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Lampreys in Human Life, Their Cultural and Folklore Importance

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Abstract: This contribution provides summary information on the historical and contemporary significance of lampreys for human life. The unusual to bizarre appearance of lampreys initially posed a problem for zoologists to correctly classify lampreys in the zoological system. In certain places, lampreys are used as bait in sport fishing, and a total of seven species are fished extensively for gastronomic purposes in Europe, North America, Australia, and Asia. New information about role of lampreys in human gastronomy was obtained by studying historical sources from Central Europe, especially from the region of Bohemia. The first specific cooking recipes have been preserved from the turn of the 15th and 16th Centuries. Instructions for cooking lampreys were mentioned by Georg Handsch von Limus, Paulus de Praga, Jan Severin the Younger and Pavel Severin of Kapí mountain. The quality of their meat is excellent, however, the slime and serum are poisonous, so there are known historical data about probable poisoning after their consumption. At present, lampreys are routinely available fresh, fried, smoked, marinated, canned or in vinegar. Lampreys play an important role in the culture and folklore of some nations. For example, lampreys are ecologically and culturally important for the North American Indian tribes of Yurok and Karuk.. The Pacific lamprey is also of spiritual significance for these tribes. The enormous esteem people have for lampreys is also reflected in the various coats of arms, in which the lamprey appears. Cooking skills and traditions are practiced at various public festivals where lampreys are caught and immediately consumed after cooking (e.g., Estonia, Latvia, Lithuania, Portugal, Spain). Lampreys have become an important model group in evolutionary studies of vertebrate development, and due to their remarkable properties, they are also used in biomedical research. Lampreys can be used for long-term bioindication of water environment, but their larvae are not a suitable bioindicator of short-term water quality worsening (see research results from the Czech Republic). Based on the analysis of the lamprey's specific method of swimming, biologists and engineers created a biomimetic robot with an electronic nervous system that imitated the movement and orientation of lampreys in the water. Nevertheless, there is also an example of the harmful effect of lampreys, namely the parasitic sea lamprey, which causes significant damage to economically important fish in the Great Lakes, requiring a yearly implementation of financially expensive measures to eliminate the lamprey.

Keywords: Lampreys, Importance for People, Cultural and Folklore Objects

1. Introduction

Lampreys (Petromyzontiformes) are jawless eel-like vertebrates with the range of origins somewhere between 360 and 550 million years ago [37, 70]. They have an antitropical distribution with approximately 40 species (44, 105, 120), grouped into three families; one in the Northern Hemisphere, Petromyzontidae, and two in the Southern Hemisphere, Geotriidae and Mordaciidae. The occurrence of lampreys in the world can be classified as disjunct distribution. Lamprey fossils are rare because cartilage does not fossilize as readily as bone. It is evident that lampreys are one of the most remarkable vertebrates which can be characterized as an

evolutionarily successful group, as they have survived from the Palaeozoic to the present [163]. Moreover, they have not changed much morphologically in this long time. For example, the species *Priscomyzon riniensis,* dating back 360 million years, is very similar to lampreys found today, but its body length is little more than 4.2 cm [48]. Their unique characteristic is that they live most of their lives in the form of eyeless, toothless worm-like larvae (ammocoetes) hidden in the fine bottom sediments of freshwater streams. Larval lamprey are important ecosystem engineers, via their burrowing activity [15, 141, 60]. They bioturbate sediments, filter-feed fine organic material, and cycle nutrients and energy between the water column and bed sediments [122]. Other ecological roles of lamprey populations involve prey resources for other animals [28], parasitation and predation [133]. Some species of lampreys are anadromous (i.e. ascending rivers from the sea for breeding) and feed in marine waters. Anadromous lampreys can be categorized into four groups, based on feeding modalities: 1) scavenger, Caspian lamprey, *Caspiomyzon wagneri*; 2) parasite-predator, Pacific lamprey, *Entosphenus tridentatus*; 3) predators, Western river lamprey, *Lampetra ayresii*; River lamprey, *L. fluviatilis*; Arctic lamprey, *Lethenteron camtschaticum*; Pouched lamprey, *Geotria australis* and *G. macrostoma*); and 4) parasites, Sea lamprey, (*Petromyzon marinus*; Shorthead lamprey, *M. mordax* and Chilean lamprey, *Mordacia lapicida*), [133]. Pure freshwater residents also feed parasitically or remaining non-parasitic and not feeding as adult [88]. All species of lampreys breed in fresh waters and are semelparous, i.e. both adults die after the eggs are fertilized [37]. The unusual to bizarre appearance of lampreys, especially their oral disc equipped with teeth (Figure 1), evokes different feelings or fears in people [43]. Nevertheless, historically, lampreys have been used in human life in various ways. The following text presents both positive and negative significance for humans, especially regarding cultural and folklore aspects.

Figure 1. *Oral sucking disc of adult European brook lamprey (Lampetra planeri). Photo Bernt Rene Voss Grimm.*

2. Material and Methods

We compiled published informations on lampreys (Petromyzontidae, Petromyzontiformes) in human life, their culture and folklore importance. Data presented in this contribution has been obtained by studying of various historical and present files, works, reports, papers, books, old cookery books, lexicons, encyclopedias, textbooks and various museum texts (see References). Scientific and English common names of lampreys were used according to FishBase [44].

