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Review

Sergey Ivanovitch Ognev and the formation of theriology in Russia

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Abstract

Sergey I. Ognev (1886–1951), one of Russia's most famous biologists, was both a theoretical scientist and a great field researcher. Ognev's "Fauna Mosquensis" (1913) is the most comprehensive study of the mammals of European Russia after Pallas. Throughout his life, Ognev's work involved two important components: biological observation in nature and study of geographical distribution. His combination of excellent knowledge of natural habitats and morphology created a unique insight. This effort resulted in seven volumes of "Mammals of Eastern Europe and Northern Asia" and "Mammals of the USSR and Adjacent Countries," published from 1928 to 1950. This work included comprehensive taxonomic accounts, detailed morphological descriptions, geographical ranges and natural history data for 264 mammalian species and 635 forms. 4879 pages were illustrated, including almost 2000 photographs and drawings of skulls and dentition, a huge number of distributional maps made by the author and 56 color figures drawn by famous animal painters. The taxonomic position of a surprisingly large portion of forms classified by Ognev have been confirmed by modern molecular genetic approaches. Ognev also authored significant books on ecology and field photography. It is impossible to overestimate the significance of Ognev's contribution to mammal studies; his "Mammals of the USSR…" volumes remain one of the most cited works in the field.

Keywords: European fauna; history of mammalogy; mammalian systematics.

By the beginning of the 20th century, because of such as P. Pallas, J.F. Brandt, N.A. Severtzov, N.M. Przhevalsky, A. Middendorff, P.P. Semenov-Tyan-Shansky and others, substantial knowledge had been accumulated on the mammals of Europe and various regions of Asia. However, these descriptive studies were not systematic. The 1910 and 1912 works by E. Trouessart and G. Miller were among the first to change the approach to mammalogy (Denys et al. 2012). During this period and in subsequent years, Sergey Ivanovitch Ognev became known as one of the founders of Russian mammalogy (Figure 1) and left a legacy as one of the world's prominent mammalogists. Ognev was best known for his multi-volume monograph "The Mammals of USSR and Adjacent Countries," the desk companion for many generations of zoologists.

Early years

Ognev was born in Moscow on November 5, 1886 into an old family of Muscovites. His father, Professor Ivan Florovitch Ognev, was a renowned histologist, one of the founders of the Moscow school of histology and the founder of the Department of Histology and Medicine at Moscow University (later to become the First Medical Institute). Sergey's mother, Sophia Ivanovna Ogneva, was a daughter of the passionate naturalist I.N. Kireevsky, scion of the ancient noble Kireevsky family, and was related to the famous slavophile I.V. Kireevsky, a philosopher and friend to prominent Russian philosophers S. Aksakov, N. Stankevitch and T. Granovsky. Sophia had a huge influence on her three sons (of whom Sergey was the second). His elder brother Alexander became a philosopher and an associate professor at Moscow University and was deeply interested in natural sciences.

The Ognev family was closely linked with Moscow University through their many relatives, friends and acquaintances. These ties must have influenced the early development of Sergey's scientific interests. His love of nature also had roots in his family. Like G. Miller (Dunnum and Cook 2012), Ognev was from childhood a committed bird-watcher. While in gymnasium, he met the renowned ornithologist M. Menzbir, and this lasting acquaintance largely determined the direction and style of Ognev's research. In 1905, Ognev graduated from gymnasium and entered the branch of

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Figure 1 S.I. Ognev in the 1930s.

natural sciences at the School for Physics and Mathematics at Moscow University.

