skin.
Pacific hagfish
_Eptatretus stoutii_

**FAMILY**
Myxinidae

**TAXONOMY**
_Eptatretus stoutii_ Lockington, 1878, West Coast of North America, South China Sea, Philippines.

**OTHER COMMON NAMES**
English: Slime eel.

**PHYSICAL CHARACTERISTICS**
Does not generally exceed 25.6 in (65 cm) in length. Jawless, single nasal opening; 10–14 gill pouches open directly to external gill openings. Dark brown, tan, gray, or brownish red, often tinted with blue or purple, never black, lighter ventrally, rarely with large patches of white. Eyes exist as degenerative eye spots covered with thick skin.

**DISTRIBUTION**
Widely distributed in the Eastern Pacific: southeastern Alaska to central Baja California, Mexico.

**HABITAT**
Occupies a wider range of substrate types than Atlantic hagfishes. Occurs at over 330 ft (100 m) on substrates ranging from soft muddy bottoms to boulder/sand substrates.

**BEHAVIOR**
Burrows in soft sediments and is often found in a coiled position nestled among rocks in boulder/gravel substrates.

**FEEDING ECOLOGY AND DIET**
Feeds on dead and dying fishes, crustaceans, and other small benthic organisms.

**REPRODUCTIVE BIOLOGY**
Females produce 20–30 large yolky eggs. Fertilization is thought to be external, but has never been observed. It is not known if there is a seasonal reproductive cycle.

**CONSERVATION STATUS**
Not threatened.

**SIGNIFICANCE TO HUMANS**
Hagfish skin is processed into various leather goods and marketed as “eel” skin.

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**Resources**

**Books**


Stacia A. Seever, PhD
Mickie L. Powell, PhD
Scott I. Kavanagh, BS