CYCLOSTOME

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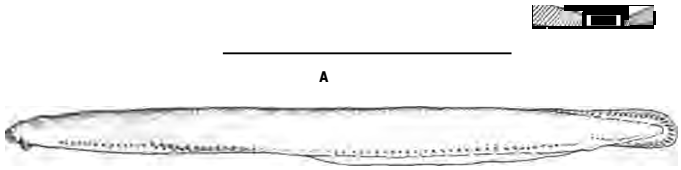
CYCLOSTOME, any of the lampreys and hagfishes, round-mouthed, eel-shaped, jawless fishes that compose the class (or order) Cyclostomata (Marsipobranchii or Cyclostomi). Together with fossil ostracoderms *(q.v.;* armoured, jawless fishes), these primitive vertebrates are often grouped in a superclass (or class) Agnatha.

Cyclostomes are all aquatic creatures, smooth, slimy and scaleless, with a cartilaginous skeleton. The known species—about 50—inhabit the waters of the temperate zones. Most are marine, but a few lampreys are confined to lakes and streams, and the sea lampreys spawn in fresh waters. The maximum size ranges from less than six inches to about three feet.

Importance.—Most of the cyclostomes are regarded as harmful to man because they destroy food and game fishes. The larger lampreys attach themselves to fishes and drain their blood. In the Great Lakes vast damage is thus inflicted by the sea lamprey, *Petromyzon marinus* (fig. 1[A]), which entered these waters by way of a canal and soon became very abundant, feeding extensively on lake trout and spawning in the lake tributaries. Efforts are made to control the increase of these lampreys by destroying the mature adults, which are caught in a weir placed in the spawning stream, and by the use of chemicals to destroy the larvae.



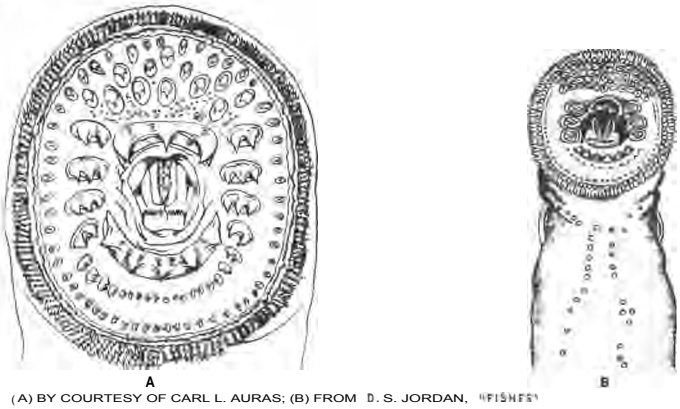
(A) AFTER DEAN; BY COURTESY OF CARL L. HUBBS

FIG. 1.—TWO PRINCIPAL TYPES OF CYCLOSTOMES: (A) SEA LAMPREY (PETROMYZON MARINUS); (B) PACIFIC HAGFISH (EPTATRETUS STOUTII)

Marine food fishes are bled by seagoing lampreys, but suffer greater damage from the attacks of the hagfishes (fig. 1[B]), which eat their way into and through the flesh of food fishes. Large numbers of valuable fish are thus destroyed. Fish that are caught in nets or on set lines are particularly subject to such loss. On the other hand lampreys are esteemed as food in many places, and their larvae are extensively used as bait by fresh-water anglers. Adult brook lampreys, which are harmless because they do not feed, furnish, along with the larvae of all lampreys, considerable natural food for trout and other game fishes.

Scientifically the cyclostomes are of great significance, because they are the most primitive of the living vertebrates. The lamprey larva or ammocoete in particular is regarded as providing the closest facsimile of the ancestor of the backboned animals. For this reason the ammocoete is recommended as one of the types to be studied in comparative anatomy courses. Adult lampreys and the hagfishes depart from the ancestral form since many of them are specialized for parasitic existence.