Another major influence was Professor G. Kozhevnikov, a zoologist specialized in invertebrates who headed the Department of Zoology. Ognev graduated from university in 1910 with a first-degree diploma and candidate's degree and was offered a position "for preparation for the professor's degree" in the Department of Zoology. Importantly, the zoological museum, also headed by G. Kozhevnikov, was then part of the Department (it did not become a stand-alone museum until many years later). This not only provided better education for the students, but also allowed the professors to study and to extend the museum's collections. Ognev became an assistant in the museum in 1914 and was appointed the Scientist Keeper of the Repositories in 1917. He taught zoology, including lab studies, in Flyorov's gymnasium beginning in 1911 and started courses on vertebrate biology and ornithology in 1920. Ognev taught the course on vertebrate zoology at Moscow University, Lenin's Pedagogical Institute and the Moscow Pedagogical Institute (with few interruptions) until the last year of his life. He was a department head in the latter two schools. He supervised undergraduate and graduate students at Moscow University and researchers from many institutes elsewhere in the USSR.

First works

Ognev had an early start in his scientific career. His first paper was published in the *Anatomischer Anzeiger* in 1906 when he was a sophomore. That work was not on mammals; it was a description of a case of hermaphroditism in the frog species *Rana temporaria*. Among his first papers, there are also works in histology, possibly tutored by Ognev's father, a renowned histologist. The solidity and thoroughness characteristic of all Ognev's works can already be seen in his first papers. It was some time before mammals became the main object of Ognev's studies; he produced faunistic works [e.g., "Materials for Ornithofauna of the Smolensk Province (1909)" and similar work on the Moscow Province (1916a), taxonomic works (identification of a new warbler species *Sylvia caucasica* (Ognev and Bankovsky 1910), and works on bird songs and on their imitation ability (1911)]. He also published popular works, such as "The Biology of Our Birds" (1938).

In 1906, Ognev actively joined the effort by the Commission on Research of Fauna of Moscow Province organized by A. Bogdanov. Ognev started systematic research and large-scale collection of mammals, thus founding his enormous collection (>7000 specimens), which was later donated to the zoological museum. This effort resulted in "The Mammals of the Moscow district," a book that brought its author the first of multiple awards for his research. It motivated many young zoologists, future students of Ognev, to take up mammalogy; many of them, including S. Turov, W. Heptner, A. Formozov, L. Portenko, I. Volchanetsky, L. Boeme, S. Stroganov, A. Kuzyakin, A. Tomilin and others, later became prominent scientists in their own right. Ognev wrote an explanatory text for the Mammalian Systematics section of the Tables on Zoology (1915), a zoology textbook for secondary schools (5 eds.) and a vertebrate zoology textbook for high schools (4 eds.). In 1926, Ognev became an associate professor and, in 1928, a full professor. In 1935, Ognev was awarded a doctoral degree, bypassing the usual procedure of defending his doctoral thesis. His work was recognized with multiple prizes awarded by a variety of institutions, scientific societies and by the state. Awards included two Stalin prizes (in 1942 and 1950), which were the highest awards in science and art in the Soviet Union. He also received the title of Distinguished Scientist, and the Order of Lenin.

Broadness of interests was characteristic of Ognev; instead of limiting himself to the study of individual groups of mammals, he tried to see the entire picture and was interested in general questions of biology, such as evolution, biogeography and the definition of species. At the beginning of the 20th century, the concept of species was vague; no formal criteria existed for distinguishing intraspecific variation and species-specific characteristics. Descriptions of different forms of variation started to appear, with special attention given to geographic variation, considered by some "a preliminary stage of speciation" (Dementyev 1952). The increasing volume of information that could not be structured efficiently led to a chaotic period in taxonomy. In his early papers, Ognev used the theoretical work by Semenov-Tyan-Shansky "Taxonomical boundaries of a species and lower taxa" (1910). Later, he established his own views on the concept of species, which were published in a series of works: "The Value of Taxonomy for Systematic Studies" (1942), "The Issue of Species in View of the Latest Data" (1944a) and "Species, Subspecies, and Current Problems of Systematics" (1947a).

