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Contribution of Karl Fedorovich Kessler (1815–1881) to Fish Systematics and Faunal Research

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Abstract—The biography and research activities of Karl Fedorovich Kessler (1815–1881), an outstanding zoologist, in the area of ichthyology are briefed. His main studies into fish systematics and faunistics are considered as well as his contribution to ichthyological collections.

Keywords: Kessler, biography, research activities, collection activities

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November 2015 marked the 200th anniversary of Karl Fedorovich (Fridrikhovich) Kessler, an outstanding zoologist (Fig. 1). He was born in Konigsberg to a family of a forester (oberforestmeister). When Karl turned 7 years old, his father was invited to Russia to be the chief forester of the Novgorod guberniya. In 1828, Karl entered the Third St. Petersburg Grammar School (now, secondary school no. 181, Gagarinskaya ul. 23) at governmental expense. After graduation from this school in 1834, Kessler was enrolled in the Department of Physics and Mathematics at St. Petersburg University. At that time, this department comprised two parts: mathematical and natural science. Of the natural sciences, Kessler attended the lectures on comparative anatomy, the system of animal life, zoology, paleontology, history of animal development, natural history of echinoderms, and natural history of slugs. However, as Bogdanov (1882, p. 301) wrote, no one could suspect a future naturalist in Kessler at the time of his university studies. Upon graduation from the university, he worked as a teacher of mathematics at school. Kessler defended his master of science dissertation titled *On Bird Legs in Relation to the Systematic Division of This Class* on December 15, 1840, and his Doctoral dissertation titled *On the Skeleton of Woodpeckers in Relation to the Place Occupied by This Genus in the Class of Birds* in the August 1842 (Bogdanov, 1982). In 1842, a position fell vacant at the Chair of Zoology with Kiev University. Kessler took this position and dedicated his life to the studies of invertebrates, fish, herpetological objects, and birds starting from this moment. His studies of freshwater and marine fish brought him the greatest success. In total, 30 most comprehensive works of his 64 zoological publications on different animal groups (birds, small mammals, frogs, scaled reptiles, crayfish, tarantulas, etc.) dealt with fish. Kessler particularly contributed to three major research areas of ichthyology: (1) faunal studies based on the data collected in his travels; (2) taxonomic studies involving field specimens and collections; and (3) creation of ichthyological collections.

FAUNAL RESEARCH BY KESSLER DURING THE KIEV PERIOD OF HIS LIFE

In 1853–1856, Kessler travelled several times to the Dnieper River within the Kiev educational region, which at that time comprised five guberniyas, namely, Kiev, Podolsk, Volyn, Chernigov, and Poltava. The ichthyological specimens collected during these travels formed the background for a vast consolidated report titled *The Natural History of the Guberniyas of the Kiev Educational Region. Zoology. Systematics Section* (Kessler, 1856). This work comprises comprehensive descriptions of 57 fish species belonging to 11 families (Table 1). The best-examined species (58%) belonged to the cyprinids (Cyprinidae family), or *coropovye,* as Kessler referred to these species; 10.5% of the species belonged to perches (Percidae) and 8.8% belonged to sturgeons (Acipenseridae). The species essays comprised the descriptions of their external morphology and its variation ("noticed local distinctions"), geographical distribution of individual species, and their specific biological features (behavior, spawning time, and fecundity). The descriptions were very passionate, illustrative, and vivid allowing for a summarized image of a particular species. This is how Kessler (1856, p. 11) described the pike *Esox lucius* and the tench *Tinca tinca:* "The pike is a tough, strong, and unusually alert fish, quick in its movements and sly. ... The tench is an awkward and lazy fish, slow in its

Fig. 1. Portrait of Karl Fedorovich Kessler from vol. 12 of *Proceedings of the St. Petersburg Society of Naturalists,* dedicated to his memory.

movements." This style in describing fish was later used by Sabaneev (1911). Kessler did not find any new species in the Dnieper River within the Kiev educational region and focused on additional characters in the fish external structure as well as their local abundance and specific spawning features of the known fish species.

The number of species (57) found by Kessler (1856) in the middle reaches of the Dnieper River remained rather stable until the construction of the dam for the Dnieper hydropower station (city of Zaporozhe) in 1927–1932. The resulting artificial reservoir changed the hydrological regime, which influenced the composition of ichthyofauna. The number of species reduced to 36 and then gradually increased owing to planned introduction of commercial species and accidental invasions. The current ichthyofauna of the Dnieper artificial reservoir comprises 52 species belonging to 14 families (Novitskii et al., 2005); many species regarded by Kessler (1856) as common for the Dnieper River are now rare or endangered and 14 species are in the Red Data Book of Ukraine (*Krasnaya kniga*..., 2009).

