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REVIEWS

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## A Comparative Analysis of Morphofunctional Characteristics of Cartilaginous Ganoid Fishes (Order Chondrostei)

G. M. Palatnikov<sup>a,\*</sup>

<sup>a</sup>*A.I. Karaev Institute of Physiology, Azerbaijan National Academy of Sciences, Baku, Azerbaijan*  
*\*e-mail: gmpal@mail.ru*

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**Abstract**—The review article provides a comparative analysis of the morphological and functional characteristics of cartilaginous ganoid fishes (Chondrostei), considering the features of their external morphology, embryology, central nervous and receptor systems, and genetics. These features reach the interclass level and, when compared to those in other ray-finned fishes, support the advisability of distinguishing the order of cartilaginous ganoids as an independent subclass.

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### INTRODUCTION

The families Acipenseridae (sturgeons) and Polidontidae (paddlefish), which are relics of the World Ocean ichthyofauna, make up the order Chondrostei (cartilaginous ganoid fishes). The heyday of ganoid fishes fell on the Permian and Triassic periods and was followed by a gradual reduction in their numbers and range. To date, as few as about 30 extant species are spread across the Northern Hemisphere. Sturgeons have always attracted close attention of researchers and gave rise to heated debate about their origin and systematic position. However, as far back as the middle of the past century, N.L. Gerbil'sky noted that all the arguments of the authors who attempted to trace sturgeon phylogeny and generate appropriate taxonomical classifications, are either based solely on the data of comparative anatomy and embryology of the skeleton, or engage quite evo-

lutionarily labile adaptive characters to validate their point of view [1]. To date, a large body of data on the biology of sturgeons has been accumulated, allowing us to look afresh at their phylogeny and systematic position.

### FEATURES OF EXTERNAL MORPHOLOGY OF STURGEONS

Compared to other ray-finned fishes (Actinopterygii), sturgeons have the largest number of archaic structural features that are absent in teleost fishes. The sturgeon axial skeleton is represented not by an ossified notochord, but by a cartilage; the internal cranium remains largely cartilaginous, while the caudal fin is heterocercal, with a larger upper lobe. On the body surface, there are five longitudinal rows of bony plates (scutes), which are considered as rudiments of ganoid scales. Like all cartilaginous fishes, stur-

geons retain a spiracle, a small hole at the edge of the opercular gill cover, leading to the gill slit. Based these characters, and also considering the presence of an arterial cone in the heart of sturgeons and a spiral valve in the intestine of sturgeons, like in sharks, A.N. Severtsov [2], as well as many other authors, believed that *Acipenseriformes* (*Chondrosteoidei*) is a very primitive group, which is similar to the subclass *Elasmobranchii*, namely the suborder *Selachii*. In other words, according to these authors, sturgeons descend not from the ancestors common with teleosts, but from primitive cartilaginous fishes. The opinion of Severtsov and other advocates of the theory of the origin of sturgeons from primitive cartilaginous fishes was disputed by L.S. Berg [3]. He wrote that it is impossible to derive lower *Actinopterygii*, for example sturgeons, from sharks. *Elasmobranchii* represent a special branch of fishes that gave rise to no other group, and, specifically, the lower *Teleostomi* could not descend from sharks. Then he adduced proofs of a higher organization of *Elasmobranchii* compared to *Actinopterygii*: (1) the presence of a oronasal groove (a prerequisite for the formation of the internal nostrils, i.e. choanae), (2) strong cartilage calcification, (3) more sophisticated skeleton of the dorsal fin compared to sturgeons, (4) in higher sharks, the spine is more developed than in cartilaginous ganoids. It should be added that the telencephalon and cerebellum in sharks are more developed than in teleosts, some shark species have a placenta, and males of all extant shark species have complex copulatory organs, pterygopodia [3]. Thus, there are cardinal differences between *Elasmobranchii* and *Teleostomi* in the structure of the skeleton, skin, branchial apparatus, central nervous system (CNS), and other organs.

Based on a comparative anatomical analysis of fossil and modern fishes, L.S. Berg put forward a hypothesis about the origin of sturgeons from the early ray-finned teleost fishes of the order *Palaeonisciformes*, an ancestor that sturgeons have in common with teleosts [3]. Later, based on paleontological finds, V.N. Yakovlev [4], who discovered in some forms of ray-finned teleost fishes the structures that he considered as transitional characters to primitive sturgeon, arrived at the same

conclusion. These primitive characters were retained in sturgeons due to fetalization, i.e. an evolutionary phenomenon implying the loss in adult organisms of the definitive, more advanced, developmental stages and the acquisition of specific adaptations. The ideas of L.S. Berg [3] and V.N. Yakovlev [4] are in line with the opinion of De Beer [5], who believed that the features of the cartilaginous skull of *Acipenseridae* emerged due to the loss of a number of ossifications in the skull and indicate the kinship of sturgeons to the ancestors of teleosts. Thus, the observed similarity between *Acipenseridae* and *Selachii* is of a secondary nature and can be regarded as a result of convergence.

