

Portraits of a juvenile *Huso huso* 23 cm TL from the Ryal Ontario Museum collection (given originally as Caspian Sea fish to Montreal Expo 1967) above the head of *Acipenser schrenckii* 81 cm TL from the Amur River stock held at the Propa-Gen International, Komadi, Hungary. Originals by Paul Vecsei, 1996.

How many species are there within the genus Acipenser?

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In their paper in this volume Bemis et al. (1997) ask: 'How many valid species of Acipenser should we recognize?' Although a partial answer to this question is presented in their Table 5, we discovered in the course of preparing this volume that some additional commentary is needed. In fact, there are two questions: (1) how many species should be recognized? and (2) what scientific names should be used for some of the species? The sympatric distributions of most species of sturgeons set the stage for much confusion about species boundaries, but the situation is actually much more complicated. Confusion about the number of species of sturgeons living within the same basin can result from the often close morphological and meristic similarities of certain species of Acipenser, particularly during juvenile period. Moreover, we still have remarkably inadequate knowledge of the comparative anatomy of the species of Acipenser: no modern study has ever attempted a comprehensive examination of all species, and it is impossible to rely on literature for the sorts of comparisons that must be made (for more on this general problem, see Grande & Bemis 1991, 1997). Most classical descriptions and comparative anatomical studies relied upon small sample sizes. Voucher specimens of large sturgeons are especially rare in most historical collections, and type specimens (if available at all) are seldom prepared in ways that are suitable for making detailed anatomical comparisons (e.g., many skins are simply overstuffed with straw, so that all internal structures are lost). Intraspecific morphological and meristic polymorphisms occur in all species of acipenserids, and in most cases we have very poor knowledge of differences that develop during ontogeny, particularly changes in such features as the shape of the rostrum (Bemis et al. 1997). Another problem is the ease of hybridization between different species of sturgeons (reviewed in Birstein et al. 1997 this volume). In many of these cases, it is not easy to discriminate between parental species and the hybrids.

Two opposite tendencies appeared in the literature on the genus *Acipenser*. (1) Recognizably different species have been considered to be the same species. This situation is illustrated below by two species pairs, *A. gueldenstaedtii* and *A. persicus* and *A. medirostris* and *A. mikadoi*. (2) Some authors elevated many forms to the rank of species. For instance, Duméril (1870) described six subgenera of Acipenser with more than 30 species of Acipenser in five of them (he considered Huso as the sixth subgenus of Acipenser). Most of the species described by Duméril (1870) have long since been recognized as conspecific with other well-known species.

We still do not know the number of species of *Acipenser*, and may never know it because of overfishing and habitat destruction in Europe and Asia, 158

which have quickly eliminated sturgeons from certain river basins (see discussions in this volume by Bacalbaşa-Dobrovici 1997, Khodorevskaya et al. 1997, Krykhtin & Svirskii 1997, Wei et al. 1997). Therefore, we probably have already lost forever the opportunity to study some species of *Acipenser*. In the meantime, it is clear that genetic and molecular phylogenetic approaches are increasingly crucial for the recognition of sturgeon species and their relationships (for discussion, see Birstein et al. 1997 this volume).

In Eurasia, the genus Acipenser is centered upon three main basins: (1) the Black Sea and Sea of Azov, (2) Caspian Sea, and (3) the Aral Sea. Each of three main species of Acipenser, A. gueldenstaedtii Brandt, 1833, A. stellatus Pallas, 1771, and A. nudiventris Lovetsky, 1828 were described as having subspecies or forms in these basins (see Berg 1948, Shubina et al. 1989, Sokolov & Vasilev 1989a, Vlasenko et al. 1989a). If we follow the view on nomenclature of species discussed by Holčík & Jedlička (1994), then the concept of subspecies and trinomial nomenclature is inefficient. Therefore, we consider all intraspecies forms and subspecies of A. gueldenstaedtii, A. stellatus, and A. nudiventris invalid until detailed molecular and morphological studies of different forms within these species can be performed.¹ The same is true for *A. ruthenus* Linnaeus, 1758, for which a few intraspecies forms were described by different authors (see Berg 1948, Sokolov & Vasilev 1989b).