In 1858, Kessler travelled to the northwestern part of the Black Sea and western coast of Crimea to study the ichthyofauna in the estuaries of the Dniester, Dnieper, and Southern Bug Rivers and the adjacent Black Sea areas. On their way from the city of Belaya Tserkov' (Kiev guberniya) to the Sudak Bay (Taurida guberniya, Crimea), Kessler and K.M. El'skii, his student, made 12 stops to study the compositions of local ichthyofaunas, commercial catch, local fishing gear, and even the national compositions of fisherman teams. The major goal of their travel was to study the fish species inhabiting river deltas and the adjacent seacoast, because these areas were the most productive and housed the most intensive fishing acts (Kessler, 1861, p. 31). They also paid much attention to the fish migration from rivers to the sea as well as upstream and downstream migrations in the rivers. In total, they observed 152 fish species belonging to 24 families in these rivers and the Black Sea. Of them, Cyprinidae and Gobiidae were represented by the largest number of species (42 and 20, respectively). Kessler (1861) divided all described species into five categories: (1) sea species (68 species); (2) anadromous, i.e., living in the sea and spawning in rivers (11 species); (3) dual type, i.e., capable of living both in rivers and sea (six species); (4) estuarine, i.e., living in river estuaries (seven species); and (5) freshwater species (60 species).

In his studies, Kessler (1861) emphasized the importance of faunal studies; he writes that fauna is a constantly changing set of animals, and the main goal in studying faunas is the insight into how they established and will further evolve. In his lecture at the First Conference of Natural Science Schoolteachers of the Kiev Region, he states that all animals are constantly struggling for their existence with both each other and ambient life conditions. This struggle results in either transient or constant displacement of some species and varieties from a locality being replaced by other animal species or varieties (Bogdanov, 1882, p. 345). The faunal studies of fishes, the importance of which was advocated by Kessler, are still most topical, and their value increases with time. The compositions of ichthyofaunas changes ever more rapidly because of a direct human impact on fish communities, such as planned introduction of "foreign" species, commercial fishing, artificial breeding, aquaculture, and accidental invasions. The comprehensive ichthyofaunal reports by Kessler, made over 150 years ago, are brilliant basic documents successfully used by ichthyologists for comparative analysis, developmental dynamics, and long-term forecasts of the changes in ichthyofaunas.

In 1861, Kessler, on a competitive basis, got a position with the Chair of Zoology at the Faculty of Physics and Mathematics of St. Petersburg University but remained in Kiev until October 13, 1862 (Bogdanov, 1882). The activities of Kessler at Kiev University were highly esteemed by his colleagues and friends, as is evident from one of their letters: "You appeared in this field of your activities at our university at a dark time

for Russia, at the time when both social life and science have become a morbid dream and all events opposed development and when the most educated and honest people were filled with apathy, whereas others chased decorations and laurels losing their honor and conscience. Your vital and generous nature avoided apathy and rose above the small vested interests driving the majority. You denoted the high value of natural science among the area of education common to humankind" (Bogdanov, 1882, p. 336).

FAUNAL RESEARCH AND TRAVELS BY KESSLER DURING THE ST. PETERSBURG PERIOD OF HIS LIFE

The early 1860s may be regarded as a renaissance in the world natural sciences, assisted by the treatise *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life* by Charles Darwin, published in 1859. The commission aimed at studying the nature of the St. Petersburg guberniya was organized with St. Petersburg University; Karl Baer recommended inviting Kessler to this commission. His participation in the work of this commission was marked by publication of the faunal report titled *The Description of Fishes Occurring in the Water Bodies of St. Petersburg Guberniya* (Kessler, 1864). During only one year, Kessler and his four assistants (two of them were A.O. Kovalevsky and K.A. Timiryazev) collected the data and specimens on 63 fish species. The fish specimens were caught in large rivers and their tributaries running within the St. Petersburg guberniya (Neva, Luga, Izhora, Narva, Volkhov, Syas', and Svir' rivers and Ladoga and Chudskoe lakes) as well as from the northeastern part of the Gulf of Finland. Of the recorded 63 species, 40 were freshwater species, 12 were anadromous, and 11 were marine species. The species constantly living there accounted for 86% and only nine species were either transient or accidental. Cyprinids were prevalent among the freshwater species and accounted for 47%; Salmoniformes, including the family Salmonidae, Coregonidae, and Thymallidae, constituted 35% (Table 2). Kessler discovered a novel species and named it after Baer, *Coregonus baerii* (Kessler, 1864). The taxonomic diversity (species, genera, and families) in the water bodies of St. Petersburg guberniya and Leningrad oblast increased over the past 120 years. The list of fishes was supplemented with five new families (Gobiidae, Lumpenidae, Liparidae, Scombridae, Catostomidae, and Odontobutidae) and 15 species (Neelov, 1987; Uspenskii and Naseka, 2014).

This increase in the number of species results from the planned introduction of commercial species, accidental invasions of noncommercial species, and species that escaped from aquaculture farms. The increase in faunal diversity is currently in progress, and its rate is constantly increasing.

Table 1. Composition of the fish and agnathan species in the Dnieper River system in the Kiev educational region (Kessler, 1856)

Family*	Number of species
Percidae	6
Cottidae	2
Gasterosteidae	1
Gobiidae	3
Lotidae	1
Siluridae	1
Cyprinidae	33
Salmonidae	1
Esocidae	1
Clupeidae	1
Acipenseridae	5
Petromyzontidae	2
Total	57

*Hereinafter, the family names are given in their current understanding (Eschmeyer, 2016).