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Detailed diagnosis of a species established by Ognev accounted for the continuous evolution of a species, its morphological uniqueness, genetic specificity, physiological isolation and geographic separation. He stressed the relativity of each criterion in isolation and the necessity, whenever possible, of using multiple traits (morphological, ecological, genetic, etc.) in a diagnosis of a species. Therefore, his understanding of the nature of species was broader than in some contemporary concepts. In addition, Ognev paid attention to behavioral peculiarities that could function as reproductive barriers; his views here predated the arrival of the "recognition species concept." The gradual evolution of Ognev's understanding of the complexity of species was reflected in his work on systematics. In later works, his taxonomic descriptions become deeper and more extensive.

Ognev wrote almost 200 scientific publications. His first major work, "The Mammals of the Moscow District" ("Fauna Mosquensis Part I: Chiroptera, Insectivora, Rodentia," 1913) was the most comprehensive study of mammals of European Russia after P.S. Pallas (1811, 1831) and E.L. Trouessart (1910). In the preface to the first volume (1928) of the main work of his life, a multi-volume series "The Mammals of Eastern Europe and Northern Asia" later re-named as "The Mammals of USSR and Adjacent Countries," Ognev remarked that the survey by P.S. Pallas (1811, 1831), published after the death of the author, was at that time (i.e., mid-19th century) the most comprehensive collection of the current knowledge. In 1851, a review by Yu.I. Simashko, "Mammals," was published but was also only of historic value. Without a doubt, works by I. Brandt, A. Middendorf, E. Eversmann, L. Shrenk, K. Kessler and K. Satunin made enormous contributions to the studies of faunas of individual regions and specific taxonomic groups. Ognev also cited multiple works by N. Kastshchenko on mammals of Western Siberia, including "Key to Mammals of the Tomsk Province" (Kastshchenko 1900) and acknowledged studies of specific groups, such as "Survey of Russian Pinnipeds" by N. Smirnov (1908), "Geographic Distribution of Wild Sheep of the Old World" by N. Nasonov (1924) and "Rodents of European USSR" by B. Vinogradov (1926).

Ognev possessed an excellent library (>9000 items), which he had collected over the course of his life. It included the library of F. Brandt, a well-known zoologist and the director of the Zoological Museum of the Academy of Sciences, and of E. Bikhner, a keeper of that museum. Ognev sent his works to multiple foreign libraries, museums and societies, such the American Museum of Natural History, the Smithsonian Institution, Oxford University, the Zoological Society of London, the American Society of Mammologists (of which he was a member from 1924), Museum Alexander Koenig and others, and he received specimens from these institutions. Outstanding books by E.L. Trouessart (1910) and G. Miller (1912) were in his library. Ognev and G. Miller had a private correspondence that spanned decades. The broadness of Ognev's knowledge and his ability to thoroughly analyze enormous datasets amazed his contemporaries. Most of the specimens in the collections of the Zoological Museum of Moscow University that Ognev donated were collected by Ognev personally, although some were sent to him by his numerous correspondents. In addition, Ognev thoroughly studied zoological collections of other museums. In the introduction to each volume of "The Mammals," he meticulously listed all the collections of museums and individuals that he had studied and the names of all those who had helped him collect samples for these groups.

Ognev was not just a bench scientist; he was also a superb field researcher. His observations of habitats, behavior, peculiarities of biology and photography of animals, burrows, nesting sites, etc. were an invaluable material for analysis.

The mammals

"Fauna Mosquensis" (1913) was the first systematic survey of the mammals of Russia. It had no equal in its volume (over 3000 specimens) and represented the first example of serial collecting of small mammals. Following this work, Ognev (Figure 2) published a large number of regional surveys on mammals: Primorye (1914a), Taurida Province (1916), Woronezh Province (1923), Caucasus (1924, 1926b), Samara Province and the Ural Region (1925a), North-Eastern Siberia (1926a), Turkestan (Ognev and Heptner 1928, Ognev 1929a), Shantar Islands (1929b), Central Tian Shan (1940a) and Anadyr Region (1941). Many papers devoted to different mammalian groups were published in various foreign journals, for example, systematic notes on carnivores, rodents, insectivores, and bats (Ognev and Vorobiev 1923, Ognev 1925b,c, 1926c,d, 1927a,b, 1933). Regional surveys were a necessary stage for preparation of Ognev's monumental monograph – "The Mammals of USSR and Adjacent Countries" (Ognev

Figure 2 S.I. Ognev in 1914.