An example helps to illustrate the taxonomic frustration of sturgeon biologists. *Acipenser persicus* was described as a valid species by Borodin in 1897 (Borodin 1897, 1926), but it was later considered to be a subspecies (Berg 1934), and, still later, again regarded as a valid species (see Vlasenko et al. 1989b, Birstein & Bemis 1997 this volume, for discussion). Moreover, Artyukhin & Zarkua (1986) described two subspecies within *A. persicus*: the population inhabiting the Caspian Sea they named as *A. persicus persicus* Borodin, 1897, and the population inhabiting the Black Sea, as *A. persicus colchicus* Marti, 1940. Although some Russian authors follow this nomenclature (Pavlov et al. 1994), additional support from genetic and molecular data is desirable.

The validity of some Asian species and subspecies of *Acipenser* is questionable. For example, Ruban (1997 this volume) reviewed and presented new data on the Siberian sturgeon, *A. baerii* Brandt, 1869, which has an extremely wide range. Ruban's new work supports the traditionally recognized subspecies (*A.b. baerii*, *A.b. baicalensis* and *A.b. stenorrhynchus*, e.g., Sokolov & Vasiliev 1989c). No genetic study on the subspecies of *A. baerii* is yet available.

The three far eastern Asian species, *A. schrencki* Brand, 1869 of the Amur River, and *A. dabryanus* Duméril, 1868, and *A. sinensis* Gray, 1834 of the Yangtze River are certainly valid (see Krykhtin & Svirskii 1997, Wei et al. 1997, Zhuang et al. 1997, all this volume). Chinese sturgeon, *A. sinensis*, from the Pearl River differ morphologically from those of the Yangtze River, but whether this difference warrants separate species status is not clear (Wei et al. 1997).

The nomenclature and species status of the socalled 'green sturgeon' and 'Sakhalin sturgeon' of the Pacific Northwest of America and northeastern Pacific in Asia has been particularly confusing. Ayres (1854) described the American green sturgeon, A. medirostris. Nearly 40 years later, Hilgendorf (1892) described an Asian species caught in the northern waters of Japan as A. mikadoi, and Schmidt (1904) soon thereafter referred a sturgeon caught in the Aniwa Bay of Sakhalin Island to A. mikadoi. However, Berg (1911, 1948) considered this Sakhalin sturgeon to be conspecific with the American green sturgeon, A. medirostris. Schmidt (1950) eventually reconsidered his 1904 view, and named Sakhalin sturgeon as a subspecies of A. medirostris, A. medirostris mikadoi (Schmidt, 1950). Therefore, three names coexisted in the literature for the Sakhalin sturgeon: A. mikadoi (Okada & Matsubara

¹ In the literature on genetics, molecular phylogenetics and systematics, the taxonomic unit subspecies is often preserved (Avise 1994, Mallet 1995). Avise & Ball (1990) and Avise (1994, p 253) suggested that we recognize 'by the evidence of concordant phylogenetic partitions at multiple independent genetic attributes'. 'When phylogenetic concordance is exhibited across genetic characters solely because of extrinsic barriers to reproduction, subspecies status is suggested'. It is evident that according to these terminology, populations of the same species of sturgeon in disjunct sea basins (e.g., Caspian and Black seas), could be considered as subspecies.

1938, Matsubara 1955), A. medirostris (Berg 1948, Andrivashev & Panin 1953, Masuda et al. 1984, Houston 1988, Artyukhin & Andronov 1990, Pavlov et al. 1994), and A. medirostris mikadoi (Lindberg & Legeza 1965, Shilin 1995). Recently Birstein (Birstein et al. 1993. Birstein 1993) noted the difference in ploidy between the Sakhalin sturgeon and American green sturgeon, and suggested that they should be considered different species, A. mikadoi Hilgendorf, 1892, and A. medirostris Ayres, 1854, respectively. Molecular data on three mitochondrial genes presented in this volume (Birstein & DeSalle 1997) also show great differences between these two species. Other molecular data obtained show a close genetic relationship of A. medirostris to another American Pacific sturgeon species, A. transmontanus (Brown et al. 1996, Birstein et al. 1997). Therefore, A. mikadoi and A. medirostris should be considered as morphologically similar, but genetically different, species. The Sakhalin sturgeon inhabits the Sea of Japan up to the Korean Peninsula and waters to the north from Hokkaido Island (Berg 1948, Lindberg & Legeza 1965). It occurs in the mouths of small rivers of the Asian far east and Korean Peninsula, as well as the Amur River, and rivers of the Sakhalin Island. Now it spawns in the Tumnin (Datta) River in the Russian far east (Artuykhin & Andronov 1990), and historically it also spawned in the Ishikari and Teshio rivers of Hokkaido Island (Okada 1955). Acipenser medirostris ranges from the Gulf of Alaska to southern California (Houston 1988), with three known spawning rivers: the Sacramento and Klamath rivers in California and the Rogue River in Oregon (Moyle et al. 1994).