At the time of Kessler (1864), Salmonidae (Atlantic salmon *Salmo salar* and char *Salvelinus lepechini*), Coregonidae (whitefish species *Coregonus lavaretus* and *C. baerii*), Cyprinidae (common bream *Abramis brama*, vimba bream *Vimba vimba,* ide *Leuciscus idus,* and roach *Rutilus rutilus*) and Percidae (perch *Perca fluviatilis,* zander *Sander lucioperca,* and Eurasian ruffe *Gymnocephalus cernua*) were the most commercially important species; they were mainly harvested in the estuaries of the Neva and Narva rivers. Of the other fish species, European eel *Anguilla anguilla* and lamprey *Lampetra fluviatilis* were in demand (Kessler, 1864).

During his fieldwork in the water bodies of the St. Petersburg guberniya, Kessler paid attention to the fact that the Onega Lake fauna was poorly studied. He travelled to the northern part of the lake in summer 1866 but managed to process the collected specimens only 2 years later. These results were published in 1868 in the faunal report on the fish of Onega Lake and the surrounding region. The ichthyofauna of northern Onega Lake was similar to the freshwater fauna of St. Petersburg guberniya and comprised 43 agnathan and fish species belonging to 15 families (Table 3).

According to Kessler (1868), Salmonidae, Coregonidae, and Thymallidae species were prevalent in the Onega Lake fauna in number of species, abundance, and distribution, which distinguished this lake from the other freshwater bodies; these group of species accounted for 33% of all fish living in the lake. Unlike the ichthyofauna of St. Petersburg guberniya, the cyprinid species in Onega Lake yielded to salmonids in the number of species, accounting for approximately 30%. The char *Salvelinus lepechini* (Gmelin,

Table 2. Composition of the fish species in St. Petersburg guberniya and Leningrad oblast

Family	Number of species and subspecies	
	Kessler, 1864	Neelov, 1987*
Petromyzontidae	2	3
Acipenseridae	2	3
Anguillidae	1	1
Clupeidae	2	3
Cyclopteridae	1	1
Cyprinidae	19	22
Cobiidae	2	2
Balitoridae	1	1
Siluridae	1	1
Esocidae	1	1
Osmeridae	2	2
Coregonidae	7	7
Thymallidae	1	1
Salmonidae	4	5
Gadidae	1	1
Lotidae	1	1
Gasterosteidae	3	3
Syngnathidae	1	1
Ammodythidae	1	2
Cottidae	3	4
Percidae	3	3
Zoarcidae	1	1
Gobiidae	–	1
Belonidae	1	1
Pleuronectidae	2	2
Lumpenidae	–	1
Liparidae	–	1
Scombridae	–	1
Catostomidae	–	1
Odontobutidae	–	1
Total	63	78

* Family names in this paper are given in Russian.

1789) was dominant among the salmonids. This char was a cosmopolitan species, with a tendency to concentrate in the deepwater part of the lake. In addition to commercial species, Kessler (1868) paid attention to a negative role of two stickleback (*Gasterosteus*) species, which he regarded as exceptionally important. He demonstrated that an increase in the abundance of the three-spine stickleback *Gasterosteus aculeatus* was associated with a synchronous decrease in the abundance of another species, the vendace *Coregonus albula*. The recommendations by Kessler for the increase in the abundance of vendace were to harvest more the stickleback and their use for fat rendering, field fertilization, and production of fish flour for feeding cattle.

Kessler (1868) assigned high priority to the migration of individual fish species from Onega Lake to Ladoga Lake and back via the Svir' River, connecting these lakes. He found that three commercial species—*Vimba vimba*, *Coregonus baerii*, and *Anguilla anguilla*—were active migrants. This was commercially important, since fishermen frequently accompanied the schools of these fishes. Of interest was the fact noticed by Kessler (1868) that the fish species (mainly sterlet *Acipenser ruthenus,* whitefish *Stenodus leucichthys,* and catfish *Silurus glanis*) that escaped from the vessels that conveyed living fish in cages or specialized boats (*soimas*) colonized the lake. Only the catfish succeeded in naturalizing in the southern part of Onega Lake; large individuals of sturgeons and whitefishes were fished by the local population.

The current ichthyofauna of Onega Lake comprises 36–37 species belonging to 15 families (Kudesrkii, 2005; *Bioresursy...,* 2008). The cyprinids are dominant now in the Onega fish community rather than whitefishes; the share of the former is over 35% of the total number of species.

After his travels in the St. Petersburg guberniya, Kessler spent 6 weeks travelling along the Volga River from Tver to Samara in August–September 1869. He collected the material, visited fishponds, fish shops and markets, questioned fishermen, analyzed the communications of assistants, and inferred that the Volga ichthyofauna consisted of 53 species from 18 families (Kessler, 1879; Table 4).

Kessler compared the number of fish species in the Volga River and the faunas of several other large European rivers, such as Dnieper (65 species) and Danube (over 80 species). He (Kessler, 1870) concluded that the Volga ichthyofauna was rather poor; he believed that the main reasons were considerable monotony of the climatic and orographic factors as well as a poorness of the Caspian Sea fauna. Kessler (1870, p. 309) writes in the final paragraph of his work that, although the Volga River is not rich in fish species, this disadvantage of its fauna is compensated for in a sense by the fact that many of its fish species are of a high trade value and are innumerable in its waters; we have only to wish that the important value the Volga River plays in the Russian fishing industry is maintained and, if possible, increased. Unfortunately, the desire of this great scientist was not heard.

