

# The Revision of the Validity of Genus *Huso* (Acipenseridae) Based on Recent Morphological and Genetic Data with Particular Reference to the Kaluga *H. dauricus*\*

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**Abstract**—The comparative morphological study in different Acipenseriform species demonstrates that there are only two morphological features combining the kaluga and the great sturgeon and separating them from other sturgeons, namely the shape of a mouth and the manner attaching of gill membranes to isthmus in adult specimens; whereas many morphological characters are different in these species. The relations of morphological similarity/distinction among different sturgeon species and polyphyletic origin of genus *Huso* revealed by both molecular and cytogenetic studies presume the restoration of initial taxonomic states for the great sturgeon and kaluga as members of the same genus *Acipenser*, namely *A. huso* and *A. dauricus*.

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Most authors (Berg, 1948; Holčík, 1989; Bemis et al., 1997; Reshetnikov, 1998, 2002; Bogutskaya and Naseka, 2004; Artjukhin, 2008) traditionally combine the great sturgeon *Huso huso* (L.) and the kaluga *H. dauricus* (Georgi) and separate them from other sturgeon species as a special genus *Huso* Brandt et Ratzeburg, 1833, which is even classified by some of the authors (Findeis, 1997; Bemis et al., 1997) as a distinct subfamily Husinae. The main diagnostic characters for this fish group are: gill membranes joined to each other and forming a free fold below the isthmus; large crescent-shaped mouth sometimes extending to the sides of the head; unpaired cartilage of the palatoquadrate consisting of a single large median element; palatoquadrate articulated with symplecticum by means of the Meckel's cartilage; stylohyale articulated with the anterior part of symplecticum (Berg, 1948; Nikolsky, 1956; Sokolov, 1989). Findeis (1997) added additional character, namely "unique morphology" of basitrabecular processes, but this bone was studied in a few sturgeon species and demonstrated wide variability among them (Findeis, 1997). At the same time the kaluga differs from the great sturgeon by lower number of dorsal fin rays (43–57 versus 62–73), larger mouth, barbers lacking of foliate appendages, and the largest

first dorsal scute, but these differences are considered as species-specific for genus *Huso* (Berg, 1948; Nikolsky, 1956).

Contrast to aforementioned morphological taxonomic conception, the results of artificial hybridization within Acipenserid species together with the data on the existence of two chromosome groups within the genus *Acipenser* led to the conclusion that traditional separation of genera *Huso* and *Acipenser* was unfounded (Nikoljukin, 1972; Burtzev et al., 1973, 1976). But this conclusion was not accepted in further compilations included Acipenserid system (Masuda et al., 1984; Holčík, 1989; Reshetnikov, 1998). The discussion on the validity of the genus *Huso* was reactivated after recent molecular studies. Their results show that the great sturgeon and the kaluga do not form a separate monophyletic group, but are inserted among species of genus *Acipenser* and are more closely related to some other sturgeons than to each other (Ludwig et al., 2000, 2001; Robles et al., 2004; Krieger et al., 2008). And newly obtained karyological data confirm polyphyletic origin of *Huso*, since the kaluga was at first characterized as species with about 250 chromosomes in its genome (Vasil'ev et al., 2008, 2009), whereas the great sturgeon belongs to sturgeons with about 120 chromosomes (Fontana and Colombo, 1974; Vasil'ev, 1985). Thus, recently only morphological features still separate *Huso* and *Acipenser*, but they

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Materials examined: institutions and number of specimens (in brackets); size variability