Characters.—The cyclostomes differ from all other living vertebrates in many important respects. None of their gill arches have been converted into jaws, for which reason they are classified among the jawless vertebrates, or Agnatha (a group that contrasts with the jaw-bearing vertebrates or Gnathostomata). The cyclostomes are also devoid of any trace of the paired fins (pectorals and pelvics), which, except for occasional loss through degeneration, are present in all other fishes and, in the form of limbs, are represented in all higher vertebrates. The muscular, protrusible tongue in all cyclostome fishes, and in the adult lampreys the buccal disc or funnel (fig. 2) as well, bear teeth that are composed of thin horny tissue rather than dentine or enamel. Instead of forming partitions between slits, the gills lie in spherical pouches that connect with the pharynx and with the exterior through tubes. The internal ear has only one or two



(A) BY COURTESY OF CARL L. AURAS; (B) FROM D. S. JORDAN, "FISHES"

FIG. 2.—BUCCAL DISCS AND TEETH OF (A) PARASITIC PACIFIC SEA LAMPREY (ENTOSPHENUS TRIDENTATUS) AND (B) NONPARASITIC AMERICAN BROOK LAMPREY (ENTOSPHENUS LAMOTTENII)

semicircular canals, not three as in typical vertebrates (the horizontal canal is missing). The brain is small, primitive and distinctive, and the brain case is incomplete, especially in the hagfishes. The skeleton is wholly cartilaginous, without any trace of calcification. The notochord is persistent throughout life and is nowhere constricted. No vertebrae proper (centra) are formed. The olfactory organ is a single median sac with an internal opening into the cavity of the pituitary and an external opening that lies on the midline either on the top or at the front of the head. On the basis of the narial structure some authorities classify the cyclostomes, along with certain extinct groups discussed below, as the Monorhini. All other vertebrates are said to be diplorhine, for they have paired nostrils, with one sac on each side of the head.

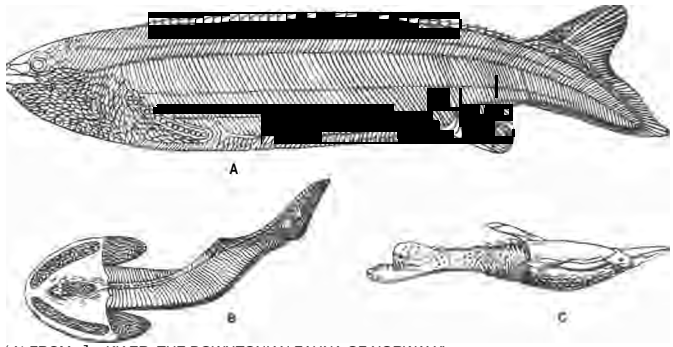
Life History.—All lampreys spawn in the spring on gravel beds in streams. The marine species migrate into the streams to breed, passing over dams and other obstructions. They inch their way up the sheer vertical walls by adhering by their sucking mouth disc. A lamprey life cycle is shown in fig. 3.

The males arrive first on the spawning grounds and start to prepare the nest. By adhering to and tugging out pebbles, the lamprey fashions a shallow depression. The newly arrived female then maintains a hold on a stone while the male clamps onto the female and twists around her, fertilizing the eggs as she extrudes them. The parents then loosen the pebbles lying on the rim of the nest so that the particles fall into the depression, thus surrounding and covering the eggs. By the time the spawning act is completed the adults are emaciated, and in a short time they die.

After about two weeks the eggs hatch and the larval or ammocoete life begins. The several size groups, each resulting from one year's spawning, indicate that the larval stage lasts several years. The wormlike, toothless, nearly blind larvae live in burrows in the bottom of mixed sand and mud, coming out at night to feed on the organic ooze, which is strained through the thick cirri in the hoodlike mouth.