3. Results

3.1. Historical View on Systematic Classification of Lampreys

Due to the strange appearance (serpentine body, oral suction disc with corneous teeth), it was not clear how to classify lampreys within the zoological system. Aristotle (384–322 B. C.) was not sure whether they were related to sharks (the presence of gill holes) or to sea worms (body shape). Roman authors (Strabo, Pliny and Oppian) considered lampreys to be leeches with gill plugs (branchiae perforatae) [20, 23]. It was not until the second half of the 16th century that earlier views were corrected based on observation (Hippolito Salviani, 1514–1572; Gillaume Rondelet, 1507–1566), when the relationship with fish (eels, moray eels) was already considered, but an analogy with leeches still permitted. The name *Lampetra* was introduced by Rondelet (1507–1566) [136]. Conrad Gesner (1516–1565), see [47], considered classifying lampreys within the system as sharks. In 1758, Carl Linné (1707–1778), in his best-known work "Systema Naturae" included the genus *Petromyzon* described by him in the class Amphibia (order Nantes) [95]. Georges Cuvier (1769–1832) and Achille Valenciennes (1794–1865) created the Cyclostomes order for lampreys in the first volume of the book "Histoire naturelle des poisons" (1828), including lampreys in the subclass of cartilaginous fish [30]. Johannes Peter Müller (1801–1858), after a detailed study of anatomy, included lampreys into a separate subclass, Marsipobranchii, or Cyclostomi, and within the subclass, categorized lampreys as the order of Hyperoartii (Petromyzontidae). Louis Agassiz (1807–1873) calls these orders Cyclostomi and Myxinides [3]. He is the first author to establish a separate class for these animals (Myzontes). Later, the Swedish paleontologist Erik Stensiö (1891–1984) assigns lampreys to the order of Petromyzontida, the Pteraspidomorphi subclasses, resp. Cephalaspidomorphi [152]. Nelson et al. [120] accepted superclass Petromyzontomorphi, class Petromyzontida and order Petromyzontiformes (Hyperoartii).

3.2. Lampreys in Angling and Other Types of Fisheries

In many regions, lampreys were used as bait for fishing in angling. Bubeníček [19] mentioned that lampreys were in Bohemia (Central Europe) excellent bait on the hook for catching eels and monks, the hunting for which was then successful, especially at night. A long tradition is known from England, where Walton [162] already mentions eel fishing in his work. In Britain, river lamprey (*Lampetra fluviatilis*) was captured alongside other fish species in medieval times. Landings of the river lamprey were mainly from the rivers Severn, Thames, Welsh Dee, and several rivers in the Humber river basin [101]. Today, frozen river lampreys can be bought in England in specialized fishing shops. However, Foulds and Lucas [40] pointed out the problematic use of lampreys in the local sport fishing. In total, they estimate that 90,000 lampreys are caught in England each year for sport fishing lures,

equivalent to about 9 tonnes. This creates a controversy and ethical conflict between sport fishermen and the endangered species of lampreys, which must be addressed both by intensifying compliance with the legislation (a law regulating catches of lampreys was issued in the UK in 2009) and by raising awareness among sport fishermen, including appropriate education for the young generation. A potential conflict arises over the use of river lamprey, a protected species, by UK coarse predator (freshwater non-salmonid) anglers [4].

Three anadromous lamprey species support important commercial fisheries in the Northern Hemisphere. Native range of the sea lamprey (*Petromyzon marinus*) is in western European and eastern North American river basins that drain to the northern Atlantic Ocean of western Mediterranean Sea [134]. This lamprey has been harvested in the Iberian Peninsula (Portugal and Spain) and in France many centuries ago. At present it is commercially harvested on the Spanish coast (Ulla, Tea and Minho rivers) and in Portugal rivers Minho, Lima, Cávado, Douro, Vouga, Mondego, Tagus and Guadiana. Landings per fishing boat operating only in the Portuguese estuaries from last 30 years show a decline in the last decade of the 20th century to ca. 13 kg/boat in 1997, but increasing to ca. 158kg/boat was found in the year 2016 [5]. Official records refer fishing of the sea lamprey in France since the beginning of the 12th century (Loire, Seine and Dordogne River basins). Presently, the harvest of this lamprey is carried out only in three rivers, i.e. Loire, Garonne-Dordogne and Adour (in total 140 tonnes) [5]. In North America sea lamprey was likely harvested by native people living on the Atlantic coast [139].

Historically, fishing of river lamprey (*Lampetra fluviatilis*) was common in most of France (Seine and Loire rivers and in Languedoc region). Official commercial and recreational landings from 1999 to 2002 varied between 300 and 4600 kg (data may include also catches of the sea lamprey) [5]. The river lamprey harvesting was known also in several Baltic countries. In Poland fishing of this lamprey is known in Vistula and Oder rivers [168]. Almost 90% of the Finnish river lamprey catch is harvested from rivers entering the Bothnian Bay and lamprey fishing is not practiced as much in the southern parts of Finland. River lamprey is common along the coast of Finland and 28 rivers are known to support spawning populations. River lamprey catch in Finnish coastal rivers make up about 2–2.5 million individuals (100 tonnes) and lampreys are used only for human consumption [159]. Lamprey fishing exist in Sweden in most of the tributaries from the Dalälven River northwards [144]. In Lithuania, river lamprey is commercially fished in the river Šventoji, the Nemunas river delta and Curonian lagoon. Total catches in Lithuania in the period 2010–2019 have been quite small, on average 5 tonnes (ranging from 2−6.2 tonnes). Even so they have increased in comparison to 2000–2009 when the mean annual catch was 3.5 tonnes [77]. The Latvian river lamprey fishery represents on average 25% of the country's total inland fisheries landings. The river lamprey is here fished in larges Latvian rivers (i.e., Gauja, Daugava, Venta, Salaca rivers). The annual harvest of this lamprey in Latvia currently accounts for 39 to 111 tonnes [2]. About 95% of Estonia's total catch of this lamprey comes from the Narva, Pärnu, Jägala, Reiu, Rannametsa, Pirita, Kunda, Vääna, Selja and Valgejõgi rivers. Over the last 50 years, the catch of the river lamprey ranged here between 3 and 68 tonnes per year [5].

