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Leo Semenovich Berg and the biology of Acipenseriformes: a dedication

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This volume is dedicated to the memory of Leo Semenovich Berg (1876–1950), a Russian ichthyologist and geographer. In the foreword to the English translation of Berg's remarkable treatise, 'Nomogenesis or evolution according to law', Theodosius Dobzhansky wrote: 'Berg was one of the outstanding intellects among Russian scientists. The breadth of his interests and the depth as well as the amplitude of his scholarship were remarkable. He had the reputation of being a 'walking library', because of the amount of information he could produce from his memory' (Dobzhansky 1969, p. xi). Berg was prolific, publishing 217 papers and monographs on ichthyology, 30 papers on general zoology and biology, 20 papers on paleontology, 32 papers on zoogeography, 320 papers and monographs on geography, geology, and ethnography, as well as 290 biographies, obituaries, and popular articles (Berg 1955, Sokolov 1955).

Berg was born 120 years ago, on 14 March 1876, in the town of Bendery. According to laws of the Russian Empire, Berg could not enter the university as a Jew, so he was baptized and became a Lutheran, which allowed him to study and receive his diploma in zoology at the Moscow University in 1898. From 1899 to 1904, he explored the fisheries and the general ecology of the Aral Sea and lakes in Turkestan and western Siberia. In 1904, Berg was appointed curator of the Ichthyology Department of the Zoological Museum (later Zoological Institute) at the Academy of Sciences in St. Petersburg. Later he held several positions in this and other institutions (Shapovalov 1951, Oliva 1951, 1952, Holčík 1976, Lindberg 1976, Oliva & Holčík 1977, 1978). As one of the most talented biologists of his time, Berg was a target of Trofim Lysenko and his followers. In January 1939, after discrediting Berg and an outstanding geneticist Nicolai Koltsov in the press, Lysenko and his accomplice, Nikolai Tsitsin, were elected in their stead as members of the Soviet Academy of Sciences. Berg was never formally recognized by the Soviet Academy for his accomplishments in biology, and only later (1946) was he elected a member of the Geography Branch of the Soviet Academy of Sciences (Figure 1).

Sturgeons and the order Acipenseriformes were a central theme in Berg's theoretical works and papers on systematics and zoogeography (Andriyashev 1955, Lindberg 1976). In December 1936, he addressed a meeting of the Biology Branch of the Soviet Academy of Sciences on 'Classification of fishes, both living and fossil'. This fundamental work was published in Russian in 1940, although some general ideas in a short form appeared earlier in English and French (Berg 1935a, 1937). The entire book was translated into English in 1947 (Berg 1947a, 1965). It was the most comprehensive study of its era on systematics and evolution of fossil and recent fishes, and it remains useful. An additional chapter, entitled 'On the position of Polypteridae in the system of fishes' appeared as a separate paper

Figure 1. Leo Semenovich Berg, ichthyologist and biogeographer.

the same year (Berg 1947b). In 1948, Berg published a second additional chapter, 'On the position of Acipenseriformes in the system of fishes'. These two chapters, as well as additional new material on fossil fishes, were included in the second Russian edition of the book which appeared only in 1955, after the author's death.

Unfortunately, the chapter on the Acipenseriformes was never translated into English. In 50 pages, Berg described the morphology, anatomy, and embryology of Acipenseriformes, comparing them to extinct Paleonisciformes and modern Elasmobranchii (Figure 2). Berg's conclusions contradicted the theory introduced by Aleksei Sewertzoff (1925, 1926, 1928), who considered acipenseriforms to be closely related to elasmobranchs. Berg wrote: 'Acipenseriformes belong to the same group of fishes as the Paleonisciformes, i.e., to the primitive Ac-