EXAMINATION OF ICHTHYOLOGICAL COLLECTIONS AND TAXONOMIC STUDIES

Kessler was elected the dean of the Faculty of Mathematics and Physics, performed the duties of St. Petersburg University rector, and was the Chairman of the St. Petersburg Society of Naturalists; all of this,

Table 3. Composition of the fish and agnathan species in the Onega Lake

Family	Number of species and subspecies		
	Kessler, 1868	Kuderskii, 2005	*Bioresursy...*, 2008
Petromyzontidae	2	2	2
Acipenseridae	2	–	1
Anguillidae	1	1	1
Cyprinidae	13	13	13
Cobitidae	2	1	–
Balitoridae	–	1	1
Siluridae	1	1	1
Esocidae	1	1	1
Osmeridae	1	1	1
Coregonidae	8	2	2
Thymallidae	1	1	1
Salmonidae	4	3	3
Lotidae	1	1	1
Gasterosteidae	2	2	2
Cottidae	2	3	3
Percidae	3	3	3
Total	43	37	36

together with his health problems, prevented Kessler from continuing his fieldwork. However, the vast collections from the Caspian and Aral seas conveyed to him in 1874 and 1876 allowed Kessler to study the ichthyofauna of these water bodies and to compare it with the available data on the Black Sea fish (Bogdanov, 1882). Examination of the specimens brought from the Aral–Caspian expedition and ichthyological collections of St. Petersburg University and Zoological Museum of the Academy of Sciences (now, Zoological Institute of the Russian Academy of Sciences) resulted in the seminal monograph titled *The Fishes Living and Occurring in the Aral–Caspian–Pontic Ichthyological Region,* published in 1877. This monograph contains descriptions of 278 fish species and subspecies belonging to 39 families. In total, 43 new species from seven families were described, namely, one Gasterosteidae species, 18 Gobiidae species, 18 Cyprinidae species, three Salmonidae species, one Balitoridae, one Cobitidae, and one Clupeidae species (Kessler, 1877; Fig. 2).

Kessler (1877) believed that the Aral–Caspian–Pontic ichthyological region began to be established during the pre-Miocene, and it considerably later divided into three autonomous basins—Aral, Black Sea, and Caspian. After these basins had separated, each of them formed its specific fish fauna. The Aral basin had the least number of species (26); however, all species were aboriginal. The largest number of species (130) was observed in the Pontic basin; however, only 45 of them (35%) belonged to the aboriginal ichthyofauna, while 80 species had migrated from the Mediterranean Sea and five or six species migrated from middle European rivers (Kessler, 1877, p. 311). As for the Caspian Sea, 62 fish species were identified

Table 4. Composition of the fish and agnathan species in the Volga River according to Kessler (1870)

Family	Number of species and subspecies
Petromyzontidae	2
Acipenseridae	5
Anguillidae	1
Cyprinidae	26
Cobitidae	1
Balitoridae	2
Siluridae	1
Esocidae	1
Osmeridae	1
Coregonidae	3
Thymallidae	1
Salmonidae	2
Lotidae	1
Gasterosteidae	1
Cottidae	1
Percidae	4
Total	53