Arctic lamprey (*Lethenteron camtschaticum*) is widespread from the Siberian coast to the Anderson River in Canada in the Arctic basin and from the Bering Sea south to Japan and Korea in the northwest Pacific. This lamprey also occurs in the Arctic, White and Barents Sea basins of Russia and Norway [125, 134]. This lamprey was harvested by native people in 19th century in the Yukon River. In Japan, this lamprey is captured throughout Hokkaido Island to the middle of Japan and along the Sea of Japan. The lamprey harvest in the Ishikari and Shiribetu rivers in western Hokkaido peaked at 80–100 tonnes in the 1980s, but declines in the 1990s and had essentially disappeared by 2000 [8]. In the European part of Russia, Arctic lamprey is captured in the Arkhangelskaya Oblast. The first commercial records are from the 18th Century. In the early 20th Century, a commercial fishery developed in Northern Dvina [81]. The main fishing area for Arctic lamprey in the European part of Russia are in Onega, Mezen with tributaries, Vashka, Nortern Dvina, Vychegda, Vyg and Nes river basin [13, 81]. In the Far East, the Arctic lamprey fishery is still undeveloped, but it is present in Amur (and its tributaries), the Suchan and other eastern rivers [5].

Pacific lamprey (*Entosphenus tridentatus*) is species with very broad distribution from Baja California in the eastern Pacific, northward to the Bering and Chukchi seas, and westwards into Russia and Japan [126]. Tribal harvest occurs along the US Pacific coast from the Columbia River to the Klamath River. This lamprey is today primarily harvested by Native Americans during spawning migrations in streams and rivers of Washington, Oregon and Northern California. In Japan, the Pacific lamprey is known to occur around the Pacific Coastal area, especially in the rivers of the Tochigi Prefecture. This species is in Japan very rare [45].

The Russian population of the Caspian basin harvested Caspian lamprey (*Caspiomyzon wagneri*) for about 300 years. Prior to the construction of the Volgograd and Mingechaur reservoirs on the Volga and the Kura rivers respectively, the Caspian lamprey was considered a commercially important species. Thereafter, it experienced dramatic declines in the whole Caspian Sea basin, but especially in the western and northern regions. Two historical fisheries were conducted; one in the lower Volga River, Russian Federation, and the other in the Kura River, Azerbaijan. Between 1910 and 1913, a maximum annual catch of 33.4 million lampreys was recorded in the Volga region. The annual catch in the Kura River for 1930–1963 varied from 10 to 269 tonnes [13]. Korean lamprey (*Eudontomyzon morii*) inhabits mainly Yalu River and other mountain rivers in northeast China, North Korea and the Russian Far East [134]. In the past, in China, Korean lamprey was regarded as harmful because it preyed on other fish [96]. Since the 1980s, the economic value of

this lamprey has increased in northern China [63].

Pouched lamprey (*Geotria australis*) inhabits south-eastern Australia, Tasmania, New Zealand, Chile, Argentina and South Georgia Island [134]. The harvest occurs during spawning migration and lamprey flesh is a highly desirable delicacy that is considered to have health benefits. Its fishery has a high cultural importance for native people in New Zealand [124].

3.3. Lampreys as Human Food

Lampreys have appeared in human food since ancient times. Lampreys appeared at Roman feasts as early as during I and II centuries A. D. [33]. Lampreys were relatively common in Rome, at least in fish ponds and dining rooms of the city's wealthier inhabitants. But even average citizens could occasionally feast on these animals; when Julius Caesar, for example, was celebrating one of his many military triumphs, he purchased for the people 6,000 pounds of lampreys from a certain Gavius Hirrius [103]. In the Middle Ages (from 500 A. D. to 1500 A. D.), lampreys were usually served in the upper-class households, especially during Lent, because their taste is much fleshier than in various species of fish [41]. In European history, the mention of lampreys appears in 1135 [78]. The popularity of the consumption of lampreys by English monarchs is also documented in the case of King John of Lackland (1166–1216), who had lampreys caught on the continent in the French Loire River sent over. The same is documented for King Henry V (1386–1422). Lampreys are also mentioned in the cookbook entitled "On Right Pleasure and Good Health" ("De honesta voluptate et valetudine", in original), written ca. 1465 by Bartholomeus Platina. The lords of Berkeley castle routinely sent lamprey as gifts to the English kings in the 14th Century. In 1367, for example, the fourth lord of Berkeley furnished Edward III (1312–1377) with six lamprey, the first of the season [41]. The English town of Gloucester on the River Severn has been a famous place for fishing for river and sea lampreys since the 12th Century. The order of 600 river lampreys (probably pickled) is documented in 1572, as food for the Lent period at the court of Ferdinand of Tyrol (1529–1595) in Innsbruck [53]. Rondelet [136] mentions small lampreys called "lamproions" or "lamprillons" caught in rivers and streams and sold in large quantities under the trade name "châtillons" in the southern French city of Toulouse. Giovio (= Jovius) [49], in his work "De Romanis piscibus" (1524) mentions that the chefs of two cardinals once quarrelled over the fish at the fish market trying to overbid each other, until one of them purchased it for a very large sum, which the other did not want to pay. When the victorious chef came home, his master was so pleased that he gave him a precious gift as proof of his gratitude. The consumption of lampreys is also evidenced by the rules of table manners of Petr of Švamberk (1616) in his estate in Třeboň, Southern Bohemia [6].

The original recipe for baked lamprey is described e.g. by May [104]: "Draw it, and split the back on the inside from the mouth to the end of the tail, take out the string in the back, flay her and truss her round, parboil it and season it with nutmeg, pepper, and salt, put some butter in the bottom of the pie, and lay on the lamprey with two or three good big onions, a few whole cloves and butter, close it up and baste it over with yolks of eggs, and beer or saffron water, bake it, and being baked, fill it up with clarified butter, stop it up with butter in the vent hole, and put in some claret wine, but that will not keep long".

Local townsmen favoured lamprey pies, i.e., meat pies made from lampreys, baked in syrup of wine and spices, and covered with a large, raised crust. Lampreys were cooked in syrup inside the pie. When the crust was broke open, the content was mixed with more wine and spices, and then spooned onto slices of white bread in a dish warmed over a chafer or hotplate. The lamprey was then cut very thin and placed on top of the bread and sauce. The City of Gloucester (Southwest of England), in token of their loyalty to the royal family, presented a lamprey pie annually at Christmas to the sovereign. This tradition lasted until 1836. On special occasions, such as coronations and anniversaries, the city of Gloucester still sends this special pie to the royal palace. The Queen Elizabeth II at her coronation on 4 March 1953, as well as later, on the silver jubilee of the accession to the throne in 1977, had such a cake among the ceremonial meals [134].