#### FEATURES OF GAMETOGENESIS IN STURGEONS

Sturgeons are lithophilic fishes, which implies spawning in relatively fast-flowing currents. In this connection, their gametes, embryos and larvae have a number of adaptive features. G.M. Persov noted in his works [6] some features characteristic of the sturgeon sperm. Their sperm cells differ from their teleost counterparts not only structurally, but also in terms of energy reserves, as well as in such a critically important biological characteristic as the time period of their fertilizing ability. While teleost spermatozoa are able to move after their activation in water for tens of seconds or, in some species, several minutes, sperm and eggs in sturgeons retain the fertilizing ability far longer than in teleosts. Observations of the sturgeon sperm showed that forward translational movement of most spermatozoa stops 5–10 min after getting into water. However, some of the spermatozoa continue active motion for up to 20–60 min or even several hours. Thus, although the fertilizing ability of the sturgeon sperm, in most cases, sharply drops within the first 10 min after getting into water, it is not completely lost [7]. Sturgeon spermatozoa differ from those of other fishes in that, like in mammals, they have an acrosome with finger-like protrusions that undergo exocytosis and filament formation, although its physiology, biochemistry and potential role in fertilization are unknown, since sturgeon eggs have several micropyles, minute

openings in the eggshell [7–9]. The acrosomal complex is located at the tip of the sperm head and varies in size across species. Different sturgeon species show trypsin-like (acrosin) and chymotrypsin-like activities, which are the most characteristic acrosomal enzymes in mammals [9].

Sturgeon oocytes have a thick shell impermeable even to colchicine, which probably protects them from the influence of mutagens. Perhaps for this reason, the level of spontaneous chromosomal aberrations in sturgeon prelarvae does not exceed 2–3%, even under conditions of severe pollution [10]. When in water, sturgeon eggs acquire stickiness, due to which they hold on a stony substrate. Successful fertilization of eggs is ensured by numerous micropyles. The ability of mature ovulated eggs to be fertilized when delayed in the female's body cavity, as well as their keeping outside the female's body in the ovarian cavity fluid or in water, gradually declines and then completely fades away. In teleosts, this process proceeds very quickly, for example, in the pike *Esox lucius* or vimba *Vimba vimba*, the roe fails completely to fertilize after 1 min. In sturgeons, a part of the eggs can fertilize much later, e.g., in the sturgeon *Acipenser gueldenstaedtii*—after 1 h, and in the stellate sturgeon *A. stellatus*—until the end of the first hour. In the abdominal fluid outside the female's body, the sturgeon roe can retain a high fertilization capacity for 4–6 h [7].

The structure of the mature egg, type of its segmentation, processes of gastrulation and embryonic mesoderm formation in sturgeons are also quite different from those in teleosts, being similar to amphibians [11–13]. Yet before the onset of cleavage (at the gray crescent stage), the sturgeon oocyte has a bilaterally symmetrical structure, which is the basis for further development. This phenomenon has much in common with the early change of the fertilized egg of amphibians [14]. In sturgeons, unlike teleosts, uneven cleavage of the zygote leads to the formation of the yolk entoderm, and thus resembling oocyte cleavage in amphibians [15]. However, in contrast to amphibians, the process of cytolysis in the yolk entoderm during sturgeon embryogenesis is completed much earlier. At the same time, the yolk entoderm, apart from performing its main func-

tion (the formation of the intestinal mucous membrane and two accessory digestive glands, the liver and pancreas), has enough time to give rise to an extremely important provisional organ, the hatching gland, which plays a critical role in prelarva hatching from the egg. In teleosts, these glands represent a unicellular epidermal formation similar in structure to skin mucous cells. In sturgeons, the hatching secretion is produced by entodermal cells, while the gland itself is a complex three-layered organ. Before hatching, glandular cells move apart the cells of the covering layer, and their apical ends come out to the embryo's surface, thus providing the route to excrete the secretion into the perivitelline space. The starting material expended in the process of secretion is the yolk [1]. A similar formation has been described in amphibians, and it has been shown that in terms of the regulation of hatching gland functions there is a great similarity between sturgeons and amphibians [16], but a profound difference between sturgeons and teleosts.