After at least three years (often more) of such life the ammocoete rapidly transforms in the late summer and fall into the adult form. Many changes take place simultaneously: the eye becomes much larger and better developed; the hood is replaced by the disc and the cirri by teeth; the nostril opening moves from the front to the top of the head; and the body becomes rounder in cross section, the flesh firmer and the colour brighter. During this transformation, or metamorphosis, the lamprey shrinks considerably in length.

Soon after metamorphosis the sea lampreys become silvery and large-eyed in preparation for life in the ocean, to which they promptly migrate. Some of the nonparasitic brook lampreys pass through this same stage, known as the macrophthalmia, as though in racial remembrance of the former seaward journey, though this trip has been abandoned for millenniums.



(A) FROM J. KIAER, THE DOWNTONIAN FAUNA OF NORWAY;" (B) AFTER A. S. WOODWARD, "PROCEEDINGS," BY COURTESY OF GEOLOGIST'S ASSOCIATION; (C) FROM A. S. ROMER, "VERTEBRACE PALEONTOLOGY"

FIG. 4.—FOSSIL RELATIVES OF CYCLOSTOMES: (A) PHARYNGOLEPIS OBLONGUS (ANASPIDA) FROM THE UPPER SILURIAN OF NORWAY; (B) CEPHALASPIS MURCHISONI (OSTEOSTRACI) FROM THE DEVONIAN OF HEREFORDSHIRE, ENG.; (C) PORASPIS (HETEROSTRACI) FROM SILURIAN OF SPITSBERGEN ISLANDS

All parasitic lampreys feed and grow rapidly on their nutritious diet of fish blood. Those that remain in fresh water live thus for a year or more. A larger size is reached in the sea, presumably because of faster growth rather than a longer life span. After they become sexually mature, the parasitic species spawn once and then die, to complete the life cycle.

The nonparasitic species metamorphose at a size at least as large as do their parasitic relatives, but the teeth are poorly developed and the gut shrinks to a solid strand. Without taking any food they complete, overwinter, the ripening of the sex cells that had begun before the metamorphosis. Like the parasitic species they then spawn and die.

The hagfishes deposit a large, yellowish, yolk-filled egg. This is enclosed in a protective horny shell and is attached to the bottom of the sea by threadlike tendrils. The development is slower than in lampreys, and the young are much larger when hatched. They look very much like the adults, into which they gradually develop without a metamorphosis. In life history as well as in structure the hagfishes are very much unlike the lampreys.

Evolutionary History.—The fossil record as well as the evidence from comparative anatomy indicates that the Cyclostomata are cousins of the earliest and lowest vertebrates. The oldest fossilized remains of vertebrate animals, found in the Silurian deposits with traces in the yet more ancient Ordovician rocks, prove on close study to be similar in many respects to lampreys