The first specific cooking recipes, manuscript and printed, have been preserved in Bohemia (Central Europe) from the turn of the 15th and the 16th Centuries [6, 135]. Georg Handsch von Limus (1529–1578) mentioned culinary use of lampreys in his unfinished work "Historia naturalis" [143]. The role of lampreys in human gastronomy is also mentioned by Master Pavel Žídek (Paulus de Praga or Paulerinus, 1413–1471). Instructions for cooking sea lampreys appear in the first three printed Czech-language cookbooks, i.e., in the Cookery of Jan Severin the Younger, which has survived in a single copy without a title page and is unfortunately undated, in the next Cookbook by Pavel Severin of Kapí mountain (1535), and in the Cookbook of Kantor (approx. 1550), where there are specific recipes [60]. A lot of various ingredients, such as cinnamon, cloves, ginger, pepper, cumin, mace, raisins, saffron, almonds, honey, and gingerbread, were used. Red wine was often an important ingredient in lamprey cooking. Lampreys were cooked in sauce, smoked, pickled in brine or vinegar, and jelled or just salted. The Swiss naturalist Conrad Gessner (1516–1565) wrote about lampreys approx. in 1550: "In the springtime they are very good and praiseworthy, the bigger, the better. They are very agreeable and lovely to eat: give a thick and slimy blood, which is why they should be washed with good wine and spices" [54].

Lamprey grilling over charcoal is still popular in some European regions. At present, lampreys are routinely available fresh, fried, smoked, marinated, canned or in vinegar, sold by supermarkets as highly prized delicacy [53]. In the past, the Caspian lamprey (*Caspiomyzon wagneri*) has been dried and used as a substitute for candles or a source of oil. It was later used in gastronomy, and today, it is considered an extraordinary delicacy [10]. It is offered fresh or smoked, and often processed by baking. Almeida et al. [5] state that river lamprey is often

sought after by gourmets in many European countries (e.g. Estonia, Finland, France, Latvia, Lithuania, Poland, Portugal, Russia, Spain and Sweden). Specially prepared lampreys called "Lamproie ala Bordelaise" (ingredients: lampreys, leeks, red wine, onions, starch, Bayonne ham, shallots, sugar, salt, pepper, and spices) or "Lamproie de Loire au vin rouge" (ingredients: lamprey, egg, red wine, milk, wheat flour, olive oil, shallot, prune, and salt) are popular delicacies in France. The specialty of "Lamproie au Loupiac" is stewed lampreys on a low heat served on a slice of toasted bread (ingedients: lampreys, leek, white Loupiac wine, sugar, salt, pepper, aromatic plants, and sunflower vegetable oil). Delicious "Lamprey Jelly" in Latvia is used for preparation lamprey sandwiches and a variety of other dishes. In Latvia and Lithuania on the Christmas table there must be a lamprey dish. Latvian traditional recipe of preparing fried lamprey is 4–5 minutes frying of both sides on alder charcoal, then putting fried lamprey in a bowl, pouring with boiling water, adding salt then stewing until they are prepared. Boiling water with lamprey fat jellies (bullion) is used for pouring the prepared lamprey (sometimes tea or coffee is used for jelly colouring). Ready product is packed in wooden tubs then pressed [90].

From non-European countries, lampreys of the genus *Lethenteron* belong among the gastronomically prized species, and are consumed more, for example, in Japan, and South Korea. There is a traditional "Yatsume kabayaki" Japanese dish prepared from lampreys. There is a diversity of regional lamprey dishes in Japan. Restaurants in Ebetsu City, Hokkaido, offer grilled, fried and raw Arctic lamprey. It is also eaten simmered and in soup seasoned with soy sauce or soybean paste (miso). Arctic lamprey are also preserved dried and later consumed grilled [5].

Pouched lamprey (*Geotria australis*) is hunted for consumption by the natives in the Australian Yarra River, Victoria State [134]. Historically, lampreys had great value as a food source also for the Māori people. Extensive fisheries existed in the Whanganui and Taranaki regions of the North Island and in the far south of the South Island of New Zealand. Māori developed sophisticated methods for the capture of lamprey [68].

In general, it can be stated that lampreys have a high utility value. The edible proportion of their body is on average 93%. The protein content is between 13 and 16%, while fat ranges between 7 and 30%. Lampreys also contain many valuable minerals (mainly phosphorus and magnesium). Compared to fish, they provide more vitamin B12 and abundance of vitamin A, the content of which equals to 9,000–44,000 international units per 100 g of edible body mass, and to around 6,300 international units in the skin. Wold et al. [169] discovered the greatest amount of vitamin A (respectively retinol) in the intestine of the Arctic lamprey, with slightly lesser content in the liver and kidneys. Yamada [173] had previously discovered that more than half of the total amount of the A vitamin is concentrated in the intestine, which weighs only about 1% of the entire body weight, of the Arctic lamprey. To be precise, up to one million international units of vitamin A per 1g have been confirmed in the intestine. The author has also reported that the amount of the vitamin during the year varies. The contents of vitamins in various species of lampreys (calculated per 100 g of edible proportion of the body, in fresh catch) are recorded as follows: 46–850 μg of thiamine (vitamin B1), 427–612 μg of riboflavin (vitamin B2), 4.7 mg of niacin (vitamin B3), 170–220 μg of pyridoxine (vitamin B6), 3.8–4.4 μg of vitamin B12, 24–29 μg of folic acid, 280–570 μg of pantothenic acid (vitamin B5), and 120–400 of international units of vitamin D3 [39, 59, 61, 91].