The prelarvae hatched from the eggshells have ample nutrient reserves inside the so-called “yolk sac”, which is not homologous to the yolk sac of teleost fishes, but represents a lower wall of the stomach composed of yolk-containing cells. Throughout the yolk-feeding period, the liver cells fill up with fat inclusions, and the liver can function as a reserve fat depot used by larvae in the absence or shortage of food objects during downstream migration [16]. During embryogenesis, the sturgeon stomach, just like in amphibians, develops from the wall of the yolk sac. Histogenesis of the complex structures of the cardiac, fundal and pyloric parts of the sturgeon stomach originates from the primitive symplastic structure of the yolk sac [1], and in this case, we observe a significant difference between these processes in sturgeons and teleosts.

#### CENTRAL NERVOUS SYSTEM AND ANALYZERS

In all vertebrates, including Elasmobranchii (sharks and rays), the telencephalon develops during embryogenesis from the rostral brain vesicle by inversion, and only in Actinopterygii it forms by eversion [17]. As a consequence of this

process, the hemispheres of the everted brain lack the lateral brain ventricles and form the unpaired medial ventricle which separates the hemispheres from each other. Brain eversion is an evolutionary dead end and had not evolved further in any of the higher vertebrate classes. The telencephalon of sturgeons also develops by eversion. However, in the rostral region of the sturgeon neural tube, eversion is less pronounced, and the internal ventricles persist in the olfactory bulbs. In general, as compared to teleosts, the telencephalon of sturgeons has a low level of differentiation [18, 19]. However, in the zone, which the authors call the lateral pallium or dorsolateral pallial zone, there is an ordered layer-by-layer arrangement of neurons that form, depending on the sturgeon species, from 12–14 to 20–22 rows [18–20]. No other lower vertebrates have such an ordered structure in the telencephalon, and only in reptiles, it emerges for the first time as a cortex rudiment [21].

At the same time, the diencephalon of sturgeons has a much more pronounced nuclear differentiation than that of teleosts and even amphibians [22].

The anatomical organization of the sturgeon medulla oblongata shares certain similarities with Polypteridae and substantially differs from teleosts [22]. Sturgeons are characterized by a large size of the dorsal and intramedial portions of this brain section.

The structure of olfactory cells in vertebrates shows strict evolutionary patterns. It has been established that Chondrichthyes and Dipnoi have microvillar olfactory cells, in contrast to teleosts whose olfactory cells are ciliated. Sturgeons have a mixed type of olfactory cells as they bear both cilia and microvilli [23]. The same pattern is observed in reptiles [24].

The ionic composition ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ), as well as the content of polypeptides, sugars and tryptophan, in the olfactory mucus of sturgeons qualitatively and quantitatively coincide with those in the respiratory mucus of the gills and mouth cavity [25]. A similar coincidence was found in amphibians [26].

Visual thalamo-telencephalic projections in sturgeons differ from those in teleosts and are similar to those in other vertebrates [27, 28].

Electroreception of sturgeons has been studied in the genera *Scaphirhynchus* and *Acipenser*, as well as in the American paddlefish (*Polyodon spathula*). All the species studied have highly sensitive electroreceptors, the ampullae of Lorenzini. These ampullary organs are mainly located on the head, including the rostrum. Sturgeons have a relatively high sensitivity to electric fields in water and actively use electrosensitivity in foraging and defensive behaviors [29, 30]. At the same time, the so-called anodic reaction, which is not associated with the presence of electroreceptors but is characteristic of cartilaginous and teleost fishes, as well as some other aquatic organisms, is absent in sturgeons [29].

A profound difference between teleosts and sturgeons is also observed in the definitive structure of the pituitary gland. In sturgeons, as in all other vertebrates, the pituitary gland forms due to the budding of the foregut dorsal wall evagination and thus, from the very beginning, contains a cavity, the Rathke's pouch. In teleosts, it is not an evagination but a bulge-like thickening that buds from the foregut dorsal wall, and thus the pituitary cavity is absent [31]. In most teleosts, gonadotropic hormones are produced by the intermediate lobe of the pituitary, while in sturgeons—by the anterior lobe. Sturgeons, in terms of the division of functions between different pituitary parts, are closer to amphibians [1]. Functional plasticity of the sturgeon pituitary gland (gonadotropic hormone production in fall and either releasing them or depositing in the brain ventricles until spring) is one of the essential evolutionary prerequisites of fish plasticity with respect to switching from fall to spring spawning and vice versa [32].