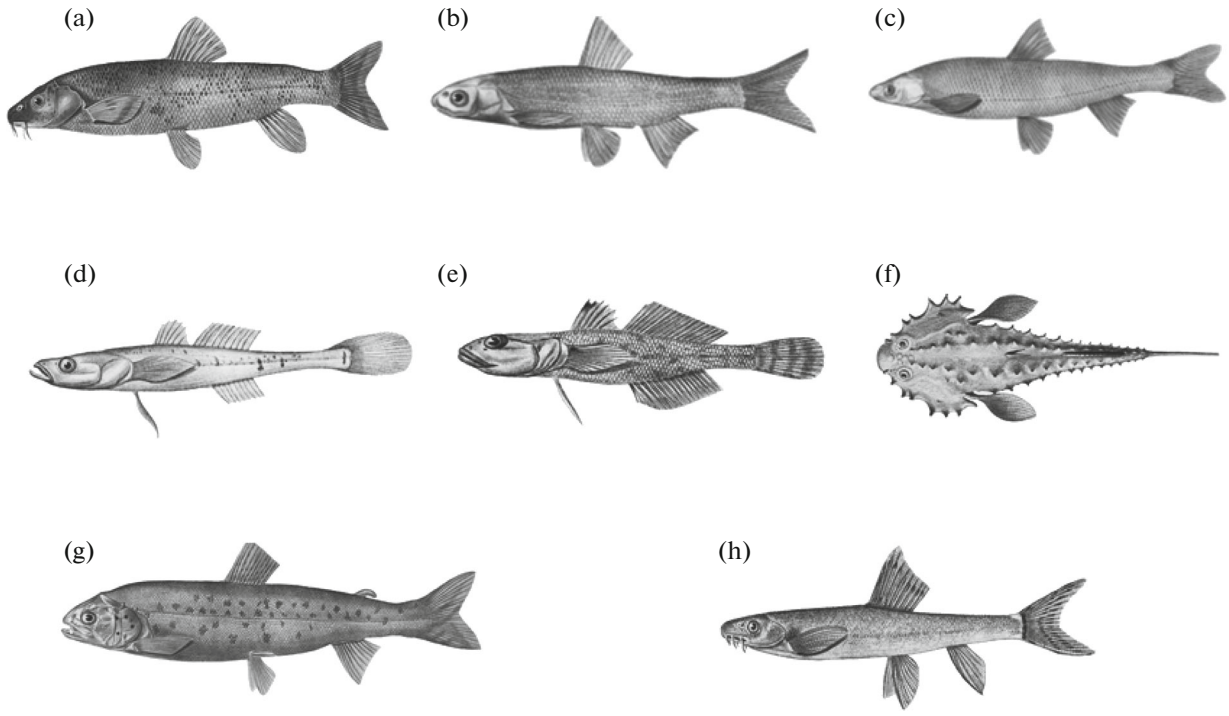

Fig. 2. Some (a–c) Cyprinidae, (d–f) Gobiidae, (g) Salmonidae, and (h) Balitoridae species described by Kessler: (a) *Barbus goktschaicus,* (b) *Chondrostoma cyri,* (c) *C. oxyrhynchum,* (d) *Knipowitschia longecaudata* (=*Gobius longecaudatus*), (e) *Mesogobius nigronotatus* (=*Gobius nigronotatus*), (f) *Benthophilus baeri,* (g) *Salmo ischchan,* and (h) *Oxynoemacheilus brandtii* (=*Nemachilus brandtii*).

and 58 of them were aboriginal, while only four were endemic.

A comparative analysis of the data by Kessler (1877) and the current data on the Caspian and Black Sea ichthyofaunas show the distinct trend of an increase in the number of species in both areas (Table 5). The increase in diversity of the Caspian ichthyofauna, which comprises both the riverine and marine forms, is determined by revision of their taxonomic status as well as by planned introductions, accidental invasions, acclimation activities, and artificial breeding (*Opredelitel'...,* 2013).

As a result of the taxonomic studies of the families rich in species, the number of Clupeidae species and subspecies increased fivefold; Cobitidae species, sixfold; Cyprinidae species, almost threefold; and Gobiidae species, 1.3-fold (Table 5). The Gobiidae family is constantly growing; in particular, a new goby species, *Ponticola iranicus,* was recently described (Vasil'eva et al., 2015) and the validity of another goby species, *Ponticola ilijini,* was restored (Vasil'eva et al., 2016). Both direct and indirect human impacts also have led to the appearance of new nonaboriginal species and subspecies as well as genera and families. In particular, 12 species from five families—Anguillidae (one species), Cyprinidae (seven species), Mugilidae (two species), Poeciliidae (one species), and Gasterosteidae (one species)—have naturalized in the Caspian Sea; four of them are freshwater; four, freshwater semianadromous; two, marine species; one, catadromous; and one, euryhaline species (*Opredelitel'...,* 2013).

Kessler (1877) described 123 species belonging to 38 families in the Black Sea ichthyofauna (except for generatively freshwater fish group), Svetovidov (1964) lists 151 species belonging to 45 families, and Vasil'eva (2007) reports of 180 species from 58 families. The increase in faunal diversity over the last 140 years after Kessler is explained by three main reasons: (1) taxonomic revisions and description of novel species in individual fish groups, (2) mediterranization of the Black Sea, and (3) accidental or planned introduction of new species (Vasil'eva, 2007). The Mediterranean species at the time of Kessler accounted for approximately half of the Black Sea fauna and now they are prevalent.

In 1867–1878, Kessler studied the fish collections sent to him by N.A. Severtsov, A.A. Kushakevich, A.P. Fedchenko, and V.F. Russov from Turkestan (Central Asia); by N.M. Przhevalsky from North China; by G.N. Potanin, I.S. Polyakov, and A.I. Shrenk from Dzungaria (Chinese Altai); and F.F. Brandt from Armenia. Bogdanov (1882, p. 347), the biographer of Kessler, writes that, from the early

1870s, Karl Fedorovich became a monopolist in the ichthyology of Russia and scarcely a fish harvest obtained by the museum of the Academy of Sciences or University missed his hands. The paper by Kessler titled "Ichthyological Fauna of Turkestan" was published in 1872 and the paper "Travel to Turkestan" (in *Zoogeographic Research*) with the section on fishes was published in 1874. These papers describe 18 known and 27 newly discovered fish species of six families (Table 6). The largest number of new species (19 of 31) was discovered in the family Cyprinidae.

Kessler (1876) prepared another section on fishes for the monograph by Przhevalsky named *Mongolia and the Land of Tanguts. Three-year Travel in the Eastern Mountainous Asia*. This study was based on a small fish collection by Przhevalsky in the north part of the Huang He River and Dalai and Kokonor Lakes, comprising 17 species of five families (eight Cyprinidae, one Cobitidae, six Balitoridae, one Siluridae, and one Gasterosteidae). Of them, 13 species and two genera—*Megagobio* (=*Rhinogobio* Bleeker, 1870) and *Diplophysa* (=*Triplophysa* Rendahl, 1933) were described by Kessler (1876) as newly discovered.