Species	Institution* and number of specimens	Total body length variability, mm
<i>Scaphirhynchus platyrhynchus</i> (Rafinesque)	ZMMU (4)	52–~400
<i>Pseudoscaphirhynchus kaufmanni</i> (Kessler)	ZMMU (3)	280–305
<i>P. hermanni</i> (Kessler)	ZMMU (3)	160–175
<i>Huso huso</i> (L.)	K (18); ZMMU (15)	118–860
<i>H. dauricus</i> (Georgi)	ZMMU (6), ZIN (4), AFF (11)	45–673
<i>Acipenser stellatus</i> Pallas	K (29); ZMMU (41)	183–845
<i>A. sturio</i> L.	ZIN (7), MNHN (23)	165–1550
<i>A. oxyrinchus</i> Mitchell	ZIN (3), MNHN (10)	170–892
<i>A. ruthenus</i> L.	ZMMU (10)	225–595
<i>A. nudiventris</i> Lovetzky	ZIN (9), MNHN (1)	203–1125
<i>A. schrenckii</i> Brandt	ZMMU (8), MNHN (1), AFF (16)	52–572
<i>A. sinensis</i> Gray	ZIN (2), MNHN (2)	233–480
<i>A. dabryanus</i> Dumeril	ZIN (2), MNHN (2)	221–755
<i>A. mikadoi</i> (Hilgendorf)	ZIN (5), MNHN (1), AFF (11)	81–705
<i>A. medirostris</i> Ayres	ZIN (1)	1100
<i>A. baerii</i> Brandt	ZMMU (15)	255–463
<i>A. brevirostrum</i> Lesueur	ZIN (1), MNHN (4)	346–970
<i>A. fulvescens</i> Rafinesque	ZIN (2), MNHN (11)	400–1500
<i>A. transmontanus</i> Richardson	MNHN (1)	556
<i>A. naccarii</i> Bonaparte	ZIN (5), MNHN (2), SN (4)	425–715
<i>A. gueldenstaedtii</i> Brandt et Ratzeburg	ZMMU (4), ZIN (5), MNHN (10)	193–728
<i>A. persicus</i> Borodin	ZMMU (8); MNHN (3)	170–306
True hybrids:		
<i>H. huso</i> × <i>A. stellatus</i>	K (17)	810–1160
<i>A. stellatus</i> × <i>H. huso</i>	K (5)	885–1100
<i>A. persicus</i> × <i>A. gueldenstaedtii</i>	ZMMU (6)	167–264.5
Androgenetic nucleocytoplasmic hybrids		
( <i>A. persicus</i> ) × <i>A. gueldenstaedtii</i>	ZMMU (4)	164–267
( <i>A. stellatus</i> ) × <i>H. huso</i>	ZMMU (4); K (4)	166–732

\*Institutions: ZMMU, Zoological Museum of the Moscow State University; ZIN, Zoological Institute of Russian Academy of Science (St-Petersburg); MNHN, Museum National D'History Naturelle (Paris); SN, the Piscifactoria de Sierra Nevada (Granada, Spain); K, the Adygeyskii Sturgeon Hatchery (Krasnodar, Russia); AFF, Anyui fishery factory (Khabarovsk region).

contradict phylogenetic relations between different sturgeon species defined by genetic studies.

The purpose of this study, is re-examination of traditional diagnostic characters for genus *Huso* in relation with recent molecular and cytogenetic data with following revision of taxonomic relations among sturgeon species.

## MATERIAL AND METHODS

Morphological characters usually employed for the identification of the genera *Huso* and *Acipenser* and their species (Berg, 1948; Holčík, 1989) were examined in Acipenseriform specimens from the collections of the Zoological Museum of Moscow State University, the Zoological Institute of Russian Acad-

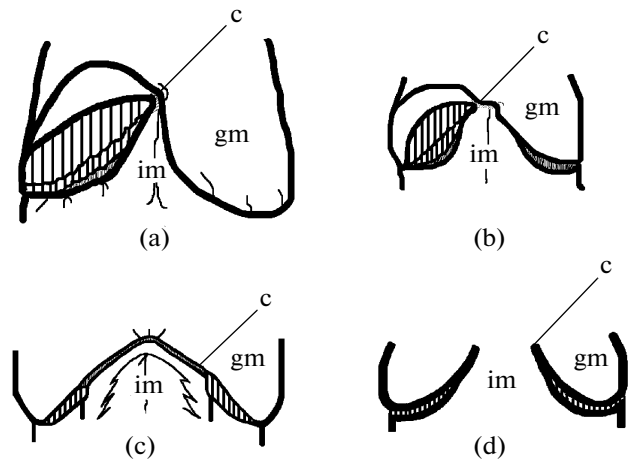
emy of Sciences (St. Petersburg) and the Museum National D'History Naturelle (Paris) as well as in some alive sturgeons from some fish farms (table). The studied material included 22 species at different ages and several artificially produced true and androgenetic hybrids, represented by 359 specimens (table). The descriptions for most of these materials were presented earlier (Vasil'eva et al., 2001, 2005; Vasil'eva, 2004, 2009).