Two other species of sturgeons are usually mentioned in descriptions of the fish fauna of Japan, *A. kikuchii* Jordan & Snyder, 1901, and *A. multiscutatus* Tanaka, 1908 (Okada 1959–1960, Masuda et al. 1984, Rochard et al. 1991). Only one specimen of *A. kikuchii* is known (Jordan & Snyder 1901, 1906), and this species was re-identified as *A. sinensis* (Takeuchi 1979). Only a few specimens of *A. multiscutatus* were described (Tanaka 1908, Fowler 1941, Matsubara 1955). It seems that these specimens are morphologically similar to *A. schrenckii* (Lindberg & Legeza 1956) and are probably conspecific with *A. schrenckii*. It is most improbable that a sturgeon species could be restricted only to Japan and not inhabiting Asian continental waters (Artyukhin & Andronov 1990). There are no new reports on the catch of *A. multiscutatus* in Japanese literature (see a compilation of data in Honma 1988) since the review of Okada (1959-1960). Therefore, *A. multiscutatus* is most probably a synonym of *A. schrencki*.

It is easy to distinguish the second Pacific North American species, *A. transmontanus* Richardson, 1836, the freshwater North American *A. fulvescens* Rafinesque, 1817, and one of the two Atlantic North American sturgeons, *A. brevirostrum* Le Sueur, 1818 (Vladykov & Greeley 1963, Scott & Crossman 1973, Lee et al. 1980). Molecular data on the structure of the control region of mtDNA not only supported close relationships of two Pacific North American sturgeon species, *A. medirostris* and *A. transmontanus*, but also showed a significant genetic difference between these species, *A. fulvescens*, and the second Atlantic North American species, *A. oxyrinchus* (Brown et al. 1996).

American and the European Atlantic sturgeon were long considered to be one species, A. sturio Linnaeus, 1758. In this older terminology, the American Atlantic sturgeon was regarded as subspecies A. sturio oxyrinchus, with the European Atlantic sturgeon being known as A. sturio sturio (see Smith 1891, Vladykov & Greeley 1963). Magnin & Beaulieu (1963) suggested elevation of these subspecies to species ranks, with the European form retaining the name A. sturio Linnaeus, 1758, and American form named A. oxyrinchus Mitchill, 1815. Two subspecies, the Atlantic sturgeon, A.o. oxyrinchus, and the Gulf coast sturgeon, A.o. desotoi, were described within A. oxyrinchus (Vladykov 1955, Vladykov & Greeley 1963).² These two subspecies of A. oxyrinchus are morphologically similar, with the most significant known difference be-

² Since the description of the species, the name *A. oxyrinchus* has changed a few times. Mitchill described this species in 1815 under the name *A. oxyrinchus* (Mitchill, 1815). Later, the name was changed to *A. oxyrhynchus* and an incorrect date of publication (1814) began to be cited widely (e.g., Vladykov & Greely 1963). Also, *A. oxyrinchus desotoi* was first described under the name *A. oxyrhynchus desotoi* (Vladykov 1955). In this volume we follow Smith & Clugston (1997) and use the names *A. o. oxyrinchus and A. oxyrinchus desotoi*.

ing the length of the spleen (in A.o. oxyrinchus the spleen is statistically smaller than it is in A.o. de sotoi, Wooley 1985). Molecular data are more informative for the discrimination between subspecies. Comparison of the control region of mtDNA sequences of both subspecies showed three fixed nucleotide changes in that region (Ong et al. 1996). Bowen & Avise (1990) suggested that there is genetic structuring among A. oxyrinchus from various drainages of the North American Atlantic coast. Recently, analyses of the control regions of mtDNA supported this hypothesis: Atlantic sturgeon populations in the Saint Lawrence and Saint John rivers (Canada), the Hudson River (U.S.A.), and rivers of Georgia (U.S A.) are genetically distinct (Waldman et al. 1996a,b).