Holčík [62] mentioned that the consumable parts of the body of Caspian lamprey, as a highly gastronomically important species, comprised 55% water, 13% protein, 30% fat, and approximately 2% ash. The energy value from 100 g of edible parts of the body corresponded to 1406.8 kJ (= 336 kcal), the edible parts contained 237 mg of potassium, 15 mg of calcium, 19 mg of magnesium, 163 mg of phosphorus, and 0.8 mg of iron (determined from fresh catch). The same author also summarized similar information about the river lamprey. The edible parts contained 67–78% water, 14–15% protein, 7–17% fat, and less than a percentage of ash. The energy from 100 g of edible parts of the body fluctuated between 511–921 kJ (= 122–220 kcal), higher values were found in autumn. The caloric value of edible body parts in Pacific (three-pointed) lamprey was 2–5 times higher than in salmon meat [165]. Therefore, lampreys are a very valuable and healthy edible delicacy. The health significance of lampreys for humans is already reported in the publication "Tacuinum Sanitatis" in the 15th Century [54].

It should also be noted that poisoning by lampreys have been reported, namely by Caspian lamprey, river lamprey, European brook lamprey, and sea lamprey [32]. However, this list is by no means complete, and this may be a general phenomenon. Poisonings are generally attributed to insufficient removal of mucus covering the body before culinary processing. Mucus and serum are listed as toxic in lampreys, so the meat must be thoroughly washed before preparation and then well-done. Symptoms of possible lamprey poisoning include nausea, vomiting, diarrhoea, convulsions, abdominal pain, and overall weakness, which may occur several hours post consumption. Within a few days, everything usually returns to normal. There is a certain parallel of ichthyotoxins in some fish, such as the European eel (*Anguilla anguilla*), barbel (*Barbus barbus*) or especially the notorious "fugu" fish from the Tetraodontidae, although poisoning is much more dangerous and much more fatal with the latter examples [29, 66, 85, 156]. According to the chronicles, King Henry I of England (1068–1135) died during the feasting on lampreys, which he craved as a delicacy [140]. The incident happened in Saint-Denis-en-Lyons in Normandy on 1 December 1135. Knight [78] wrote in his book: "The castle of Lions, about six leagues from Rouen, was his favourite hunting-seat and he arrived there on the 25th of November, 1135. He had not lost his active habits at the age of sixty-five, and he gave orders for the chace on the next day. But the next day saw him sick. He had feasted upon a dish of lampreys, and in four days was dead, after beating his breast,

and lamenting his sins." It is, naturally, difficult to prove whether his death was caused by food poisoning or whether it was a mere consequence of overeating. However, it remains a fact that occasional cases of food poisoning by lampreys have been reported [167]. From this point of view, it is also worth mentioning a rather logical interpretation concerning lampreys in the Czech dream book, where eating lampreys means danger [82].

3.4. Lampreys in Biological Research and Human Medicine

Lampreys have become important subjects of studies in diverse fields of biology. They are used e.g., as a model for vertebrate evolutionary research [35, 69, 70, 71, 83, 84, 113, 123, 147, 148, 150, 171, 175]. Detailed analysis of various papers published between 1864–2013 that employed lampreys directly or indirectly was published by Docker et al. [34].

Lampreys are also used as model organisms in biomedical research. Their large reticulospinal axons help synaptic transmission research. Lamprey axons are particularly large and allow for microinjections of substances for experimental manipulation [17]. Lampreys can fully regenerate its spinal cord even after it's been severed – within three months the lamprey is swimming, burrowing, and flipping around again, as if nothing had happened. These results opens up a new path for identifying pro-regenerative molecules and potential therapeutic targets for human spinal cord injury [57].

Moreau and Dabrowski [114] confirmed the ability of ascorbic acid (vitamin C) biosynthesis in sea lampreys. This is very interesting as bony fish (formerly the Osteichthyes class), with rare exceptions (sturgeon, oars), do not contain the important enzyme of gluconolactone oxidase, without which the conversion of glucose to vitamin C cannot take place [89]. Pacific lampreys were harvested in large numbers at Willamette Falls in Oregon (USA). The primary use of lampreys was for vitamin, oil, protein food for livestock, poultry, and fish. Later, lampreys were used as a source of anticoagulants [102]. Pacific lamprey is one of the many religious foods of the indigenous peoples inhabiting the mid-Columbia Plateau, while lamprey oil is an important part of their diets. Oil collected during the lamprey drying process is applied to skin or ailing parts of the body in conjunction with a purifying sweat bath. Historically, the oil was also used to condition hair and cure earaches [79]. In Japan, the Arctic lamprey is also highly valued as a medicine against night blindness [134]. Asian people use lampreys as a source of essential oils for traditional medicines. In Japan, a pharmaceutical product called "Kyoryoku yatsume unagi kimono abura" is used, which is made by combining refined lamprey oil extracted from lamprey and vitamin A [117]. Lamprey immune protein (LIP) derived from lamprey supraneural body induces remarkable morphological changes in tumour cells and inhibits tumour growth [128, 149]. Cai et al. [21] report that sea lamprey is genetically programmed for biliary atresia, i.e., that it loses bile ducts and gallbladder during metamorphosis [99]. However, unlike human patients with biliary atresia or other forms of cholestasis who develop this serious disease, metamorphic lampreys continue to grow normally into adulthood. Analysis of urine and faeces showed that waste products, including biliverdin and bile acid salts, were excreted by the kidneys and, to a lesser extent, through faeces. These findings suggest that adult lampreys tolerate cholestasis by altering the composition of bile salts in the liver, while maintaining normal plasma bile salt levels, and predominantly by renal bile acid excretion. Therefore, it was concluded that a method of accelerating the renal excretion of bile salts and other toxins could be beneficial for the treatment of human patients, including children, with cholestasis [108, 154, 174]. When parasitic lampreys attack host fishes to suck blood and flesh, their buccal glands could secrete proteins to suppress blood coagulation, nociception, oxidative stree, immune response, as well as other advers effects encountered during their parasitic lives [92]. The buccal gland secretions of parasitic lampreys are potential source for the development of novel anticoagulants, local anesthetics, immunosuppressants, and thrombolytic agents [170]. Lampreys could provide insights into treatment for people suffering from hemochromatosis (called "bronze diabetes" due to the discoloration of the skin). It is disorder associated with deposits of an excess of iron that causes multiple organ dysfunctions. Given sanguivorous foraging strategy, parasitic lampreys ingest large amounts of iron, and have a unique capacity to store and tolerate high concentrations of iron in various body tissues (e.g., liver) [158].