## RESULTS AND DISCUSSION

Nikoljukin (1972) was the first who started the critical revision of morphological characters diagnostic for the genus *Huso*. He noted that the great sturgeon fry at the age of seven-eight days had gill membranes attached to the isthmus in the same manner as in *Acipenser* species with free fold developed below at later ages. He concluded this fold as a secondary state confirmed by the absence of the fold in hybrids between *H. huso* and both *A. gueldenstaedtii* Brandt et Ratzeburg and *A. stellatus* Pallas and the presence of very poor developed fold in hybrids between *H. huso* and *A. ruthenus* Linnaeus (Nikoljukin, 1972). The free fold below the isthmus was absent or poor developed in most specimens determined as hybrids between the kaluga and the Amur sturgeon (Soldatov, 1915); artificially obtained hybrids *A. stellatus* × *H. huso* had gill membranes attached to the isthmus (Vasil'eva et al., 2005).

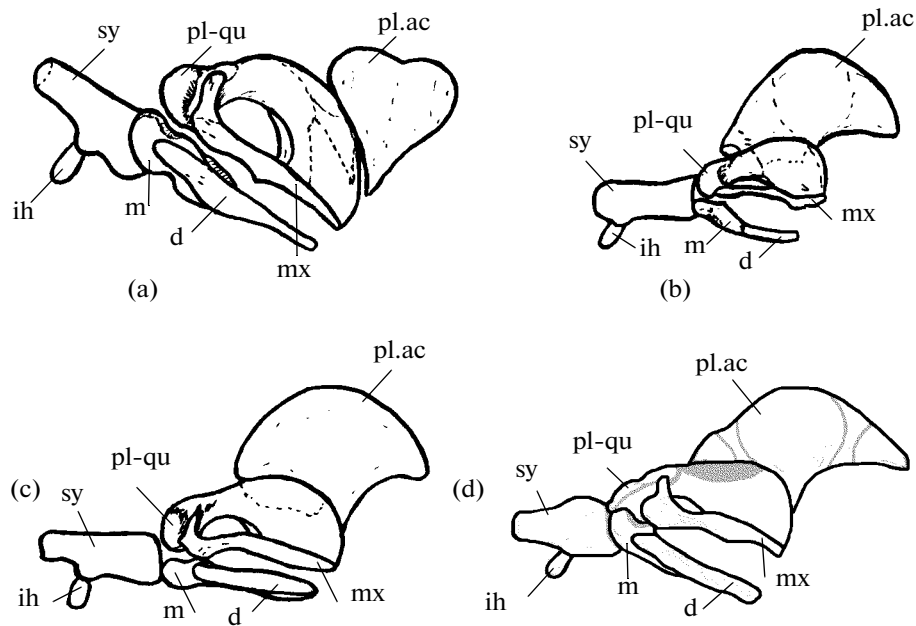
Morphological study on museum acipenseriform specimens testifies against accepted characteristic state of the fold in the great sturgeon and the kaluga. Really, gill membranes in these fishes are not free from the isthmus, but join with it by the skin from their inner sides; whereas outer sides of gill membranes are expanded in caudal direction, join to each other and cover the isthmus as a single whole fold which hides the connection with isthmus (Fig. 1a). In young studied specimens of *A. mikadoi* Hilgendorf, *A. brevirostrum* Lesueur and *A. naccarii* Bonaparte, as well as in adult fishes from related genera *Scaphirhynchus* and *Pseudoscaphirhynchus*, outer sides of gill membranes are slightly enlarged and form poor developed short fold or rudimentary fold developed only in the places where the skin from inner sides joins with isthmus (Figs. 1b, 1c). In adult sturgeons inner and outer sides of gill membranes are equally developed and both join with the isthmus at the same points (Fig. 1d). According to these results the developed fold of gill membranes looks not more significant for taxonomic relations than other species-specific morphological features in Acipenseriforms.

The next group of diagnostic characters of *Huso*, namely specific structural traits of the components and the system of articulations of the palate-quadrates arch, also does not significantly diverge from the states observed in other sturgeons. These characters were earlier studied in the stellate sturgeon *A. stellatus*, the



**Fig. 1.** The way of gill membranes to attach to the isthmus: (a) in adult kaluga *Huso dauricus* and the great sturgeon *H. huso*, (b) in young *Acipenser mikadoi*, (c) in adult *Pseudoscaphirhynchus kaufmanni*, (d) in adult *Acipenser dabryanus*; c, connection between gill membrane and isthmus; gm, gill membrane; im, isthmus.