Unpublished results of Birstein & DeSalle on the sequences of three more genes of mtDNA (cytochrome b, 12S rRNA, and 16S rRNA) also show a genetic difference between the two subspecies of A. oxyrinchus (one fixed nucleotide change in cytochrome b gene). The analysis of these genes demonstrated that the European A. sturio is the only sturgeon species closely related to A. oxyrinchus. Moreover, it appeared that there is a significant genetic differentiation within A. sturio. Birstein & DeSalle studied samples from two specimens of A. sturio caught in the Gironde estuary system (Dorgonne and Garonne rivers) and in the North Sea. The genetic difference between two individuals of A. sturio (6 nucleotide changes in the region of cytochrome *b* analyzed) was even more than the difference between subspecies of A. oxyrinchus (one change). These data seem to support the difference in some meristic characters between specimens from the Baltic Sea, from one side, and specimens from the Atlantic Ocean, Mediterranean and Black seas, from the other (Marti 1939, Magnin 1963, Ninua 1976, Holčík et al. 1989). Because A. sturio has almost disappeared in the wild (Holčík et al. 1989). more work should be done in museum collections on the comparison of specimens from different populations. This is especially important in terms of recovery projects for this species (Hochleithner 1995, Williot et al. 1997, this volume).

The last species in the genus *Acipenser* is the Adriatic sturgeon, *A. naccarii* Bonaparte, 1836. It is

restricted to the Adriatic only and resembles *A. gueldenstaedtii* in meristic characters (Tortonese 1989).

Since Berg (1904), Huso huso Brandt, 1869 and H. dauricus Georgi, 1775 were considered as representatives of a distinct genus Huso, not Acipenser as they were usually considered in the 19th century (also see Findeis 1997, this volume). Results of recent molecular studies, however (see Birstein et al. 1997 this volume) showed that the two species of Huso do not form a separate monophyletic group, but are inserted among species of Acipenser. This result reactivates the old discussion on the validity of the genus Huso. In the absence of detailed work on this problem, it makes sense for now to regard Huso as a genus based on morphological and anatomical data (Findeis 1997 this volume). Also, a few subspecies were described within H. huso (reviewed in Pirogovskii et al. 1989). For instance, some authors still consider the Sea of Azov population of H. huso as Huso huso maeoticus Salnikov & Myatskii, 1934 (Pavlov et al. 1994). Until genetic differences can be shown in combination with morphology, we recommend the name *H. huso* for the Mediterranean. Black, Azov, and Caspian sea populations of beluga.

In conclusion, we recognize 17 valid extant species within *Acipenser*. For the moment, we accept that two species (*A. baerii* and *A. oxyrinchus*) contain subspecies. Further genetic and molecular studies will generate new data for correction of our contemporary knowledge about some of the species, including *A. sturio*.

A final note regarding the names of sturgeon species concerns the need to return to the originally published spellings for names of genera and species³. In addition to two recent clarifications on the correct spelling of species names for Siberian (*A. baerii*, see Ruban 1997, this volume) and American Atlantic sturgeon (*A. oxyrinchus*, see Gilbert 1992), we note the following correct spelling for two other

³ Such decisions to use the originally published spellings of names, regardless of subsequent practices, are based on the International Code of Zoological Nomenclature (Ride et al. 1985). For a specific explanation of rules, see Chapters 31 and 33 of the International Code of Zoological Nomenclature. 1985, 3rd ed. International Trust for Zoological Nomenclature, London.

species of *Acipenser*. The scientific name of the Russian sturgeon should be spelled *Acipenser guel-denstaedtii* Brandt, 1833, and the scientific name of the Amur River sturgeon should be spelled *Acipenser schrenckii* Brandt, 1869.