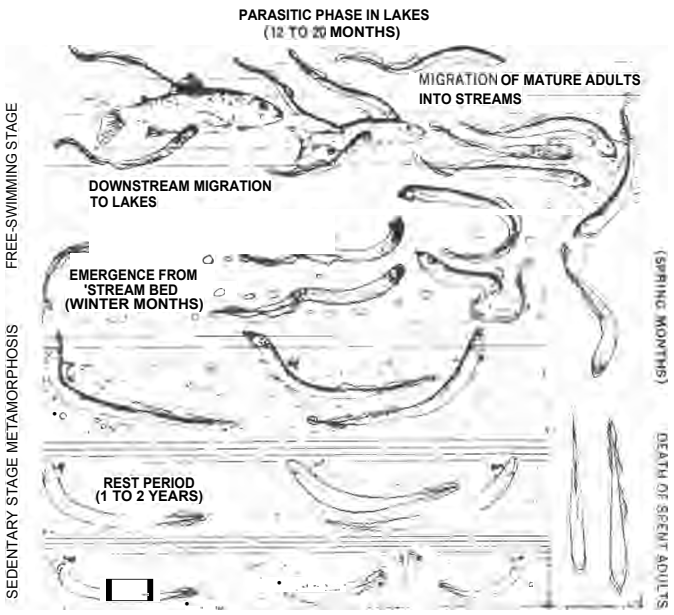


FIG. 3.—LIFE CYCLE OF THE SEA LAMPREY (PETROMYZON MARINUS) IN THE GREAT LAKES. THE LIFE SPAN OF THE LAMPREY MAY BE AS LONG AS 61 TO 71 YEARS. MOST OF THIS TIME SPENT IN THE SEDENTARY LARVAL STAGE THE ADULT LAMPREY DIES SOON AFTER SPAWNING

and hagfishes. Superficially the fossils (fig. 4) bear little resemblance to their modern relatives, which, in correlation with their parasitic habits, are highly specialized in some respects and in other ways much degenerated. In fundamental anatomy, however, they were much alike. Thus the extinct forms resembled the cyclostomes in lacking jaws, for the anterior gill arches remain unaltered. They appear also to have lacked true paired fins, though in some species flipperlike flaps were developed in place of pectoral fins. The extinct forms agreed further with the cyclostomes in gill structure and in having had only two semicircular canals in the internal ear. Most of the extinct groups had, like the cyclostomes, a single median nostril.

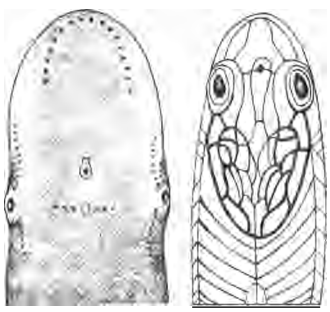
Most of these early fishes, and naturally those that are best known because most thoroughly preserved, were heavily armoured with dermal bone—hence the group name Ostracodermi that has often been applied to them as a whole. On these grounds many paleontologists have regarded the bizarre armoured fishes as the direct ancestors of the more ordinary modern types. It is more logical to assume, however, that both the armoured and the progressive types were derived from unarmoured fishes with the usual fish form. The highly specialized mailed kinds were probably evolved to provide protection from such enemies as the gigantic "water scorpions" of early times. Furthermore, such types had a much greater chance than their slender, soft-bodied and probably free-swimming ancestors to be fossilized and well preserved in the rocks. The more highly evolved, heavily armoured types persisted throughout Late Silurian time and all of the Devonian, along with the earlier jawed or gnathostome fishes which are classified as the Placodermi. None of the Ostracodermi is known to have survived beyond the end of the Devonian, but some primitive member of the Agnatha must have persisted, to give rise to the living group with which we are dealing. In conformity with an evolutionary rule, the highly specialized group died out while some generalized relative lived on.

Fossil Relatives.—Since the cyclostomes are the only living Agnatha or jawless vertebrates, their relatives are to be sought exclusively among the extinct fishes. Three groups, commonly treated as orders, all Paleozoic and none persisting beyond the Devonian, show evidence of relationship with the lampreys and hagfishes: they are the Osteostraci, Anaspida and Heterostraci, composing the Ostracodermi. The common feature of all ostracoderms is their plated or armoured skin *(see* OSTRACODERM).

In some ways the most lampreylike of the fossils were the Anaspida (fig. 4[A]). These Silurian and Devonian creatures seem primitive because of their small size (none exceeding ten inches), their almost ordinary fish form and their small scales, which apparently overlaid the muscle segments.

As in the cyclostomes, they had the eyes lateral and a single nostril in front of the third or pineal eye (fig. 5), and the gill openings formed a row of pores on each side.

The Osteostraci (fig. 4[B]) also had a median, superior nostril and a row of porelike gill openings, but differed from the Anaspida (and from the cyclostomes) in having the head enclosed in a flat bony shield.