3.5. Lampreys in Culture and Folklore

It is sometimes believed that Roman emperors fed sea lampreys to slaves sentenced to death [64]. However, they were wrong in so doing. Sea lampreys cannot seriously harm a person, although a case of harassment of an adult swimmer by lampreys has been documented [76, 161]. In the case of Roman emperors, it could have been moray eels (Muraenidae) kept in the tanks (see e.g., Cassius Dio, s.a. /born 163, died 235/ [24, 58]. This information is also debatable, but sometimes cited in recent literature. In 1555, Gerolamo Cardano (= Cardanus, 1501–1576) wrote in his letter that sea lampreys liked to suck on new ships to "soak up the resin" that was said to be pleasing to them [138]. Some authors believed that there were such strong and large lampreys in the sea which could prevent ships from sailing if firmly attached to them.

People sometimes call lampreys "nine-eyed". The explanation for this notion is not easy, because lampreys have only two eyes and seven gill openings on each side of the head. However, around 1560, Georg Handsch von Limus published a not very logical explanation of the German name "Neunauge". He added the number of gill openings on one side of the body to the number of eyes. Another speculative explanation may be based on the sum of seven gill holes, one eye and a nostril on the forehead [6]. In Japanese, they are called "yatsume-unagi", 八つ目鰻, "eight-eyed-eel", which excludes the option of the addition of the nostril. Andreska

[7] published zoological and linguistic comparison of the lamprey family names, that were used in Bohemia in the past, with names currently in use throughout Europe.

Peterson Lewis [130] states that for the North American Indian tribes of Yurok and Karuk, lampreys are ecologically and culturally important. Specifically, it is the Pacific lamprey, called "key'ween" in the Yurok language and "akraah" in the Karuk language. These indigenous peoples have been fishing for lampreys for centuries, as part of their fishery wealth. The Pacific lamprey is also of spiritual significance for these tribes. It has an irreplaceable spot in their creation stories, and it is a part of their way of life and of their identity. Knowledge about lampreys, their life and meaning is sacred and is passed from generation to generation [124]. In Portugal, stewed lampreys are still a suitable beef replacement. The dish "Arroz de Lampreia" consists of sautéed onions, olive oil, wine, smoked sausage, rice, and lamprey, which is cut into smaller pieces and then marinated in a combination of vinegar, wine, various herbs, and its blood. All the ingredients are combined and cooked until the stew thickens and develops its typical dark brown color. The dish is mainly associated with the northern parts of the country, and it is traditionally prepared between January and April when lampreys are in season [9]. Every March, many gourmets flood the small village of Montemor-o-Velho (municipality of the Coimbra District) for the annual Lamprey and Rice Festival. During the Christmas season, nuns, bakers, and families celebrate by fashioning sea lampreys out of sweet egg yolk. This treat, known as „Lampreia de Ovos", features a lamprey replica covered in icing — a more kid-friendly version than the blood-coated [86]. In other regions, we can also find a long tradition of gastronomic festivities associated with the preparation of lampreys using special recipes. The festival in Arbo (Galicia) directly on the Mino River on the border between Spain and Portugal is another good example (the local gastronomic festival has been held there every year since 1960). It begins with a procession of Galician bands through the villages and tastings of lampreys and local wines. This is also reflected in the city's coat of arms, where a lamprey and a bunch of grapes appear on a blue background [87]. The Latvian coastal Vidzeme region of Salacgriva hosts a traditional festival ("Lamprey Day") of migrating river lamprey in the autumn. For several hundred years, the ancient method of catching lampreys on the weir of the Salaca River, which flows into the Gulf of Riga, has been used there. At this place, near the mouth of the sea, there is a special long wooden footbridge made of spruce wood built without a single nail. Dozens of wicker traps of various sizes are placed in the current of the river at the time of lamprey migration. The traps are installed at night and the caught lampreys are collected at dawn. On the spot, they are gastronomically processed, so that numerous visitors can immediately taste this specialty on site [2]. Being the part of fishery, lampreys are the part of Latvian and Lithuanian historical development, part of tradition and intangible cultural heritage in coastal areas. In the 19th and 20th Centuries in Estonia, grilled lamprey were mainly marinated in wooden barrels. The marinade was a brine of vinegar, peppers, nutmeg and bay leaves. As in Latvia, Estonia has a festival devoted to lamprey that occurs in Narva-Joesuu at the end of September [5].

Fatty and highly nutritious, lampreys are valued as a traditional source of food by Native Americans. Lampreys continue to be a part of the Columbia River tribal culture and are as important in ceremonies and celebrations as many other foods collected during seasonal harvests [79]. Historically, the Tribes and Bands that make up the Yakama Nation, have shared a commonality treating lampreys as a medicine, food source, and cultural, spiritual and ceremonial icon. Since time immemorial, the Yakama Nation has lived along the Columbia River and its tributaries. For many of the tribal elders, lamprey have been not only a key food source and medicine but also an integral piece of their culture and tradition, without which there is an indubitable "void" in their very existence. The tribes believe that lampreys are fundamentally important and linked to the ecological health of the Columbia basin in a similar manner as salmon and steelhead [166, 172].