The same profound differences between sturgeons and teleosts, as well as the convergence of sturgeons with amphibians, were revealed when studying the microanatomy of hypothalamic nuclei [31, 32]. While both in sturgeons and amphibians, the preoptic vegetative nucleus (nucleus praeopticus) is well developed and the lateral nucleus (nucleus lateralis tuberis) is absent, in teleosts, the lateral nucleus is developed particularly well and forms a single vast cluster of secretory neurons [33]. According to immunohistochemical data on the distribution of such hypophysiotropic factors as galanin, neuro-

physin, somatostatin, and gonadotropin-releasing hormone, the neurons immunoreactive to these substances were found in the preoptic and hypothalamic nuclei. Immunoreactive fibers were observed along the preoptic-hypothalamic-pituitary tract and in the pituitary gland, indicating their hypophysiotrophic role in the sturgeon brain. Thus, according to O. Kah and F. Adrio, the majority of neuropeptides and neurohormones occur in four-legged animals and are also present in sturgeons [34].

When studying the amino acid composition of prolactin (one of the hormones produced by acidophilic cells of the anterior pituitary lobe), which by its chemical structure is a peptide hormone, in the Russian sturgeon (*A. gueldenstaedtii*), marbled lungfish *Protopterus aethiopicus*, and teleosts, Kawauchi et al. [35] established that in the former two species, prolactin has by three disulfide bridges at the same positions as in Tetrapoda, while in teleosts—only two.

It would probably be appropriate to mention here the difference between two other secretory organs of sturgeons, the thyroid gland and pancreas. In sturgeons, the thyroid gland is a compact organ with a capsule made of connective tissue. Teleosts, on the other hand, differ from other vertebrates in the structure of the thyroid gland. Thyroid follicles in teleosts are scattered along the wall of the ventral aorta and, in part, along the walls of the first and second pairs of branchial arteries. Functionally, the thyroid gland of sturgeons also differs from that of teleosts in a more orderly, synchronous response of all follicles [1]. The pancreas of sturgeons is histologically similar to that of mammals but differs from that of other fishes. A characteristic feature of the sturgeon pancreas is the presence of three separate lobes. The pancreatic duct ends in the papilla between the small intestine and the pyloric cecum. Pancreatic endocrine cells are grouped into clusters that resemble the mammalian Langerhans islets [36].

#### SOME PHYSIOLOGICAL AND BIOCHEMICAL FEATURES OF STURGEONS

According to E.M. Kreps [37], sturgeons belonging to the genera *Acipenser* and *Huso* rep-

resent a very homogeneous group by the lipid characteristics of the brain, with minor interspecific differences. In addition, the sturgeon brain resembles neither the brain of selachians nor that of teleosts. In terms of their lipid characteristics, sturgeons not infrequently occupy a position far away from both selachians and teleosts. Such a peculiarity of the sturgeon brain was revealed when studying the composition of cerebroside, cerebroside sulfates, and gangliosides [37].

Lukyanenko et al. [38] established the identity of the fractional hemoglobin composition of the Russian sturgeon (*A. gueldenstaedtii*), stellate sturgeon (*A. stellatus*), and beluga sturgeon (*H. huso*) during the marine and riverine periods of their life, in both the total number of components and the relative protein content per each hemoglobinogram component. By this criterion, all the three sturgeon species are fundamentally different from other migratory fishes, in which the ratio of fast and slow hemoglobin components is redistributed in favor of the latter during the transition from marine to riverine environments.

The ratio of phospholipids in the sturgeon serum lipoproteins also distinguishes them from other animals [39]. Sturgeons differ from teleost and cartilaginous fishes not only in the biochemical composition of their blood, but also in the structure and function of the hematopoietic and lymphatic systems.

The cranial hematopoietic organ was found in the cranial cavities of sturgeons, which represents a universal hematopoietic organ, the histological structure of which is similar to that of the mammalian bone marrow [36, 40]. Supposedly, this is the first example of the hematopoietic tissue—skeleton association in the vertebrate evolution [41].

The teleost spleen functions mainly as a blood depot and consists of the red pulp with separate lymphoid clusters [41]. In sturgeons, like in mammals, the spleen consists of the red and white pulps with different composition of hematopoietic tissue [42]. The red pulp performs mainly an erythropoietic function, while the white pulp is formed by follicle-like clusters of lymphocytes, granulocytes and macrophages. Thus, it is obvious that the sturgeon spleen is a true immune organ.

In addition, the unique lymphoid epicardial

formations were found in sturgeons, being analogous in their structure to the mammalian lymph nodes. Their content of reticulocytes, lymphocytes, granulocytes, and macrophages allowed Kondrat'eva et al. [41], as well as Gallo et al. [42], to hypothesize that these formations, as well as the lymph nodes, are responsible for lymph filtration. Teleosts have no lymph nodes, and their function is performed by accumulations of lymphocytes in visceral mucous membranes of visceral organs. These clusters of lymphocytes play the main role in the immune response to antigens that reached the intestine [43].