References cited

- Andriyashev, A.P. & K.I. Panin. 1953. Discovery of a Pacific sturgeon (*Acipenser medirostris* Ayres) in the Bering Sea. Zool. Zhurnal 32: 932–936 (in Russian).
- Artyukhin, E.N. & A.E. Andronov. 1990. A morphological study of the green sturgeon, *Acipenser medirostris* (Chondrostei, Acipenseridae), from the Tumnin (Datta) River and some aspects of the ecology and zoogeography of Acipenseridae. Zool. Zhurnal 69: 81–91 (in Russian, English translation J. Ichthyol. 30 :11–21).
- Artyukhin, E.N. & Z.G. Zarkua. 1986. On the question of taxonomic status of the sturgeon in the Rioni River (the Black Sea basin). Voprosy Ikhtiologii 26: 61–67 (in Russian).
- Avise, J.C. 1994. Molecular markers, natural history and evolution. Chapman & Hall, New York. 511 pp.
- Avise, J.C. & R.M. Ball, Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surv. Evol. Biol. 7: 45–67.
- Ayres, W.O. 1854. Descriptions of the sturgeons. Proc. Calif. Acad. Sci. 1: 14–16.
- Bacalbaşa-Dobrovici, N. 1997. Endangered migratory sturgeons of the lower Danube River and its delta. Env. Biol. Fish. (this volume).
- Bemis, W.E., E.K. Findeis & L. Grande. 1997. An overview of Acipenseriformes. Env. Biol. Fish. (this volume).
- Berg, L.S. 1904. Zur Systematic der Acipenseriden. Zool. Anz. 27: 665–667.
- Berg, L.S. 1911. Fishes (Marsipobranchii and Pisces). Fauna of Russia and adjacent countries. Vol. 3, Vypusk 1. Izdatelstvo Akademii Nauk, St. Petersburg. 337 pp. (in Russian).
- Berg, L.S. 1934. Acipenser gueldenstaedti persicus, a sturgeon from the south Caspian Sea. Ann. Mag. Nat. Hist., Ser. 10: 317– 319.
- Berg, L.S. 1948. The freshwater fishes of the USSR and adjacent countries, Vol. 1. Akademia Nauk USSR, Moscow & Leningrad. Part 1. (in Russian, English translation published by Israel Program for Scientific Translations, Jerusalem. 505 pp.)
- Birstein, V. J. 1993. Is Acipenser medirostris one or two species? Sturgeon Quart. 1(2): 8.
- Birstein, V.J. & W.E. Bemis. 1997. Leo Semenovich Berg and the biology of Acipenseriformes: a dedication. Env. Biol. Fish. (this volume).
- Birstein, V.J., R. Hanner & R. DeSalle. 1997. Phylogeny of the Acipenseriformes: cytogenetic and molecular approaches. Env. Biol. Fish. (this volume).

Birstein, V.J., A.I. Poletaev & B.F. Goncharov. 1993. The DNA

content in Eurasian sturgeon species determined by flow cytometry. Cytometry 14: 377–383.

- Birstein, V.J. & R. DeSalle. 1997. Molecular phylogeny of Acipenserinae. Mol. Phylogenet. Evol. 7 (in press).
- Bonaparte, C.L. 1836. Iconographia della fauna italica per le quatro classi degli animali vertebrate. 3. Pesci. Roma. Fasc. 15– 18, 80–93.
- Borodin, N.A. 1897. A report about a summer 1895 zoological expedition on board of the cruiser Uralets in the northern part of the Caspian Sea. Vestnik Rybopromyshlennosti 1: 1–31 (in Russian).
- Borodin, N. 1936. Acipenser persicus, a sturgeon from the Caspian Sea. Ann. Mag. Nat. Hist., Ser. 9, 20: 26–28.
- Bowen, B.W. & J.C. Avise. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life history patterns. Mar. Biol. 107: 371–81.
- Brandt, J.F. 1833. *In*: J.F. Brandt & J.T. Ratzeburg. Medizinische Zoologie. 2. Berlin. 364 pp.
- Brandt, J.F. 1869. Einige Worte ber die europaischen-asiatischen Störarten (Sturionides). Bull. Acad. Imper. Sci. St.-Petersb. 14: 171–175.
- Brown, J.R., K. Beckenbach, A.T. Beckenbach & M.J. Smith. 1996. Length variation, heteroplasmy and sequence divergence in the mitochondrial DNA of four species of sturgeon (*Acipenser*). Genetics 142: 525–535.
- Duméril, A. 1868. Note sur trois poissons de la collection du museum, un esturgeon, un polyodonte et un malarmat. Nouv. Arch. Mus. Nat. Hist. Nat. Paris 4: 98–100.
- Duméril, A. 1870. Histoire naturelle des poissons ou ichthyologie gnrale. T. 2. Librairie Encyclopdique de Roret, Paris. 624 pp.
- Findeis, E.K. 1997. Osteology and phylogenetic interrelationships of sturgeons. Env. Biol. Fish. (this volume).
- Fowler, H.W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondili and Ostariophysi obtained by the United States Bureau of Fisheries steamer Albatross in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Bull. U. S. Nat. Mus. 100: 1–879.
- Georgi, J.G. 1775. Bemerkungen einer Reise im russischen Reich. Vol. 1. St. Petersburg. 352 pp.
- Gilbert, C.R. 1992. Atlantic sturgeon. pp. 31–39. *In*: R.A. Ashton (ed.) Rare and Endangered Biota of Florida, Vol. 2, Univ. Florida, Gainesville.
- Grande, L. & W.E. Bemis. 1991. Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. J. Vert. Paleo. 11, supplement 1: 1–121.
- Grande, L. & W.E. Bemis. 1997. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. J. Vert. Paleo. Supplement (in press).
- Gray, J.E. 1834. Characters of two new species of sturgeons (Acipenser, Linn.). Proc. Zool. Soc. London 1834: 122–123.
- Hilgendorf, F. 1892. Über eine neue Stör-Art aus Nord-Japan (Acipenser mikadoi). Sitzungsber. Ges. naturf. Freunde, Berlin 7: 98–100.