From a tribal perspective, the decline of lamprey has at least three negative effects [27]. These include: 1) Loss of lamprey from the ecological circle and the tribal way of life. The tribes consider the lamprey as their sacred elder and without them the circle of life is unbalanced, 2) Loss of cultural heritage, especially for young tribal members—many have never even seen a lamprey. As a consequence of declining harvest within interior Columbia River tributaries, many young tribal members have not learned how to harvest and prepare lamprey and are losing historically important legends associated with these animals, 3) Loss of fishing opportunities in traditional fishing areas. Among other things tribal members are forced to travel long distances to lower Columbia River tributaries, such as the Willamette River, for severely limited lamprey harvest opportunities. To the four Columbia River Treaty Tribes, restoration of lamprey populations is as necessary to the restoration of the ecological health of the Columbia River and its tributaries as are salmon and other native fish populations [157].

Historically, Turkmen of the southeastern Caspian Sea coast believe that Caspian lamprey (*Caspiomyzon wagneri*) is useful as medicinal treatments against haemorrhoids, asthma and besmi (a local name); it has been caught from the Gorganrud River and consumed eithersmoked or soaked in brine, and their oil has been used to treat some pains. Generally, this lamprey is not commercially important in Iran and it is not eaten because of religious beliefs (lack of scales). Lampreys are collected from Iranian rivers during the annual spawning season, especially from the Shirud, with research as the aim. Many local fishermen in Iran kill or injure Caspian lamprey taken from the Shirud River in the mistaken belief that it is a parasite of other commercially important fishes. For example, in the autumn of 2011 was observed about 20 lampreys caught by a fisherman and left to die on the river bank. After a short talk with him, he was persuaded to return the lampreys into the river. Therefore public awareness would play a crucial role in the lamprey conservation management strategies [119].

The oil from Arctic lamprey (*Lethenteron camtschaticum*) was used for human consumption or as fuel for lamps [134]. In easternmost part of Russia, local folks (i.e. Nanais, a Tungusic people) dried Arctic lamprey to make candles [5]. Previously, Caspian lamprey were dried and used also as candles or for their oil [80]. This species was used for food and for lighting by the non-Muslim population of the Russian Caucasus, whereas Muslims only used this resource for non-gastronomic purposes, such as candle manufacture [5]. In Iran, and other countries of Muslim majority, lamprey is not consumed due to religious reasons (considered "haram", i.e. any act that is forbidden by God) and thus it is not commercially harvested [119]. The annual lamprey festival in Ebetsu (Japan) along the Ishikari River in central Hokkaido died out due to collapse of Arctic lamprey harvest after 2001. In Ishikari River, over 100 ton lamprey were caught and landed in 1985 and in 1986. However, it decreased sharply to 3.5 tons in 2002 [75].

Clemens and Wang [25] pointed out the negative attitude of some people in the Pacific Northwest (USA) to the native species of lampreys. This misunderstanding is caused by persistent misperceptions reinforced in media and exacerbated by a long-running and pervasive outreach campaign on the control of the invasive sea lamprey in the Laurentian Great Lakes. Native lamprey species are thus erroneously confused with the invasive/nuisance sea lamprey.

The enormous esteem people have for lampreys is also reflected in the various coats of arms, in which the lamprey appears, especially in north-eastern and southern Europe and Scandinavia. Lamprey adorn coats of arms straight position (e.g. black lamprey in the coat of arms of the municipality Nakkila in Western Finland [118] or curved (e.g. yellow lamprey in the coat of arms of the municipality Sainte-Terre, in the region Bordeaux wine, France [137]; silver lamprey in the coat of arms of Carnikava municipality, Latvia [22]; three silver lampreys in the coat of arms of Lampreel, Bruges, Belgium [121]; black lamprey in the coats of arms of the municipalities Pajares de la Lampreana [127] and Villalba de la Lampreana [160] in Spain; brown-yellow lamprey in the coast of arms of the municipality Penacova in Portugal [129], encircling another heraldic figure (e.g. brown lampreys in the coat of arms of the municipality Arbo, Galicia, Spain [116]; sometimes are lampreys stylized as prey (e.g. in the coat of arms of the municipality Eurajoki in Western Finland [36], where crayfish is holding blue lamprey in its claws). Lampreys also appear in some family coats of arms, an example is the Pride family originating from Lanarkshire in Scotland [132], where we find three silver lampreys.

Lampreys also appear in postage stamps, and, as a consequence, in the collections of philatelists thematically focused on collecting series dedicated to aquatic animals, especially fishes (e.g., Latvia, Scotland, England, Finland) [54]. The unusual appearance of lampreys inspired filmmakers to shoot the horror fiction of "Blood Lake: Attack of the Killer Lampreys". It premiered on the Animal Planet cable TV channel (US) in 2014.

3.6. Lampreys as Pests

The sea lamprey is one of the largest marine diadromous amphihaline and ectoparasite species. It is an aggressive parasite that can have severe negative impacts on Great Lakes fish populations. Single sea lamprey can kill 40 or more pounds of fish during its adult life. Fish that survive a sea lamprey attack expend more energy on healing than on producing eggs and mating, causing declines in fish populations. By the late 1940s, sea lamprey populations had exploded in all of the upper Great Lakes [139]. The invasion of the remainder of the Great Lakes has been well-documented [18, 50, 145, 146], with first observations of sea lamprey in Lake Erie in 1921, Lake Huron in 1937, Lake Michigan in 1936, and Lake Superior in 1938. In the upper of the Great Lakes, sea lamprey abundances increased markedly soon after their colonization and coincided with population declines in their host species [115]. For example, in Lake Huron, lake trout catches declined from more than 2268 tonnes in 1938 to 76 tonnes in 1954, and in Lake Michigan, from 2948 tonnes in 1944 to 181 kg in 1953 [146]. In Lake Superior, catches were as high as 2041 tonnes in 1950, but drastically decreased to 227 tonnes in 1960 [12]. Lake trout (*Salvelinus namaycush*) is the presumed preferred host of the invasive sea lamprey in the Great Lakes. But, sea lampreys attack many other Great Lakes species, especially large-bodied ones and population level impacts have been observed or hypothesized for several species: Chinook salmon (*Oncorhynchus tshawytscha*), lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*), and coregonines and suckers (*Coregonus* spp. and *Catostomus* spp.) [1]. Sea lampreys killed more than 100 million pounds of Great Lakes fish annually, which was five times the commercial harvest in the upper Great Lakes. The ongoing control efforts reduced sea lamprey numbers in most areas implementing various measures (lampricide, barriers, aplication of migratory pheromones, sterile male release, assessment) [14, 31, 38, 65, 73, 74, 93, 106, 107, 153].