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1928, 1931, 1940b, 1947b, 1948, 1950). Ognev handwrote his texts directly, totaling almost 5000 print pages, as clean copies without any prior drafts. The monograph includes tens of maps and hundreds of figures. They are based on an enormous volume of data – many thousands of processed skins and skulls and hours and hours of field observations. A total of eight volumes of the monograph were published; seven of them, dealing with insectivores and chiropterans, carnivores, lagomorphs, and rodents (except murids and cricetids, which remained unprocessed), were written by Ognev. The eighth volume on cetaceans (published in 1957 and numbered IX to account for the unfinished last volume on rodents, which was supposed to be number VIII) was written upon Ognev's request by A.G. Tomilin, one of the best specialists in marine mammals (Tomilin 1957). The monograph was translated into English by the Israel Program for Scientific Translations and published for the Smithsonian Institution and the National Science Foundation in Washington, D.C., U.S.A. (Ognev 1962a,b,c, 1963a,b, 1964, 1966).

The manuscript of the first volume of Ognev's monograph, with data on insectivores and chiropterans, was fully ready for publication in 1922. However, due to its large volume and unforeseen financial difficulties, its publication was delayed, and the volume was published under the name "The Mammals of Eastern Europe and Northern Asia" in 1928. Among the difficulties associated with Ognev's combined use of old and contemporary material was collation of the geographic positions of sample collection points. No devices for geographic positioning were then available; names of nearby villages had to be used for this purpose, and those changed with time. Ognev also discussed the problem of priority in nomenclature; he thoroughly collected all the synonyms for all the names of genera and species and listed them next to the names of the taxa.

In the preface to the first volume, Ognev proposed a new term, "theriology," to replace the (in his view) "unmusical" terms "mammalogy" and "mammaliology." However, in most countries, this new term never became broadly accepted.

Ognev believed that drawings of animals were of major scientific value; he specifically noted this in the preface to the first volume. He insisted that a narrative description does not always fully render the peculiarities of morphology and that a drawing is much more precise and vivid. The monograph included a total of 1992 black and white drawings by A. Formozov, A. Komarov and K. Flyorov; additional drawings were done with a camera lucida by T. Timofeeva, S. Kostylyov and Ognev himself. Remarkable color drawings (for a total of 56 tables) were produced by the brilliant animalists V. Vatagin (Figure 3), A. Formozov, N. Kondakov and K. Flyorov.

Figure 3 Russian desman *Desmana moschata* by V.A. Vatagin, published in Ognev (1928).

Ognev specifically noted the importance of studying series of samples, especially for highly variable morphological traits, such as teeth of rodents. He paid special attention to variation, distinguished the types of variation and provided drawings for such morphotypes. He stressed that, in the analysis of skulls, age variation and sexual dimorphism are important. He also claimed traits such as structure of genitalia or of auditory ossicles to be of special interest as they can provide important taxonomic differences. He provided many pictures of soft tissues: structures of nostrils, ears, paws and distribution of vibrissae. More than once, he discussed the difficulties associated with the description of color standards and the need for standards of coloration.

Ognev paid special attention to description of analyses and, specifically, to the methods of measurement. He described in detail his standards for cranial parameters, overall, basal, condylobasal lengths, height, interorbital width, etc., as well as the parameters of other measurements such as body length, tail length, etc. In some cases, to make explanations more vivid and precise, schematic drawings of measurements were given. Tables with results of measurements were provided in all volumes. Importantly, all measurements were linked to their particular specimens and collection location through museum catalogue numbers. This allowed for reevaluation of his work by future researchers. The volume of the material processed was gigantic; for example, in the introduction to Volume VII (devoted to voles), Ognev mentioned that he had analyzed over 15,000 individual voles.