Electron microscopic analysis of the intestinal epithelial cells in the white sturgeon (*A. transmontanus*) enabled the identification of five different types of endocrine cells that share similarities with mammalian endocrine cells and differ from those of teleost and cartilaginous fishes [44]. The midgut epithelial cell layer of the Russian sturgeon (*A. gueldenstaedtii*), Siberian sturgeon (*A. baeri*), beluga sturgeon (*H. huso*), and their hybrids, have been found to contain cells with not only microvilli but also cilia on the apical surface, which is considered a primitive character inherited from ancient ancestors. However, at the same time, in these fishes and their hybrids, there were detected the cells similar to mammalian M cells that provide the primary immune responses [44].

Monoamine oxidase (MAO) is a widespread membrane-bound thiol enzyme catalyzing oxidative deamination of biogenic amines. There are two forms of MAO, MAO-A and MAO-B. The results of numerous studies have shown that both MAO forms are present in the liver of terrestrial vertebrates (reptiles, birds, and mammals). In the case of fish, the situation is more complicated. In some teleost species, hepatic MAO has been found to be similar to MAO-A of terrestrial vertebrates. In other teleost species, MAO is completely different from both MAO-A and MAO-B. In sturgeons, like in mammals, both forms, MAO-A and MAO-B, have been found [45].

Sturgeons have also been found to be substantially different from teleosts in the mechanisms of maintaining a relative constancy of blood serum osmolarity. In diadromous brackish-water sturgeons, which specifically include the stellate sturgeon, the kidney plays an important role in the

excretion of excess  $\text{Na}^+$ , in contrast to teleosts where this excretory organ is almost irrelevant to the regulation of  $\text{Na}^+$ . Sturgeons excrete a significant amount of  $\text{Na}^+$  and  $\text{Ca}^{2+}$  with urine, while in teleosts this function is performed mainly by branchial chloride cells [46].

## STURGEON CARYOTYPE

Sturgeons are of great interest to study genetic and evolutionary processes. Their living fossil status makes them important for the understanding of the evolution of both cartilaginous ganoids and vertebrates in general.

Sturgeon genomic studies have a number of peculiarities associated primarily with their polyploid origin, which plays an important role in the evolution and phylogenetic diversity of fish. Currently, among the species of the families Acipenseridae and Polyodontidae, three groups of species are distinguished karyologically by their ploidy level [47, 48]. The first group includes species with a karyotype of approximately 120 chromosomes (the exact number varies from 112 to 146). This group includes the beluga (*H. huso*), sterlet (*A. ruthenus*), ship (*A. nudiventris*), stellate sturgeon (*A. stellatus*), and paddlefish (*P. spathula*). The second group includes the 240-chromosome species with the number of chromosomes varying from 240 to 270, e.g., Russian sturgeon (*A. gueldenstaedtii*), Siberian sturgeon (*A. baeri*), and Adriatic sturgeon (*A. naccarii*). The third group includes the bluntnose sturgeon (*A. brevirostrum*) with 360–370 chromosomes. This species has not only the highest number of chromosomes, but, correspondingly, the greatest amount of DNA among all representatives of Acipenseriformes [49, 50].

In a study by Birstein et al. [51], the DNA content per cell in the Sakhalin sturgeon (*A. mikadoi*) turned out to be the highest among Acipenseriformes, with the calculated value being almost twice as high as for such 240-chromosome species as the Russian and Siberian sturgeons. In this connection, an approximate number of chromosomes in the karyotype for this sturgeon species was assumed to be about 480–500. The same value was subsequently mentioned in other studies as well [52]. However, further research showed

that the Sakhalin sturgeon, like the kaluga (*H. dauricus*), belongs to the 240-chromosome sturgeon group [53]. The presence of a large number of chromosomes in the cell nucleus and, including microchromosomes, is one of the reasons for debates about the ploidy level of sturgeon species. Undoubtedly, the amount of DNA per cell in sturgeons is on average 2–4 times larger than in other vertebrates. Of particular interest are DNA hybridization studies on the genetic kinship among different systematic groups of organisms. Using this method, it was shown that interspecific hybridization of sturgeons with teleosts and sharks does not exceed 10–15%, which corresponds to the level of interclass homologies, i.e., sturgeons should be allocated into a special class [54, 55].