great sturgeons and their true and androgenetic hybrids (Vasil'eva et al., 2005). The comparative analysis indicates that the so called unpaired cartilage (an unpaired cartilaginous palate-pterygoid plate) in acipenserids is generally represented by one cartilaginous component, though individual deformations of the cartilage are possible, leading to its fragmentation. Meckel's cartilage in the great sturgeon is quite massive, with a large articulating capitulum whose depth makes an essential part (64.5–93.3%) of the depth of the articulating socket of the symplectic. Therefore, the caudal part of the palate-pterygoid-quadrates cartilage is topographically situated beyond the articulating socket of the symplectic, adjoins the Meckel's cartilage, but is connected by connective-tissue ligaments not only with the Meckel's cartilage but also with the symplectic (Fig. 2a). In the stellate sturgeon, the cartilage is not so bulky, and the depth of its articulating capitulum reaches less than half (40.0%) of the depth of the articulating socket of symplectic. Therefore, the caudal part of the palate-pterygoid-quadrates cartilage directly contacts the articulating socket of the symplectic and almost does not adjoin the Meckel's cartilage (Fig. 2b). These differences are not qualitative but quantitative, which is also true for the other "diagnostic" character, the topographic position of the articulation of symplectic and interhyale (=stylohyale): in the great sturgeon the articulation of symplectic and interhyale is indeed situated in the anterior half of symplectic, while in the stellate sturgeon it is situated in the posterior half (Figs. 2a, 2b). In the true hybrids, the Meckel's cartilage is developed relatively weakly (the depth of its articulating capitulum makes 42.0–62.5% of the depth of the articulating socket), and the caudal part of the palate-pterygoid-quadrates cartilage



**Fig. 2.** Structure of visceral skeleton: (a) *Huso huso*, (b) *Acipenser stellatus*, (c) their hybrid, (d) *H. dauricus*; d, dentale; ih, interhyale; m, Meckel's cartilage; mx, maxilla-praemaxilla; pl.ac, palate-pterygoid accessory cartilage; pl-qu, palate-pterygoid-quadrate cartilage; sy, symplectic.

directly contacts the articulating socket of the symplectic; the articulation of the symplectic and interhyale is situated in the posterior half of the symplectic (Fig. 2c). At the same time, aforementioned structures of the kaluga demonstrate the intermediate state between the great sturgeon and stellate sturgeon: an unpaired cartilaginous palate-pterygoid plate is fragmented in several pieces as it was declared for *Acipenser* species (Berg, 1948); Meckel's cartilage in the kaluga is more or less massive, with enlarged articulating capitulum whose depth makes an essential part (78.9%) of the depth of the articulating socket of the symplectic, but the caudal part of the palate-pterygoid-quadrate cartilage envelops upper side of the articulating capitulum of Meckel's cartilage and immediately adjoin the articulating socket of the symplectic; stylohyale articulated with the middle part of symplectic (Fig. 2d). These data testify to species-specific or/and individual variability of mentioned structures and their useless for the separation of genus *Huso*.

Thus, only two morphological features combine the kaluga and the great sturgeon and separate them from other sturgeons, namely the shape of a mouth and the manner attaching of gill membranes to isthmus in adult specimens; whereas four morphological characters (the number of dorsal fin rays, mouth size, barbel structure and size relations of dorsal scutes) differentiate them. These relations of morphological similarity/distinction seem to be of the same level as ones observed between some other sturgeon species, for example, continuous lower lip characteristic for

*A. nudiventris* Lovetsky or very elongated sword-shaped snout in *A. stellatus*.

It should be mentioned that, in spite of molecular data rejected close phylogenetic relations between the great sturgeon and kaluga, recently obtained karyological evidences for polyphyletic origin of *Huso* (Vasil'ev et al., 2008, 2009) were quite unexpected. The first data on the kaluga karyotype were presented by Serebryakova (Burtzev et al., 1973, 1976). They were obtained by imperfect methods (the study of embryonic mitosis at the late blastula and in gill mucus cells) resulted in incorrect values: only 60 chromosomes were first defined in the kaluga karyotype, as well as in the great sturgeon one (Burtzev et al., 1973). Later 60-chromosome sturgeon karyotypes were transformed in about 120-chromosome karyotypes (Burtzev et al., 1976) in conformity with earlier published karyotype of the shovelnose sturgeon *Scaphirhynchus platyrhynchus* (Rafinesque) characterized by the chromosome number  $112 \pm 5$  (Ohno et al., 1969). After aforementioned publications the kaluga is treated as undoubted 120-chromosome species by most authors (Birstein et al., 1993, 1997; Birstein and DeSalle, 1998; Fontana et al., 1999, 2001, 2008; Ludwig et al., 2001; Fontana, 2002; Artjukhin, 2008).