In the introduction to the second volume, Ognev gave a corrected (fixing some errata in the first volume) and more modern classification of mammals. The second volume was much lengthier than the first. Ognev explained that this was because it dealt with carnivores, and, because they include many species that are hunted for furs, it was necessary to go through old publications by hunters to extract valuable historic information and to compare that information with the current observations. In addition to a detailed survey of systematics and taxonomy, Ognev thus obtained much information on carnivore behavior.

The first two volumes were published under the title "The Mammals of Eastern Europe and Northern Asia", whereas subsequent volumes were titled "The Mammals of the USSR and Adjacent Countries." The third volume completed the survey of mustelids and gave descriptions of felines and pinnipeds. Most of the drawings there were original, although a small fraction were borrowed from several rare publications, including J. Allen's "History of North American Pinnipeds" (1880). Ognev utilized a huge number of sources. Collections of many museums and data were provided by N. Smirnov, S. Freiman, W. Heptner, V. Stakhanov, and L. Belopolsky.

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Rodents are the subject of volumes IV–VII (Ognev 1940b, 1947b, 1948, 1950). Volume IV begins this extensive subject and is devoted to a portion of the rodent and lagomorphs orders, which he called Glires following the proposal of Linnaeus (1758). His own vision of classification was consistent with the current systematics based on molecular data and chromosome painting (Bininda-Emonds et al. 2007, Meredith et al. 2011). As Ognev stated in the preface, some of the surveys were very lengthy due to the fact that they included data obtained from his own material, a large number of collections, literature on systematics and zoogeography and, of special note, of biological literature. Indeed, the sections devoted to descriptions of the best-studied species, such as squirrels, ground squirrels and hares, were very long – approximately 50 pages each. With his typical humor, Ognev notes that he "doesn't expect the readers to be annoyed by this fact." For example, discussing the distribution of *Lepus europeus* according to different sources, Ognev (1940b, pp. 140–1) claimed that E.L. Trouessart (1910) was right in pointing to Poland as the *terra typica* for this species. Ognev endeavored to make his survey "as complete as possible," and by all accounts succeeded in this.

Importantly, starting with the fourth volume, Ognev makes the main description ("centre") species-specific; the subspecies are differentiated separately. Volume IV was followed by a long break due to World War II, which affected the publication, but not the writing, of "The Mammals." Ognev kept working ceaselessly, often late at night, through the hungry and cold years of war (Figure 4). Volume V, which finished the survey of squirrels and included surveys of beavers, dormice and spalacids, was ready for print by the time the war was over and was published in 1947. Volume VI (jerboas and, partially, voles) was published in 1948. Volume VII, entirely devoted to voles, appeared in 1950. Volume VIII remained unfinished due to Ognev's sudden death on December 20, 1951.

Figure 4 S.I. Ognev at his office in the Zoological Museum of Moscow University on February 4, 1942.
On this day, two months after the beginning of the Soviet counter-offensive after the Battle of Moscow and still years from the end of the war, classes at the School for Biology resumed in Moscow. Photo by D. Vyazhlinsky.

In the introduction to Volume VI, Ognev wrote that he planned to prepare five volumes on rodents; the planned overall volume of the monograph was 12 volumes. Unfortunately, only seven volumes were ever published.