In total, the result of Kessler's examination of all collection specimens allowed him to discover and describe 135 new species belonging to 12 families (Eschmeyer, 2016). Currently, 81 of these species are regarded as valid (Table 7). The largest number of newly described species and subspecies (87% of the valid taxa) belong to three families: Cyprinidae (32 species), Nemacheilidae (19), and Gobiidae (16).

CREATION OF ICHTHYOLOGICAL COLLECTIONS

Kessler well understood the value of zoological collections, which he started to create at the Cabinet for Zoology with St. Vladimir Kiev University. He frequently traveled within the Kiev guberniya to sample invertebrates and vertebrates for the collections. In 1844, he rented a boat and sailed from Kiev to Cherkassy with his colleagues to collect fish specimens (Bogdanov, 1882). Most likely, this year should be regarded as the beginning of Kessler's ichthyological studies; he resumed these studies in 1853 after an interruption and continued them to the end of his life. His work titled *Zoological Travel to the Northern Coast of the Black Sea and Crimea* (Kessler, 1861) was supplemented with the list of fish species that he acquired during the trip for the Cabinet for Zoology. This list contained 95 items, mostly marine species; 49 species of them were represented by many individuals aimed "for exchange" (p. 245). Unfortunately, I failed to find out whether Kessler's collections are still retained at Kiev University; according to some data, they were partially lost during World War II. The fish harvests from the St. Petersburg guberniya that Kessler donated to St. Petersburg University have not been found; only the specimens of fishes from Crimea, Upper Volga, and Central Asia that Kessler examined still remain at the Chair of Ichthyology and Hydrobiology, including the *Squalius oxianus* holotype. Regretfully, a complete catalog of Kessler's collection at St. Petersburg University has not been composed, which hinders acquaintance of researchers with these truly priceless specimens.

The major part (82%) of the species and subspecies holotypes described by Kessler is in the ichthyological collection of the Zoological Institute with the Russian Academy of Sciences. In total, 111 specimens of 135

Table 5. Composition of the agnathan and fish species in the Caspian Sea

Family	Number of species and subspecies	
	Kessler, 1877	*Opredelitel'...,* 2013
Petromyzontidae	1	1
Acipenseridae	5	6
Anguillidae	–	1
Clupeidae	4	21
Cyprinidae	14	40
Cobitidae	1	6
Siluridae	1	1
Coregonidae	1	–
Salmonidae	1	1
Esocidae	1	1
Lotidae	1	1
Atherinidae	1	1
Gasterosteidae	1	2
Syngnathidae	1	1
Percidae	3	5
Gobiidae	27	35
Poeciliidae	–	1
Total	62	124

Table 6. Composition of fish species in Turkestan (Kessler, 1872, 1874)

Family	Total number of species	Number of new species
Percidae	3	1
Cottidae	1	1
Siluridae	1	–
Cyprinidae	31	19
Salmonidae	1	1
Esocidae	1	–
Cobitidae	5	4
Acipenseridae	2	1
Total	45	27

Table 7. Valid species described by Kessler (Eschmeyer, 2016)

Modern name	First description	Locality
	Petromizontidae	
Caspiomyzon wagneri	*Petromyzon wagneri* Kessler, 1870	Volga River, Caspian Sea
	Acipenseridae	
Pseudoscaphirhynchus fedtschenkoi	*Scaphirhynchus fedtschenkoi* Kessler, 1872	Syr Darya River, Kazakhstan
Pseudoscaphirhynchus hermanni	*Scaphirhynchus hermanni* Kessler, 1877	Syr Darya River, Uzbekistan
Pseudoscaphirhynchus kaufmanni	*Scaphirhynchus kaufmanni* Kessler, 1877	Amu Darya River, Uzbekistan
	Salmonidae	
Salmo bodschac	*Salmo bodschac* Kessler, 1877	Novo-Bayazet, Sevan basin
Salmo caspius	*Salmo caspius* Kessler, 1877	Kura River
Salmo ischchan	*Salmo ischchan* Kessler, 1877	Sevan Lake
	Thymallidae	
Thymallus brevirostris	*Thymallus brevirostris* Kessler, 1879	Altai, Mongolia
	Coregonidae	
Coregonus baerii	*Coregonus baerii* Kessler, 1864	Ladoga, Volkhov River
	Clupeidae	
Clupeonella grimmi	*Clupeonella grimmi* Kessler 1877	Caspian Sea
	Percidae	
Perca schrenkii	*Perca schrenkii* Kessler 1874	Balkhash Lake
	Gasterosteidae	
Pungitius platygaster	*Gasterosteus platygaster* Kessler, 1859	Dnieper River
Pungitius stenurus	*Gasterosteus stenurus* Kessler, 1876	Dalai Lake, Mongolia and China
	Cyprinidae	
Alburnus filippii	*Alburnus filippii* Kessler, 1877	Kura River, Tbilisi
Alburnus hohenackeri	*Alburnus hohenackeri* Kessler, 1877	Karabakh, Azerbaijan
Alburnoides maculatus	*Alburnus maculatus* Kessler, 1859	Salgir River, Crimea
Alburnoides taeniatus	*Alburnus taeniatus* Kessler, 1874	Syr Darya River, Turkey
Aspiolucius esocinus	*Aspius esocinus* Kessler, 1874	Syr Darya and Amu Darya Rivers; Kuma Rivers near Georgievsk
Barbus ciscaucasicus	*Barbus ciscaucasicus* Kessler, 1877	Kuma Rivers near Georgievsk
Barbus goktschaicus	*Barbus goktschaicus* Kessler, 1877	Sevan Lake
Barbus tauricus	*Barbus tauricus* Kessler, 1877	Salgir River, Crimea
Capoeta buhsei	*Capoeta buhsei* Kessler, 1877	Namak Lake, Iran
Capoeta platylepida	*Capoeta steindachneri* var. *platylepida* Kessler, 1872	Zeravshan River, Uzbekistan
Capoetobrama kuschakewitschi	*Acanthobrama kuschakewitschi* Kessler, 1872	City of Khujand
Chondrostoma cyri	*Chondrostoma cyri* Kessler, 1877	Kura River, Georgia
Chondrostoma oxyrhynchum	*Chondrostoma oxyrhynchum* Kessler, 1877	Kuma River, Georgievsk
Diptychus sewerzowi	*Diptychus sewerzowi* Kessler, 1872	Aksai River, China
Gobio lepidolaemus	*Gobio lepidolaemus* Kessler, 1872	Zeravshan River, Uzbekistan
Gymnodiptychus dybowskii	*Diptychus dybowskii* Kessler, 1874	Aksu River, Turkey
Gymnocypris przewalskii	*Schizopygopsis przewalskii* Kessler, 1876	Kukunor Lake, China
Leuciscus danilewskii	*Squalius danilewskii* Kessler, 1877	Azov Sea
Leuciscus chuanchicus	*Squalius chuanchicus* Kessler, 1876	Huang He River, China