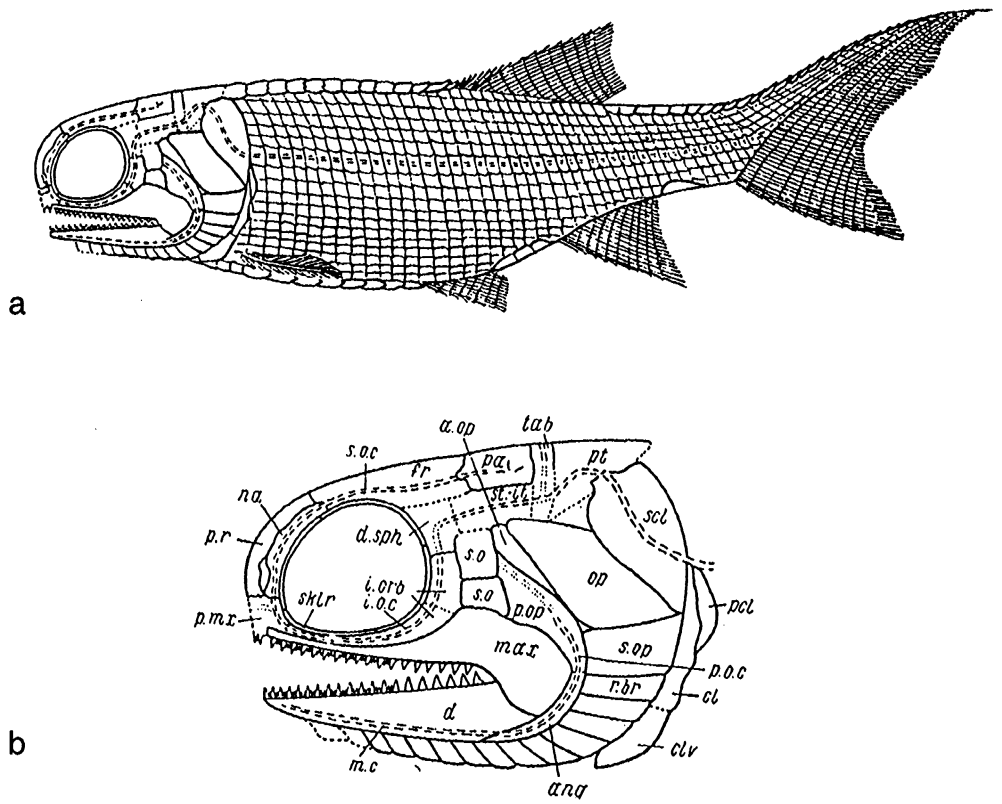

Figure 2. Berg's original reconstructions of a paleoniscid, *Ganolepis gracilis* (first published by Obruchev 1955): a – Lateral view of the entire fish, b – reconstruction of skull (ang = angular, a op = anteoperculum, cl = cleithrum, clv = clavicle, d = dentary, d sph = dermosphenotic, fr = frontal, i.o.c. = infraorbital sensory canal, i orb = infraorbital, max = maxillary, m c = Meckel's cartilage, na = nasal, op = operculum, pa = parietal, pcl - postcleithrum, p mx = premacilla, p o c = preopercular canal, p op = preoperculum, p r = postrostrale, pt = posttemporal, r br = branchiostegal rays, scl = supracleithrum, sklr = sclerotic ring, s o = suborbitalis, s o c = supraorbital canal, s op = suboperculum, st-it = supratemporal-intertemporal, tab = tabular).

tinopterygii. There is no contemporary data supporting the hypothesis on the close relationship of acipenseriforms to selachians' (Berg 1948a, p. 53). He identified three families within Acipenseriformes: 'Chondrosteidae (from the Lower Lias to the Lower Cretaceous), Acipenseridae (beginning from the Upper Cretaceous), and Polyodontidae (beginning from the Upper Cretaceous)' (Berg 1948a, p. 54). Berg's understanding of Acipenseriformes as actinopterygians is fundamental to all contemporary views (Sokolov & Berdichevskii 1989a, b, Grande & Bemis 1991, Bemis et al. 1997, this volume).