Hochleithner, M. 1995. Gesellschaft zur Rettung des Störs (Acipenser sturio) e.V.i.G. Österreichs Fisch. 48: 165–168.

Holčík, J. & L. Ledlička. 1994. Geographical variation of some taxonomically important characters in fishes: the case of the bitterling *Rhodeus sericeus*. Env. Fish. 41: 147–170.

Holčík, J., R. Kinzelbach, L.I. Sokolov & V.P. Vasilev. 1989. Acipenser sturio Linnaeus, 1758. pp. 367–394. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.

Honma, Y. 1988. Records and distributional notes on the sturgeons along the coast of Japanese Archipelago. Bull. Biogeogr. Soc. Japan 43: 51–55 (in Japanese).

Houston, J.J. 1988. Status of the green sturgeon, Acipenser medirostris, in Canada. Can. Field-Natur. 102: 286–290.

Jordan, D.S. & J.O. Snyder. 1901. Description of nine new species of fishes contained in museums of Japan. J. Coll. Sci. Imp. Univ. Tokyo 15: 301–311.

Jordan, D.S. & J.O. Snyder. 1906. A synopsis of the sturgeons (Acipenseridae) of Japan. Proc. U. S. Nat. Mus. 30: 397-398.

Khodorevskaya, R.P., G.F. Dovgopol, O.L. Zhuravleva & A.D. Vlasenko. 1997. Present status of commercial stocks of sturgeons in the Caspian Sea basin. Env. Biol. Fish. (this volume).

Krykhtin, M.L. & V.G. Svirskii. 1997. Endemic sturgeons of the Amur River: kaluga, *Huso dauricus* and Amur sturgeon, *Acipenser schrenckii*. Env. Biol. Fish. (this volume).

Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister & J.R. Stauffer. Jr. 1980. Atlas of North American freshwater fishes. North Carolina Biol. Survey, Publ. # 1980–12. 867 pp.

Le Sueur, C.A. 1818. Description of several species of chondropterygious fishes of North America, with their varieties. Trans. Amer. Phil. Soc. 1: 383–394.

Lindberg, G.U. & M.J. Legeza. 1965. Fishes of the Sea of Japan and its adjacent waters, Sea of Okhotsk and Yellow Sea, Pt. 2. Izdatelstvo Akademii Nauk, Moscow. 391 pp. (in Russian).

Linnaeus, K. 1758. Systema naturae. pp. 230–238. *In:* Nantes Pisces. X ed., Vol. 1. Holmiae.

Lovetsky, A. 1828. On the fishes belonging to the sturgeon genus and inhabiting waters of the Russian Empire. Novyi Magazin Estestvennoi Istorii, Fiziki, Khimii i Svedenii Ekologicheskikh, Izdannyi I. Dvigubskim, Chast 6, Moscow. 3 pp. (in Russian).

Magnin, E. 1963. Recherches sur la systmatique et la biologie des Acipenserids Acipenser sturio L., Acipenser oxyrhynchus Mitch. et Acipenser fulvescens Raf. Ann. Stat. Centr. hydrobiol. appliq., Paris 9: 8–242.

Magnin, E. & G. Beaulieu. 1963. tude morphomtrique compare de l'Acipenser oxyrhynchus Mitchill du Saint-Laurent et de l'Acipenser sturio Linn de la Gironde. Natur. Can. 90: 5–38.

Mallet, J. 1995. A species definition for the Modern Synthesis. Trends Ecol. Evol. 10: 294–299.