Moreover, 120-chromosome genome in the kaluga was "confirmed" by the nuclear DNA content described for this species. The value 3.74–3.81 pg obtained by flow cytometry by Birstein and co-authors (1993) was similar to ones earlier obtained for 120-chromosome species (see Birstein et al., 1993). But it should be mentioned that the authors studied

two specimens of the kaluga and obtained value 8.24–8.42 pg for two specimens of the bester, artificial hybrid between *Huso huso* and *Acipenser ruthenus* with about 118 chromosomes (Arefjev, 1989). Therefore, taking into consideration the recent data on about 250-chromosome number in the kaluga (Vasil'ev et al., 2008, 2009), both aforementioned samples seem to be confused in the cited study. This assumption looks very probable since in the molecular analysis conducted by Birstein and DeSalle (1998) “the kaluga” was demonstrated clustered with *H. huso* and *A. ruthenus*, as should be expected for the bester; whereas in further phylogenetic analyses based on mtDNA gene sequences the kaluga is found clustered with other Pacific sturgeons (*A. medirostris* Ayres, *A. mikadoi*, *A. schrenckii* Brandt, *A. transmontanus* Richardson, *A. sinensis* Gray, *A. dabryanus* Duméril), while *H. huso* is clustered within Atlantic sturgeon group and represents sister taxon for both 120- and 250-chromosome subclusters (Ludwig et al., 2001; Krieger et al., 2008), or represents sister taxon for the group including Ponto-Caspian species and *Acipenser baerii* Brandt (Fain et al., 2001). Similar low value (4.77 pg) of the nuclear DNA content was obtained for the kaluga by Yin et al. (2004). It may be caused by any methodological and/or technical mistakes, since the karyological analysis of different Far East sturgeon species (Vasil'ev et al., 2008, 2009) did not reveal any noticeable differences in cell sizes of the head lymphoid organ between the kaluga and *A. mikadoi* with the DNA content 13.93–14.73 pg (Birstein et al., 1993). But if the kaluga has low value of the nuclear DNA content, the ratio of its cell sizes and ones from *A. mikadoi* should be at least 1 : 2.

Another “confirmation” for 120-chromosome genome in the kaluga was presented by Ludwig et al. (2001) based on microsatellite analysis demonstrated disomic allelic band patterns in *Huso dauricus* at four from five studied loci (at one locus, Afu-68, tetrasomic pattern was revealed for this species). In this connection, it should stress that other karyologically studied sturgeon species with 120-chromosome demonstrated disomic patterns at all of five studied loci (Ludwig et al., 2001) and it is known, that the number of disomic inheritable microsatellite loci approaches 36% in functional tetraploid sturgeons (Welsh et al., 2003). Therefore, taking into consideration a very little number of studied loci, the predominance of loci with disomic patterns in the kaluga should be regarded as a chance phenomenon. It should also be mentioned that only three kaluga specimens were studied, while the samples of 120-chromosome species included from 15 (*A. nudiventris* Lovetsky) to 150 (*A. ruthenus*) specimens (Ludwig et al., 2001). Therefore, the allelic variability in the kaluga seems to be understated even for studied loci. Nevertheless, it should be stressed that both of the discussed methods (microsatellite analysis and DNA content value) are indirect ones, and the karyological study is the only way to define ploidy level of

any organism. And recent karyological study (Vasil'ev et al., 2008, 2009) completely refutes the misconception on 120-chromosome state in the kaluga and its close relation with the great sturgeon.

Polyphyletic origin of genus *Huso* recently revealed both molecular and cytogenetic studies and observed morphological divergence between sturgeon species may result in two different taxonomic consequences: (1) the separation of both former *Acipenser* and *Huso* in several genera of phylogenetically related and morphologically similar species, (2) the recover of the initial system with all sturgeon species combined in the same genus *Acipenser*. The last opinion seems to be the most constructive in different aspects and is proved correct by recent information on the presence of *Huso* diagnostic characters in the short-snout forms of the white sturgeon *A. transmontanus* which is thus treated as *Huso transmontanus* (Stephen and Goodman, 2008; Stephen, 2008). This presumes the restoration of the old name *Acipenser huso* for the great sturgeon and *A. dauricus* for the kaluga.

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