In total, the multi-volume monograph contains surveys of morphology, geographic distribution and biology for 264 species and 635 forms. Ognev described 167 forms of mammals as species or subspecies. The current survey "Mammal Species of the World, Third Edition" (Wilson and Reeder 2005) lists Ognev's authorship of 3 genera, 12 species and 42 subspecies. Notably, some of the species distinguished by Ognev have been confirmed genetically; this includes *Sorex (Sorex) satunini* Ognev, 1922; *Sicista severtzovi* Ognev, 1935; *Dicrostonyx vinogradovi* Ognev, 1948 and others. Ognev's foresight as a taxonomist was probably largely based on his enormous experience.

Ognev was often criticized for being a splitter. However, in the process of initial accumulation and systematization of data on mammals of the enormous territory of the USSR, it was important to cover their ranges as broadly as possible and to pinpoint the differences between the geographic forms. Ognev is known to have been interested in advances in population genetics, which were then only emerging. One of the famous Russian biologists, Nikolai Timofeeff-Ressovsky, was Ognev's student at Flyorov's Gymnasium. Years later, they participated together in fieldwork in the Smolensk, Moscow and Tver provinces and in Central Asia and kept up a correspondence for many years. All this indirectly influenced the formation of the population-level approach in the Russian biology.

The monograph was widely accepted and acknowledged both in Russia and abroad. Without a doubt, it is one of the best examples of mammalogical studies; its arrival inspired the development of mammalogy in Russia and predetermined its success for many years. This thorough analysis and revision of mammals from a common methodological position by a single person is nearly unprecedented in the world of zoology.

Other contributions

Ognev deeply loved nature. He organized and participated in numerous long-term field expeditions to remote areas; he also often went on short trips and hunting. Field observations allowed him to better understand and describe the ecological peculiarities of various groups and the specifics of a range of biotopes. This was reflected in all of his publications. His richly illustrated book "Surveys of Mammalian Ecology" (1951) was largely the result of his own observations.

Ognev was also an avid photographer. He authored "Photography in Nature," the first Russian manual on wildlife photography, which went through three editions (1926e, 1938 and 1949). It is hard to imagine the amount of patience and effort that went into the amazing photographs in "Mammals". Despite the very cumbersome and inconvenient equipment available at the time, Ognev managed to take photos of extremely wary animals in the wild, such as his "Singing of Pikas" series and the photos of leverets in the nest (Volume I).

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Figure 5 S.I. Ognev in 1950, shortly before his death.

Two other books of Ognev are also of special notice: "The Life of the Forest" (six editions, 1914b, 1925, 1940, 1948, 1950 and 1962) and "The Life of Steppes" (two editions, 1927c and 1951). As A. Formozov vividly put it in the preface to the sixth edition of the "The Life of the Forest," "It seemed that its pages were alive with the fresh wind of blooming meadows, green forest openings, and bird songs could reach one's ear through a window wide open…" This book filled the enormous gap in the popular scientific literature that existed in post-revolutionary Russia.

Ognev authored biographies of many eminent Russian biologists: N. Severtsov, B. Zhitkov, A. Semenov-Tyan-Shansky, G. Kozhevnikov, and M. Menzbir. He also wrote a very interesting book entitled "Ivan Florovitch Ognev. Excerpts from Life of the Moscow University and Moscow Intelligentsia of the Late XIX and Early XX century" (Ognev 1944b). This work was based on the author's memories, not just of his father, but also of his colleagues and friends – prominent Russian scientists and intellectuals. This book had a most dramatic history: the second, updated edition was published in 1948, but all copies were destroyed as a result of the infamous 1948 session of the All-Union Academy of Agricultural Sciences, which effectively banned all "bourgeois idealistic" science. Only a few copies were saved by the author's family.

Ognev gave much attention to the issues of environmental protection; he worked in several nature reserves, participated in the governmental commission on reserves and initiated the creation of the Astrakhan Nature Reserve.

Ognev had a huge impact as a role model. People of all ages, and especially the young, were attracted by his talent, by the power of his scientific thought and also by the personal charm of a man of exceptional kindness and generosity (Figure 5). The extensive scientific school of Ognev was also the extensive circle of his friends.

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