Marti, V. Yu. 1939. Biology and harvest of *Acipenser sturio* in the Black Sea. Zool. Zhurnal 18: 435-442 (in Russian).

Marti, V.Yu. 1940. Systematics and biology of the Russian stur-

geon from the Caucasian shore of the Black Sea. Zool. Zhurnal 19: 865–872 (in Russian).

Masuda, H., K. Amaoka, C. Araga, T. Uyeno & T. Yoshino. 1984. The fishes of the Japanese Archipelago. Tokai Univ. Press, Tokyo. 437 pp.

Matsubara, K. 1955. Fish morphology and hierarchy, Vol. I-III. Ishizaki Shoten, Tokyo. 1605 pp. (in Japanese).

Mitchill, S.L. 1815. The fishes of New York described and arranged. Trans. Lit. Philos. Soc. New York 1: 355–492.

Moyle, P.B., P.J. Foley & R.M. Yoshiyama. 1994. Status and biology of the green sturgeon, *Acipenser medirostris*. Sturgeon Quart. 2(1): 7.

Ninua, N.Sh. 1976. The Atlantic sturgeon from the Rioni River. Izdatelstvo Metsniereba, Tbilisi. 122 pp. (in Russian).

Okada, Y. 1959–1960. Studies on the freshwater fishes of Japan, Vol. I–II. J. Fac. Fish., Pref. Univ. Mie 4: 1–860.

Okada, Y. & K. Matsubara. 1938. Keys to the fishes and fish-like animals of Japan. Sanseido, Tokyo. 584 pp. (in Japanese).

Ong, T.-L., J. Stabile, I. Wirgin & J. R. Waldman. 1996. Genetic divergence between *Acipenser oxyrinchus oxyrinchus* and *A.o. desotoi* as assessed by mitochondrial DNA sequencing analysis. Copeia 1996 (in press).

Pallas, P.S. 1771. Reise durch verschiedene Provinzen des russischen Reiches, 1768 und 1769 sten Jahre. 1. St. Petersburg.

Pavlov, D.S, K.A. Savvaitova, L.I. Sokolov & S.S. Alekseev. 1994. Rare and endangered animals. Fishes. Vysshaya Shkola, Moscow. 334 pp. (in Russian).

Pirogovskii, M.I., L.I. Sokolov & V.P. Vasilev. 1989. *Huso huso* (Linnaeus, 1758). pp. 156-200. *In:* J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II. General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.

Rafinesque, C.S. 1817. Additions to the observations on the sturgeons of North America. Amer. Month. Mag. Crit. Rev. 1: 128.

Richardson, J. 1836. The fish, Vol. 3. Fauna Boreali-Americana, or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under the command of Sir John Franklin, R.N. Richard Bentley, London. 327 pp.

Ride, W.D.L., C.W. Sabrosky, G. Bernardi & R.V. Melville. 1985. International code of zoological nomenclature. Univ. Calif. Press, Berkeley. 338 pp.

Rochard, E., P. Williot, G. Castelnaud & M. Lepage. 1991. Iments de systmatique et de biologie des populations sauvages d'esturgeons. pp. 475–507. *In:* P. Williot (ed.) Acipenser, CEMA-GREF Publ., Bordeaux.

Ruban, G.I. 1997. Species structure, contemporary distribution and status of the Siberian sturgeon, *Acipenser baerii*. Env. Biol. Fish. (this volume).

Salnikov, N.I. & S.M. Myatskii. 1934. On the systematics of the beluga from the Sea of Azov-Black Sea Basin. Trudy Nauchnoi Rybokhozyaistvennoi i Biologicheskoi Stantsii Gruzii 1: 31–50 (in Russian).

Schmidt, P.Yu. 1904. Fishes of the eastern seas of the Russian Empire. Izdanie Russkogo Geograficheskogo Obshchestva, St. Petersburg. 466 pp. (in Russian).