Successful sea lamprey control has allowed for the rehabilitation of a healthy Great Lakes ecosystem and economy now valued at more than $7 billion annually.

3.7. Lampreys as Bioindicators

Bioindicator is an organism used as an indicator of the quality of an ecosystem, especially in terms of pollution. Bioindication can be applied in predicting the impact of anthropogenic activities particularly pollutants and predicting environmental changes in a timely manner. Lampreys can be considered animals sensitive to changes in the environment. They worldwide face multiple anthropogenic stressors. Some lamprey species are endangered, their population declines in many regions [26, 33, 42, 56, 112, 155, 163]. Eleven threats to anadromous lampreys have been identified: climate change, shifting oceanographic regimes, artificial barriers, low water quantity/flow management, habitat degradation, poor water quality, reduced habitat availability, host and prey availability, predation, overharvest, and disease.

Lampreys can be used as indicators of water environment [100]. Jenkins and Burghead [72] mentioned that Ohio lamprey (*Ichthyomyzon bdellium*) is used as an indicator of water and substrate quality. The European brook lamprey (*Lampetra planeri*) was studied with respect to its bioindicator value. This species lives in running waters from trout to barbel fish zones (mostly in trout and grayling zones). These fish zones correspond to better/worse oligosaprobity and better β-mesosaprobity [131]. Larvae of the European brook lamprey are specific bioindicators of water quality and environmental conditions. A well-balanced length and age structure of numerous populations of larvae demonstrate long-term high quality environmental conditions. Low number of specimens or total absence of some age groups indicate the influence of negative factors during breeding time in the past. Yearly observations of breeding populations and the comparison of the number of adult specimens across years can serve as a good bioindicative parameter. The absence of breeding adult specimens or their remarkably low amount indicates the historical influence of some negative factors. Blind larvae colonize muddy riverbed sediments. Owing to their specific way of living, they are not a suitable bioindicator of short-term water quality worsening [54]. The Saprobic Index (Si) is a measure of saprobity, an estimate of the level of organic pollution as measured by a combination of the biological oxidation demand of a water sample and the presence of specific indicator organisms in the habitat. As for the saprobic index of the European brook lamprey, its value was set at Si = 1.3 (Indication weight = 4, oligosaprobity - 7, β-mesosaprobity - 3) [51, 52, 55]. Lampreys can also serve as sentinel species, i.e., biological monitors that accumulate pollutants in their tissues [94, 97, 98, 110, 111, 142], even regarding the safety of gastronomic use [109].

3.8. Lampreys in Biomimetics

Lamprey swim by rhythmic lateral undulations of the body axis. The lamprey swims forward by propagating lateral axial undulations that increase in amplitude from nose to tail. Similar waves travelling from tail to nose can propel the lamprey backward. Rhythmic alteration of muscle activity on either side of the body axis produces a propulsive wave [16]. Lamprey swimming is uncomplicated by pectoral, pelvic, or anal fins, which are missing. Endurance rather than high speed is characteristic of pure anguilliform mode [46]. Biologists and engineers on the base od analysis of specific undulatory swiming behavior of lampreys created a biomimetic lamprey-based robot with an electronic nervous system that imitated move and orientation in the water [11, 151, 164]. In addition to providing new insights into functioning of the vertebrate central nervous system, these lamprey-inspired robots may also lead to new engineering solutions for high-performance artificial locomotion [67].

4. Conclusion

Despite the fact that in terms of the number of species lampreys form a small group of vertebrates, considerable attention by the public has been paid to them, especially recently, as evidenced by almost six million links shown after for the word "lamprey" is entered in the search bar. The interest of scientists in these remarkable animals has been confirmed by the number of works dedicated to examining lampreys from various perspectives published between 1864 and 2013, which exceeds 22 thousand. Lampreys have been a part of human food since ancient times. They are considered a delicacy, although rare cases of poisoning after consumption have been documented, mainly due to insufficient removal of mucus from the body. River lamprey is often sought after by gourmets in many European countries, namely Estonia, Finland, France, Latvia, Lithuania, Poland, Portugal, Russia, Spain, and Sweden. In some places, lampreys are considered culturally important animals with spiritual significance (e.g., among North American Indian tribes), and there are also places where lampreys are a part of various popular festivals associated with their catching and consumption (e.g., Portugal, Spain, and Latvia). Lampreys are also used as bait in sport fishing. In some parts of the world, commercial fishing for lampreys has a long tradition (e.g., the Iberian Peninsula, the Baltic states, Russia, China, the Pacific coast of North America). On the other hand, in the Laurentian Great Lakes, sea lamprey is considered to be an aggressive parasite causing great damage to the local ichthyofauna, which requires effective measures be applied to reduce its populations. Lampreys (larvae and adults) are an important food chain component in both freshwater and marine environments. Lampreys have become an important subject of studies in diverse fields of biology (e.g., in evolutionary studies), and model organisms in biomedical research (e.g., studies of anti-coagulants, biliary atresia, hemochromatosis, spinal cord regeneration, and more). For their sensitivity to the quality of the environment they inhabit, lampreys can also be used as bioindicators. Thanks to their popularity, lampreys have appeared in city coats of arms and on postage stamps, inspired research in the field of biorobotics, and even prompted filmmakers to shoot a horror film starring lampreys. To conclude, lampreys are an immensely interesting species.

Conflict of Interest

The authors declare they have no conflict of interest.

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