### FEATURES OF STURGEON ECOLOGY

When studying the biology of sturgeons, Herbilsky pointed out their wide ecological adaptability [1]. Due to the expansion of spawning temperature limits, sturgeons have an opportunity to repeatedly use spawning grounds within the same population. For example, the range of spawning temperatures in different biological groups of the Persian sturgeon (*A. persicus*) ranges from 12 to 15°C in the early spring sturgeon and from 18 to 24°C in the late spring sturgeon [1]. Such a wide range of spawning temperature is also accompanied by a significant embryonic eurythermia and more perfect regulation of the embryo's state at hatching than in teleosts. A number of studies have shown that the phenomenon of premature hatching of underdeveloped embryos observed in teleosts, specifically under the influence of temperature fluctuations or oxygen deficiency, is not characteristic of sturgeons. This is due to the structural and functional peculiarities of the hatching gland [1, 55].

Natural spawning of sturgeons occurs in river sections with strong currents that quickly disperse eggs and sperm. However, due to the properties of their gametes to retain the fertilization ability for a long time, sturgeon spawning efficiency is relatively high [7]. The possibility of using spawning grounds located at different distances from the river mouth is of great importance for maintaining the population size. For

example, winter sturgeon groups travel considerable distances during spawning migrations, entering rivers in summer and fall and spending a winter in pits located in the river bed along the migration route. This allows them to move further upstream in spring and to spawn in the upper reaches of rivers. However, this peculiarity of sturgeons requires prelarvae, as well as larvae and fry, to be able to withstand a long period when they may be carried downstream. In this respect, the larvae of anadromous sturgeons have adapted perfectly. For example, the larvae of the spring sturgeon of the Volga-Caspian population, which under natural conditions at a temperature of 16–18°C switch to active feeding on the 8th–9th day after hatching, lived under laboratory conditions in crystallizing dishes with tap water without food and nevertheless retained a high motor activity for three weeks [1]. This ability of larvae to resist exhaustion during downstream migration is due to the ability of hepatic parenchymal and intestinal (brush border) epithelial cells to accumulate considerable amounts of fat yet in the yolk-feeding period.

Another adaptation of sturgeon larvae to prolonged downstream migration is an early polyphagy. While in teleost larvae the narrow feeding spectrum makes their survival dependent on the availability of appropriate food, sturgeon larvae are characterized by a wide feeding spectrum from the very beginning of their active feeding. This not only promotes a more complete utilization of the reservoir's forage resources, but also represents the most important factor that extends the breeding period and increases the length of the spawning zone [1]. Under favorable conditions, sturgeon larvae, when switching to outside feeding and later on, feed mainly on zoobenthos; the species and size spectrum of the consumed organisms changes as the larvae grow. For want of the available forms of benthos, zooplankton is a constrained food. The predominance of zoobenthos in the sturgeon diet during early ontogenesis, including switching toward outside feeding, is associated with its higher energy value compared to zooplankton, as well as with its greater availability to larvae at the mixed feeding stage, determined by their morphology and the maturity of sensory systems, specifically some-

what delayed development of the olfactory system compared to the gustatory and seismosensory systems, touch and electroreception [56].

One more adaptive feature of sturgeons is their early euryhalinity. In the Volga, Kura, Ural, and Danube, sturgeons use not only spawning grounds remote from the river mouth, but are also able to spawn in the lower reaches of rivers, and even just a few kilometers away from the river mouth. In this case, the larvae get into the brackish waters of the river premouth very early.

Long-lasting salt tolerance studies of the sturgeon, beluga, and stellate sturgeon at the early stages of ontogenesis attest to their broad euryhalinity. Early euryhalinity forms due to the organs involved in water-salt metabolism (branchial chloride-secreting cells, kidney, interrenal and thyroid glands, hypothalamic-pituitary complex) and is regarded as an adaptation aimed at reducing offspring mortality. Salinity changes elicit active behavioral responses in juveniles, as well as the seeking of optimal salt zones, changes in motor and foraging activity [57].

The highest form of adaptation of an organism to its environment is its behavior. Behavior is a complex linkage of innate and acquired components. A comprehensive study of the formation of sturgeon behavioral responses in early ontogenesis was carried out by Kasimov [58]. Having analyzed the developmental periods and patterns of the formation of conditioning activity, he has distinguished three stages in the formation of behavioral responses during sturgeon ontogenesis.

*First stage* (aged up to 3–4 days since hatching): larval adaptive behavior based on unconditioned reflexes; no reflex conditioning.

*Second stage* (4–5 to 28–35 days of age): at the beginning of the stage, unstable positive motor reflex conditioning; later on, food and defensive reflex conditioning (in the latter case – to light stimulation).

*Third stage* (35 to 90 days of age): stable negative and positive reflex conditioning to various conditioned stimuli.

Thus, sturgeons differ dramatically from teleosts also by a number of phylogenetic adaptations and have significant advantages over them in the struggle for existence.