- Schmidt, P.Yu. 1950. Fishes of the Sea of Okhotsk. Izdatelstvo Akademii Nauk, Moscow. 370 pp. (in Russian).
- Scott, W.B. & E.J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184. 966 pp.
- Shilin, N.I. 1995. Programme for conservation of Acipenser medirostris mikadoi in the Russian Far East. pp. 262-267. In: A.D. Gershanovich & T.I.J. Smith (ed.) Proceedings of International Symposium on Sturgeons, 6–11 September 1993, Moscow-Kostroma-Moscow, VNIRO Publishing, Moscow.
- Shubina, T.N., A.A. Popova & V.P. Vasilev. 1989. Acipenser stellatus Pallas, 1771. pp. 395–443. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Smith, H.M. 1891. Report on the fisheries of the South Atlantic States. Bull. U. S. Fish. Comm. 11: 269–356.
- Smith, T.I.J. & J.P. Clugston. 1997. Status and management of Atlantic sturgeon, *Acipenser oxyrinchus*, in North America. Env. Biol. Fish. (this volume).
- Sokolov, L.I. & V.P. Vasilev. 1989a. Acipenser nudiventris Lovetsky, 1828. pp. 206-226. *In*: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Sokolov, L.I. & V.P. Vasilev. 1989b. Acipenser ruthenus Linnaeus, 1758. pp. 227–262. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Sokolov, L.I. & V.P. Vasilev. 1989c. Acipenser baeri Brandt, 1869. pp. 263-284. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Takeuchi, T. 1979. Description of two acipenserid fishes, Acipenser sinensis Gray and A. kikuchii Jordan et Snyder, recorded from Sagamy Bay. Ann. Rep. Keikuy Aburatsubo Marine Parc. Aq. 10: 20–25 (in Japanese).
- Tanaka, S. 1908. Notes on some Japanese fishes, with descriptions of fourteen new species. J. Coll. Sci. Imp. Univ. Tokyo 23: 1–54.
- Tortonese, E. 1989. Acipenser naccarii Bonaparte, 1836. pp. 285-293. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Vladykov, V.D. 1955. A comparison of Atlantic Sea sturgeon

with a new subspecies from the Gulf of Mexico (*Acipenser ox-yrhynchus de sotoi*). J. Fish. Res. Board Can. 12: 754–761.

- Vladykov, V.D. & J.R. Greeley. 1963. Order Acipenseroidei. pp. 24-60. *In:* H.B. Bigelow, C.M. Breder, D.M. Cohen, G.W. Mead, D. Merriman, Y.H. Olsen, W.C. Schroeder, L.P. Schultz & J. Tee-Van (ed.) Fishes of the Western North Atlantic, Mem. Sears Found. Mar. Res. 1.
- Vlasenko, A.D., A.V. Pavlov, L.I. Sokolov & V.P. Vasilev. 1989a. Acipenser gueldenstaedti Brandt, 1833. pp. 294–344. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Vlasenko, A.D., A.V. Pavlov & V.P. Vasilev. 1989b. Acipenser persicus Borodin, 1897. pp. 345-366. In: J. Holčík (ed.) The Freshwater Fishes of Europe, Vol. 1, Pt. II, General Introduction to Fishes, Acipenseriformes, AULA-Verlag, Wiesbaden.
- Waldman, J.R., J.T. Hart & I.I. Wirgin. 1996a. Stock composition of the New York Bight Atlantic sturgeon fishery based on analysis of mitochondrial DNA. Trans. Amer. Fish. Soc. 125: 364–371.
- Waldman, J.R., K. Nolan, J. Hart & I.I. Wirgin. 1996b. Genetic differentiation of three key anadromous fish populations of the Hudson River. Estuaries 19: 759–768.
- Wei, Q., F. Ke, J. Zhang, P. Zhuang, J. Luo, R. Zhou & W. Yang. 1997. Biology, fisheries, and conservation of sturgeons and paddlefish in China. Env. Biol. Fish. (this volume).
- Williot, P., E. Rochard, G. Castelnaud, T. Rouault, R. Brun, M. Lepage & P. Elie. 1997. Biological characteristics of the European Atlantic sturgeon, *Acipenser sturio*, as the basis for a restoration program in France. Env. Biol. Fish. (this volume).
- Wooley, C.M. 1985. Evaluation of morphometric characters used in taxonomic separation of Gulf of Mexico sturgeon, *Acipen*ser oxyrhynchus desotoi. pp. 97–103. *In:* F.P. Binkowski & S.I. Doroshov (ed.) North American Sturgeons: Biology and Aquaculture Potential, Dr W. J. Junk Publishers, Dordrecht.
- Zhuang, P., F. Ke, Q. Wei, X. He & Y. Cen. 1997. Biology and life history of Dabry's sturgeon, *Acipenser dabryanus*, in the Yangtze River. Env. Biol. Fish. (this volume).