Table 7. (Contd.)

Modern name	First description	Locality
Oreoleuciscus potanini	*Chondrostoma potanini* Kessler, 1879	Dayan Lake, Mongolia
Petroleuciscus squaliusculus	*Squalius squaliusculus* Kessler, 1872	Syr Darya River, Tajikistan
Phoxinus poljakowii	*Phoxinus poljakowii* Kessler, 1879	Balkhash Lake, Kazakhstan
Rhinogobio nasutus	*Megagobio nasutus* Kessler, 1876	Huang He River, China
Schizothorax anisolepidus	*Schizothorax eurystomus* var. *anisolepida* Kessler, 1872	Urgut River, Uzbekistan
Schizothorax argentatus	*Schizothorax argentatus* Kessler, 1874	Urzhar River and Alakol Lake
Schizothorax eurystomus	*Schizothorax eurystomus* Kessler, 1872	Samarkand
Schizothorax fedtschenkoi	*Schizothorax fedtschenkoi* Kessler, 1887	Zeravshan River, Uzbekistan
Schizothorax pelzami	*Schizothorax pelzami* Kessler, 1870	Shah Rud River, Iran
Schizopygopsis pylzovi	*Schizopygopsis pylzovi* Kessler, 1876	Gansu province, China
Squalius borysthenicus	*Squalius borysthenicus* Kessler, 1859	Dnieper River, Ukraine
	Nemacheilidae	
Labiatophysa microphthalma	*Diplophysa microphthalma* Kessler, 1879	Cham River, China
Labiatophysa nasalis	*Diplophysa nasalis* Kessler, 1876	Dalai Lake, China
Lefua costata	*Diplophysa costata* Kessler, 1876	Dalai Lake, Mongolia
Qinghaichthys zaidamensis	*Nemachilus zaidamensis* Kessler, 1876	Tsaidam region, China
Oxynoemacheilus oxianus	*Nemacheilus brandtii* var. *oxiana* Kessler, 1877	Amu Darya River, Uzbekistan
Oxynoemacheilus brandtii	*Nemachilus brandtii* Kessler, 1877	Kura River, Tbilisi
Paracobitis longicauda	*Cobitis longicauda* Kessler, 1872	Akdarya River, Uzbekistan
Triplophysa dalaica	*Diplophysa dalaica* Kessler, 1876	Dalai Lake, China
Triplophysa dorsalis	*Cobitis dorsalis* Kessler, 1872	Syr Darya River, Tajikistan
Triplophysa dorsonotatus	*Nemachilus dorsonotatus* Kessler, 1879	Ili River basin, Kazakhstan
Triplophysa elegans	*Cobitis elegans* Kessler, 1874	Salar River, Tashkent
Triplophysa intermedia	*Diplophysa intermedia* Kessler, 1876	Dalai Lake, China
Triplophysa kungessana	*Diplophysa kungessana* Kessler, 1879	Ili River basin, Kazakhstan
Triplophysa labiata	*Diplophysa labiata* Kessler, 1874	Urzhar River, Kyrgyzstan
Triplophysa papillosolabiata	*Diplophysa papillosolabiata* Kessler, 1879	Tarim River, China
Triplophysa robusta	*Nemachilus robustus* Kessler, 1876	Gansu Province, China
Triplophysa strauchii	*Diplophysa strauchii* Kessler, 1874	Balkhash Lake
Triplophysa uranoscopus	*Cobitis uranoscopus* Kessler, 1872	Iskanderkul Lake
	Gobiidae	
Benthophilus baeri	*Benthophilus baeri* Kessler, 1877	Caspian Sea
Benthophilus ctenolepidus	*Benthophilus ctenolepidus* Kessler, 1877	Caspian Sea, Baku
Benthophilus granulosus	*Benthophilus granulosus* Kessler, 1877	Baku, Azerbaijan
Benthophilus grimmi	*Benthophilus grimmi* Kessler, 1877	Caspian Sea
Benthophilus leptocephalus	*Benthophilus leptocephalus* Kessler, 1877	South of Caspian Sea
Benthophilus spinosus	*Benthophilus spinosus* Kessler, 1877	Caspian Sea
Caspiosoma caspium	*Gobiosoma caspium* Kessler, 1877	Caspian Sea
Knipowitschia longecaudata	*Gobius longecaudatus* Kessler, 1877	Caspian Sea
Mesogobius nigronotatus	*Gobius nigronotatus* Kessler, 1877	Caspian Sea, Kazakhstan
Ponticola bathybius	*Gobius bathybius* Kessler, 1877	Caspian Sea, Baku
Ponticola cyrius	*Gobius cyrius* Kessler, 1874	Kura River, Borjomi