## PHYLOGENESIS AND SYSTEMATICS OF CARTILAGINOUS GANOIDS

To construct phylogenetic schemes, and as one of the species-specific criteria, one can use the data of studies on the morphofunctional organization of the fish CNS. Specifically, sturgeons show a significant interspecific variability in the structure of their CNS, which suggests an uneven evolutionary pattern of this group of fish. By this criterion, shovelnose sturgeons (*Scaphirhynchus*) are most deviant from other sturgeons. They have a simplest structure of the telencephalon, as manifested in its microanatomical, cytoarchitectonic, and neuronal organization [59]. Moreover, minimal interspecific differences within the genus *Scaphirhynchus* imply a conservative evolutionary pattern of shovelnose sturgeons, which diverged from the common ancestral trunk of sturgeons back in the Jurassic period, remained in primary freshwater reservoirs, and hence did not change significantly their ecological and functional characteristics over this period.

Based on such biochemical parameters as the fractional composition of hemoglobin, as well as serum and oocyte proteins, Luk'yanenko [60] proposed to single out the stellate sturgeon into an independent monotypic genus *Helops* (*Acipenseridae*), and, based on the similarity of the same parameters in the sterlet and ship to the beluga, as well as on the sharp difference between the beluga and sturgeon species proper, to include the sterlet and ship into the genus *Huso*. However, it is quite obvious that both morphofunctional and biochemical criteria do not suffice for such constructions. The more that, although the number of chromosomes in these species is the same (118 + 2), the DNA content in the cell nuclei of the sterlet and ship is higher compared to the beluga [64]. At the same time, the DNA content in these two species coincides with that in another member of the genus *Huso*, beluga [61]. This difference is due to the presence of micro- and macrochromosomes in sturgeons.

Within the very order of cartilaginous ganoides (*Chondrostei*), there is a far-reaching genomic divergence corresponding to the inter-order level [62]. In fact, the systematics and phylogeny of individual species within the family *Acipenseridae*



have long been a subject of debate. Based on the comparative analysis of karyotypes and DNA content in vertebrates, Birstein [47] concluded that phylogenetic lineages of the most ancient representatives of Actinopterygii, cartilaginous ganoids (Chondrostei) and bony ganoids (Holostei), descended from related ancestral 60-chromosome forms. Such “ancestral” karyotypes contained both macrochromosomes, some of which were represented by bi-armed homologs, and microchromosomes, while the genome size (1C) amounted approximately 1.5 pg. Later on, karyological changes in both lineages followed different directions: during the evolution of Acipenseriformes, karyotypes remained extremely conservative and changes concerned the formation of polyploid (tetra- and octoploid) forms, while in Holostei, there was a reduction in the number of chromosomes and a karyotype symmetrization due to the disappearance of microchromosomes.

Based on the karyological data (the number of chromosomes in the genome), it was proposed to divide sturgeons into two genera including, respectively, 120- and 240-chromosome species. At the same time, the genus of so-called low-chromosomal sturgeons should include the Atlantic sturgeon (*A. sturio*), sterlet, stellate sturgeon, ship, beluga, and kaluga, while the genus of multi-chromosomal sturgeons should include the Russian, Adriatic (*A. naccarii*) and Siberian sturgeons [62, 63]. Such a division appears artificial, since, being based on genetic criteria only, it does not consider morphological, physiological, biochemical, and ecological traits inherent in these species. Having conducted an ecological and zoogeographical analysis with parallel evaluation of a number of morphological, anatomical, and karyological characters, Artyukhin [64] proposed to single out several subgenera in the genus *Acipenser*.

Cytogenetic and molecular data allow discussing the problem of phylogeny within the order of cartilaginous ganoids and the family Acipenseridae. The families Acipenseridae and Polyodontidae may have originated from a common tetraploid ancestor with a karyotype of 120 chromosomes containing about 3.2–3.8 pg of DNA per nucleus. Presumably, tetraploidization

occurred in the originally 60-chromosome ancestor at the earliest stage of sturgeon evolution, perhaps at the time when this group of fish emerged in the Mesozoic era [61]. Subsequently, the speciation within the family was accompanied by the emergence of octoploid and then 16-ploid species. Phylogenetic analysis showed that the polytomic branch included Acipenseridae, while Polyodontidae gave rise to five clades. Both clades, Polyodontidae and Scaphirhynchus, were a monophyletic group, whereas Acipenser and *Huso* species represented a polyphyletic group [65].