Systematics of Acipenseridae was the topic of one of Berg's early theoretical papers (Berg 1904). He included four genera in this family: *Huso* with two species, *H. huso* and *H. dauricus; Acipenser* with sixteen species; *Scaphirhynchus* with one species, *S. platorhynchus*; and *Pseudoscaphirhynchus* with three species, *P. fedtschenkoi, P. hermanni*, and *P. kaufmanni*. This division of Acipenseridae into four genera is used by most contemporary researchers (but see Jollie 1980). In his first monograph on the fishes of Russia (Berg 1911), Berg divided *Acipenser* into three subgenera: (1) *Lioniscus* Bonaparte, 1846, with one species, *A. nudiventris*; (2) *Helops* Bonaparte, 1846, also with one species, *A. stellatus*; and (3) *Acipenser* sensu stricto, which includes all other species of *Acipenser*. Later, in 1948, in the last edition of his monograph on the Russian

fish fauna, Berg changed the name *Helops* Bonaparte 1846, to *Gladostomus* Holly, 1936. Historical reviews of these divisions within *Acipenser* are given by Findeis (1997) and Birstein et al. (1997) in this volume, but it is clear that we are still far from an unambiguous, synapomorphy-based diagnosis of the genus *Acipenser* (also see Birstein & Bemis 1997 this volume).

In many monographs and papers, Berg gave classic descriptions of sturgeons inhabiting Russia, eastern Europe and Asia, including their zoogeography and biology (Berg 1905a, b, 1908a, b, 1909, 1911–1913, 1916, 1923, 1932a, b, 1933, 1945, 1948b, c). His encyclopedic knowledge of the material allowed him to discuss hybrids as well as different forms within the same species. Extreme polymorphism is characteristic of many sturgeon species, which poses problems for morphological diagnoses. Berg's approach was typical for his time: recognize and name distinctive subspecies from portions of the range. Many examples are known. For instance, in the Caspian Sea, besides the typical form of the Russian sturgeon, *A. gueldenstaedtii*, Berg recognized a subspecies *A. gueldenstaedtii persicus* Borodin, 1897 or Persian sturgeon (Berg 1933, 1934a, 1948). Later this form was elevated to the rank of species, *A. persicus* (Artyukhin 1979, 1984). This species also occurred in the Black Sea (Artyukhin & Zarkua 1986, Vlasenko et al. 1989). Berg (1948b) considered the Black Sea and Sea of Azov populations of *A. gueldenstaedtii* to be a distinct subspecies, *A. gueldenstaedtii colchicus*. Within the European sterlet, *A. ruthenus*, Berg (1911, 1923, 1948a) recognized two morphs. One, with a typical long and pointed rostrum he named '*A. ruthenus* morpha *kamensis* Lovetsky, 1834', which was synonymous to *A. gmelini* Fitzinger & Heckel, 1834, and to *A. ruthenus* var. *brevirostris* Antipa, 1909. Berg described Siberian sterlet from the Ob River as *A. ruthenus* natio *marsiglii* (Berg 1949).

Berg published several well-known articles on winter and vernal (or spring) races of anadromous fishes (Berg 1934b, 1934c, 1935b). The English-speaking audience learned about these definitions only 25 years later, when Berg's article was translated into English (Berg 1959). He concluded that anadromous fishes, including sturgeons, typically consist of two main races, winter and vernal. Their characteristics are: (1) winter fish spend the coldest time of the year either in the river itself, or in the sea close to the river mouth, whereas vernal fish enter the river at higher temperatures in the spring. (2) During the coldest seasons, the winter fish are in a state of vegetative quiescence, eating little or nothing. Many 'hibernate' in holes. Vernal races have only a short period of vegetative quiescence and do not 'hibernate'. (3) The vernal races spawn in the same season in which they enter the rivers. The winter races spawn the next year. (4) The winter races usually spawn earlier than the vernal races, i.e. in a given year they mature earlier. (6) The winter race is usually larger than the vernal race. (7) The winter race is usually more fertile than the vernal race. As typical examples of the two races, Berg analyzed the behavior of the four species of sturgeons in the northern part of the Caspian Sea: *A. stellatus*, *A. gueldenstaedtii*, *H. huso*, and *A. nudiventris*. Depending on the species, one of the two races usually predominates. One of the races can disappear completely. For example, there was only a winter race of the ship sturgeon, *A. nudiventris*, in the Aral Sea (now the Aral Sea population has disappeared completely, see Zholdasova 1997 this volume). Although the sterlet, *A. ruthenus*, is a freshwater resident species, there were two races (and two morphs, as mentioned above) in the Volga, Danube, and Dnieper rivers, which migrated along the rivers to the deltas and back. Differences in races of sturgeons remain even now, despite drastic changes in the Volga, Danube, and other rivers (see Bacalbaşa-Dobrovici 1997, Hensel & Holčík 1997, Khodorevskaya et al. 1997, Kynard 1997, all this volume). Long migrations of *A. ruthenus* in major European rivers are disrupted by dams (for the situation in the Danube River see Hensel & Holčík 1996, Bacalbaşa-Dobrovici 1997, this volume). Migrating and riverine races (or populations) are discussed by: Ruban (1997 this volume) for Siberian sturgeon, *A. baerii*; Krykhtin & Svirskii (1997 this volume) for Amur River sturgeons; and Hensel & Holčík (1997 this volume) for sturgeons of the Danube River.