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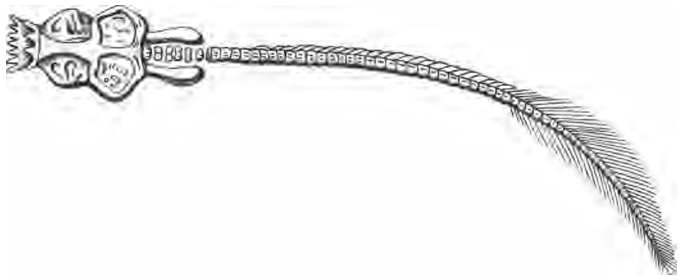
FROM J. KIAER, "VIDENSK. SKRIFT.," OSLO

FIG. 5.—HEAD OF LIVING LAMPREY COMPARED WITH A FOSSIL RELATIVE: (A) SEA LAMPREY (PETROMYZON) (B) SILURIAN ANASPIDA (RHYNCHOLEPIS)

The Heterostraci were armoured fishes (fig. 4 [C]) that closely resembled the Osteostraci. Both groups were abundant in Late Silurian and Early Devonian times and disappeared completely by the end of the Devonian. In this group the armour lacked the bone cells that were characteristic of the Osteostraci. The paired eyes were far apart, and there was no dorsal nostril. The olfactory organs, which were close together but paired, are supposed to have opened into the mouth cavity.

The Devonian group known as Cycliae or Palaeospondyloidea is



BY COURTESY OF THE TRUSTEES OF THE BRITISH MUSEUM

FIG. 6.—FOSSIL REMAINS OF PALAEOSPONDYLUS GUNNI FROM THE SILURIAN OF SCOTLAND (TWICE NATURAL SIZE)

recognized for one of the most problematical of the fossil vertebrates, *Palaeospondylus* (fig. 6), which by some has been thought to be an ancient lamprey or lampreylike animal. If so, the living lampreys must be very degenerate, for they lack the vertebral centra that are well developed in the fossil. Other zoologists have regarded it as a larval arthrodire. The remains of this one- to two-inch fishlet abound in one quarry in Scotland and have been very thoroughly studied. Nevertheless, opinions differ as to whether or not the group had gills or paired fins, and relationships of the group remain uncertain.

CLASSIFICATION

The Cyclostomata are divided into two subgroups, which are different in anatomy, appearance and habits:

	Hyperoartii (lampreys)*	*Hyperotreti* (hagfishes)
Nasal opening	On top of head	At front of head
Pituitary canal	Closed internally	Opening into pharynx
Cartilaginous rings around this canal	Lacking	Developed
Pineal eyes	Easily visible	Degenerate
Eyes	Well developed	Vestigial
Oral funnel	Developed	Not present
Teeth	On disc also	Only on tongue
Tentacles about mouth and nostril	Lacking	Six, supported by cartilage
Number of gills	Always 7	5 to 14
Gill openings	Close to head	Remote from head
Internal gill tubes	United	Separate
Duct on left side, pharynx to exterior	Lacking	Developed
Branchial skeleton	A conspicuous basketwork	Greatly reduced
Dorsal fin	One or two well developed	None or only a trace
Neural arches	Present	Lacking
Dorsal and ventral roots of spinal nerves	Distinct	United
Kidneys	Compact organ	Separate
Eggs	Minute, without horny shell	Very large, with horny shell
Development	With larva and metamorphosis	Direct (young much like adult)
Spawning place	Gravel in streams	Ocean floor
Feeding on	Fish blood	Fish flesh, etc.
Type of parasitism	External	Internal

* The characters are those of adult lampreys. In several respects the lamprey larvae agree with the Hyperotreti.

The differences between the lampreys and the hagfishes are so extensive and so fundamental as to lead some authorities to think that the two groups are unrelated. They appear, however, to have had a remote common ancestor.