According to a comparison of the processes of functional genome reduction, 120-chromosome species are older compared to the younger 240- and 360-chromosome sturgeon species, in which this process is still active [51]. Thus, two scales are used when classifying the sturgeon ploidy, the actual and the more commonly used now, functional [52]. It is assumed that polyploidization in an allopolyploid manner occurred in sturgeons at least three times with a concomitant interspecific hybridization [66]. Apart from allopolyploidy, Krieger and Fuerst [67], as well as Le Comber and Smith [68], indicate that whole-genome duplication, i.e. autopolyploidy, can occur repeatedly and independently in different fish taxa.

According to Vasiliev et al. [66] and De La Herran et al. [69], Acipenseriformes are characterized by slow molecular evolution. The results of the comparative analysis of nucleotide sequences of the mitochondrial and nuclear genes indicate that the substitution rate in this group is almost twice as low as in teleosts [66]. This phenomenon is apparently associated with the polyploid origin of sturgeons. It is hypothesized that due to this, this group has retained the most ancient traits peculiar to cartilaginous ganoids [66, 69]. At the same time, based on the analysis of speciation and changes in fish anatomy, a group of researchers from the University of California have constructed a phylogenetic scheme for about eight thousand different fish genera covering the relationships between about thirty thousand species of Actinopterygii. Rabobsky et al. [70] and M. Friedman [71] came to the conclusion that sturgeons evolve at an enormous speed, exhibiting

an extraordinary flexibility and the ability to adapt to environmental conditions.

## CONCLUSION

Carl Linnaeus [72], in his taxonomy, had once assigned sturgeons to the class Amphibia. Later, Jackel [73] suggested that they may have descended from terrestrial quadrupeds. These are, of course, extreme opinions.

Polenov [31] believed that sturgeons occupy in the phylogenetic system the nearest position to the main trunk of vertebrate evolution compared to other fish. Vinnikov [74] was more categorical in his statement that it is sturgeons that may represent the ancestors of the modern terrestrial vertebrates. Luk'yanenko [60], summarizing the results of sturgeon hemoglobin studies, also came to an opinion that the fundamental similarity of hemoglobinograms and hemoglobin amino acid sequences of sturgeons and higher vertebrates, including humans, indicates that sturgeons are in the main trunk of the phylogenetic tree of vertebrates. All these statements were based on the analysis of only a single, separately taken trait.

The concept of mosaic evolution suggests that novel progressive traits characterizing a novel class of organisms develop unevenly in phylogenesis, i.e., this is one of the forms of the evolution of organisms, in which changes arise in individual parts of the organism or in separate systems without parallel changes in other parts thereof, or at an uneven pace. Species that exemplify mosaic evolution are considered as transitional forms. The latter are characterized by the presence of more ancient and primitive (in the sense of primary), but at the same time, more progressive (in the sense of later) traits compared to their ancestors [75, 76].

So far, there are no commonly accepted criteria to define higher taxa in the classification of living organisms. Specifically, sturgeon taxonomy considers mainly meristic and plastic characters. Meristic characters are based mainly on the variability of those morphological traits that are the least variable in fish ontogenesis. Plastic characters that characterize the shape of the body and the relative size of its parts are the most informative in individual identification. However, they alter significantly, depending on age, size, sex,

season, and habitat.

In some of the studies cited in this review, morphological, physiological, and ecological features have been used with varying degrees of success to discriminate between genera, species, and populations. In modern systematics, methods to assess genetic polymorphism using molecular markers are widely used along with morphological analysis. However, as already mentioned above, a high ploidy of the sturgeon genome hampers the polymorphism analysis with the use of nuclear markers [65, 80].

Currently, the fish taxonomy proposed by J. Nelson is widespread. Based on the analysis of meristic and plastic characters, the author allocates Chondrostei (cartilaginous ganoids) into a subclass which includes Acipenseriformes (sturgeons) as an order [81]. A.A. Lyubischev wrote that the most perfect is such a system, in which all characters of the object are determined by its position in the system; the closer the system to this ideal, the less artificial it is, and the natural is such a system, in which the number of the object's properties (ideally, all of them) functionally related to its position in the system is maximal (quoted from [82]). If following this absolutely correct Lyubischev's statement, the Nelson's taxonomy of cartilaginous ganoids may seem somewhat artificial. However, using the criteria applied in species identification, and having conducted a comparative analysis of data on the external morphology, morphology of visceral organs, as well as physiological, biochemical, genetic and ecological features, most of which go beyond the inter-class differences, there is every reason to consider bony-cartilaginous as a transitional form between fish and terrestrial vertebrates, and to single out the order of cartilaginous ganoids, if not as an independent class, then at least as a subclass, as proposed by Nelson [81].

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## CONFLICT OF INTEREST

The author declares that he has neither evident nor potential conflict of interest associated with the publication of this article.

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