Profound knowledge of the distribution of Acipenseriformes played a major role in Berg's evolutionary (Berg 1922) and zoogeographic theories.

Figure 3. At the Institute of Zoology in St. Petersburg, the presence of Lev Semenovich Berg is still strong 40 years after his death. Minutes after arrival on 18.6.1990 E.A. Dorofeeva seated Eugene Balon in the chair used by L.S. Berg.

Amur River acipenserids (Berg 1909, 1911) were one of the elements of Berg's hypothesis on the relic character of the fauna of the Amur River Basin (Berg 1912, 1928). According to this hypothesis, the species constituting the Amur River fauna are remnants of the subtropical Upper Tertiary fauna that characterized the entire northern hemisphere, and which mostly disappeared as a result of cooling during the Quaternary. Berg also discussed problems of interrelationships of the Asian, European, and North American fish faunas (Berg 1950). Contemporary information about sturgeons of the Amur River is presented in two articles of this volume (Krykhtin & Svirskii 1997, Zhuang et al. 1997).

Some of Berg's other zoogeographic ideas are useful for understanding the distribution and evolution of sturgeons in the northern hemisphere. For instance, in a hypothesis explaining the similarity of elements of the Pacific and Atlantic faunas, Berg suggested two periods of exchanges between elements of the faunas of the northern parts of the two oceans (Berg 1918, 1934d, e, 1947b). Also, Berg's ideas on historic changes in the fauna of the Caspian Sea (Berg 1928c, d) are useful for understanding the

Figure 4. A portrait of L.S. Berg in his office at the Zoological Institute, St. Petersburg. Lithograph by G. Vereisky, 1950.

history and evolution of sturgeons in the Caspian and Black Sea basins.

Berg gave his first short presentation on sturgeons in 1897, when he was a student (Berg 1898). It described experiments on artificial breeding of *A. stellatus*. Much later he returned to the problem of sturgeon development, describing juveniles of *Pseudoscaphirhynchus kaufmanni* caught in the Amu Darya River (Berg 1929). In this volume detailed information on the reproductive cycle of the white sturgeon, *A. transmontanus*, is given by Doroshov et al. (1997).

Berg never stressed the ability of sturgeons to hybridize, but he described many sturgeon hybrids in detail (Berg 1911, 1932, 1948b). Some genetic aspects of acipenseriforms, including hybridization, are discussed in this volume by Birstein et al. (1997).

Berg lived and worked when the sturgeon crisis in Russia, Europe, and Asia had only started (Figure 3, 4). The desperate need for conservation measures to save sturgeons was in the future. He published only a small article describing his concern about *A. sturio* in the Baltic Sea and especially in the Neva River (Berg 1935c). He suggested that a complete ban on the catch of this species should be established for at least the next 10–15 years. Unfortunately, since then most of the species of sturgeons and paddlefishes have become threatened or endangered, a theme of many papers of this volume, and one that surely would have saddened L.S. Berg.

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