Lampreys.—The Hyperoartii, or lampreys, may be classified into three families. The chief family, Petromyzonidae, comprises all the northern hemisphere species. The well-known sea lamprey, *Petromyzon marinus,* occurs on both sides of the Atlantic. Three related genera, *Eudontomyzon, Entosphenus* and *Lam petra,* occur in Eurasia as well as in North America. The primitive genus *Ichthyomyzon,* with more species than any other, inhabits only the fresh waters of eastern North America. *Caspiomyzon* is confined to the Caspian sea basin. About half the species of Petromyzoni-

dae are of the dwarfed, nonparasitic brook type, with weak teeth. Nearly all of these have arisen through degeneration from different parasitic kinds, and hence they are named as distinct species (in the genera *Ichthyomyzon, Eudontomyzon, Entosphenus* and *Lampetra).*

The distinctive lampreys of the southern hemisphere are placed in two families, Geotriidae and Mordaciidae, each with a single genus *(Geotria* and *Mordacia).* These southern genera live along the coasts of Chile, New Zealand and Australia. Like all other lampreys they spawn in fresh water. (See also **LAMPREY.**)

Hagfishes.—All the Hyperotreti, or hagfishes, are marine. Except for a few species in deep water within the tropics, all are inhabitants of the temperate zones—in the North Atlantic, western North America, Japan, New Zealand, Chile, Patagonia and South Africa. Fewer than 24 species are recognized. They are generally regarded as constituting a single family Myxinidae. Some authorities restrict Myxinidae to genera (principally the genus *Myxine)* that have a single external gill opening on each side, placing the genera *(Eptatretus,* etc.) with 6 to 14 such openings on each side in a separate family, Eptatretidae. In view of the similar basic structure of all hagfishes, and the closely approximated gill openings of the genus *Paramyxine,* the family separation has generally been abandoned. *See* also **HAGFISH.**

See also references under "Cyclostome" in the Index volume.

BIBLIOGRAPHY.—Vernon C. Applegate, "Natural History of the Sea Lamprey, *Petromyzon marinus,* in Michigan," U.S. Department of the Interior, Fish and Wildlife Service, Special Scientific Report, Fisheries, no. 55 (1950) ; L. S. Berg, "A Review of the Lampreys of the Northern Hemisphere," Annuaire du *Musée Zoologique* de *l'Académie* des Sciences de *l'URSS,* vol. 32 (1931) ; Charles W. Creaser and Carl L. Hubbs, "A Revision of the Holarctic Lampreys," Occasional Papers of the Museum of Zoology of the University of Michigan, no. 120 (1922) ; Bashford Dean, Fishes, Living and Fossil (1895); Simon Henry Gage, "The Lake and Brook Lampreys of New York," The Wilder Quarter-Century Book (1893), "The Lampreys of New York State—Life History and Economics," A Biological Survey of the Oswego River System, suppl. to annual report of New York State Conservation Department, vol. 17 (1928) ; E. Ray Lankaster (ed.), A Treatise on Zoology, part ix, E. S. Goodrich, "Vertebrata Craniata (First Fascicle: Cyclostomes and Fishes)" (1909) ; Carl L. Hubbs, "The Life-Cycle and Growth of Lampreys," Papers of the Michigan Academy of Science, Arts, and Letters, vol. 4 (1925) ; Carl L. Hubbs and Milton B. Trautman, "A Revision of the Lamprey Genus *Ichthyomyzon,"* Miscellaneous Publications of the Museum of Zoology of the University of Michigan, no. 35 (1937) ; David Starr Jordan, Fishes (1925) ; J. A. Moy-Thomas, Palaeozoic Fishes (1939); T. Jeffery Parker and William A. Haswell, A Textbook of Zoology, 6th ed., rev. by C. Forster-Cooper (1940); C. Tate Regan, "A Synopsis of the Marsipobranchs of the Order Hyperoartii," Annals and Magazine of Natural History, series 8, vol. 7 (1911) ; Alfred S. Romer, Vertebrate Paleontology, 2nd ed. (1945).

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