Table 7. (Contd.)

Modern name	First description	Locality
Ponticola eurycephalus	*Gobius eurycephalus* Kessler, 1874	Kerch, Crimea
Ponticola goebelii	*Gobius goebelii* Kessler, 1874	Baku, Azerbaijan
Ponticola gymnotrachelus	*Gobius gymnotrachelus* Kessler, 1877	Dniester River, Ukraine
	Cottidae	
Cottus sibiricus	*Cottus sibiricus* Kessler, 1889	Yenisei River, Minusinsk
Cottus spinulosus	*Cottus spinulosus* Kessler, 1872	Syr Darya River, Tajikistan

Kessler's species and subspecies have been carefully preserved despite the violent social storms and wars undergone by this country over 140 years.

FISH SPECIES NAMED AFTER KESSLER

The contribution of Kessler to ichthyology was highly estimated not only by his students and colleagues but also by his followers. Bogdanov (1882, p. 351), a student of Kessler, concluded the biography of his teacher with the following words: "Your name will be everlasting in Russian science, which you advanced towards infinite and self-consistent development." One genus (*Kessleria* Bogdanov, 1882) as well as 30 species and subspecies were named after Kessler (Eschmeyer, 2016). Currently, 14 following species and subspecies remain valid: *Ponticola kessleri* (Günther, 1861), *Romanogobio kesslerii* (Dybowski, 1862), *Barbus kessleri* (Steindachner, 1866), *Leocottus kesslerii* (Dybowski, 1874), *Notarius kessleri* (Steindachner, 1876), *Hexanematichthys kessleri* (Steindachner, 1876), *Alosa kessleri* (Grimm, 1887), *Erythrinus kessleri* (Steindachner, 1877), *Paraschistura kessleri* (Günther, 1889), *Schizopygopsis kessleri* (Herzenstein, 1891), *Lethenteron kessleri* (Anikin, 1905), *Arnoglossus kessleri* (Schmidt, 1915), *Benthophilus kessleri* (Berg, 1927), and *Schizothorax intermedius kessleri* (Turdakov, 1968).

CONCLUSIONS

Karl Fedorovich Kessler significantly contributed to two large areas in ichthyology: freshwater and marine fish systematics and faunal research. He described 135 novel species and subspecies as well as four genera (*Clupeonella, Diplophysa, Megagobio,* and *Pseudodon*). Most of the new species (59) described by Kessler belong to the family Cyprinidae. Cyprinids of North Eurasia and America were very intensively studied at the time when Kessler lived and worked. By 1882, over 1770 Cyprinidae species and subspecies had been described (Eschmeyer, 2016). The contribution of Kessler to the species diversity of cyprinids accounted for 3.3%; he described 38 Gobiidae species and subspecies, which accounts for 6.0% of the known Gobiidae taxa. The contribution of Kessler's studies to the research into Nemacheilidae fish (earlier included into the family Cobitidae) is still underestimated: he described 18 species (53%) of the 34 species and subspecies known before 1882.

Kessler conducted his faunal studies in large water bodies, such as the Black, Caspian, and Aral seas; Dnieper and Volga rivers, Onega and Pskov lakes; estuaries; and a multitude of rivers and brooks. He was interested in taxonomic diversity, external structure, life style, distribution, migrations, behavior, and reproduction as well as the economic use, fishing gear, fishponds, and many other issues associated with comprehensive studies of fishes. He actively spread his knowledge in the Society of Naturalists, which he organized, at conferences of teachers, and among his students. Some works conducted by Kessler, such as *The Fishes of the St. Petersburg Guberniya,* have not been so far repeated in full.

Karl Fedorovich created and considerably expanded scientific zoological collections of Kiev and St. Petersburg Universities as well as supplemented the ichthyological collection of the Zoological Museum, now the Zoological Institute of the Russian Academy of Sciences, with holotypes.

Scientific freedom, humanity, diligence, and moral purity, noticed by everyone who knew him, were characteristic of Kessler along with his scientific achievements. He deserves the recognition and grateful acknowledgment of all who are interested in the fishes of Russia and other countries that once were its part or adjacent to it. L.S. Berg (1917), a well-known ichthyologist, with good reason regarded Kessler, his predecessor, as the father of Russian ichthyology.

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