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The great Empire's malacologist: Alexander von Middendorff's contribution to the study of molluscs

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ABSTRACT. The contribution to malacology made by the eminent Russian scientist and traveler, Alexander Theodor von Middendorff (1815–1894) is reviewed. Middendorff's research is rightly considered the highest achievement of Russian malacology in the 19th century. It is shown, despite the relatively short timespan of his malacological activity, Middendorff could reach substantial progress in the knowledge of the Russian malafauna, both marine, and continental, and authored more than 15 malacological publications, including a series of fundamental systematic works. Middendorff's views on taxonomy, variability, and zoogeography of molluscs are discussed, and the research program in malacology, proposed by him, is reviewed as well as the impact of his studies on the further development of malacology in the Russian Empire. The full list of all molluscan taxa described by Middendorff is provided as an "Appendix" to the article.

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Малаколог великой Империи: вклад Александра фон Миддендорфа в исследование моллюсков

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РЕЗЮМЕ. В статье рассматривается вклад в малакологию, сделанный выдающимся российским исследователем и путешественником Александром фон Миддендорфом (1815–1894). Его работы о моллюсках по праву считаются наивысшим достижением российской малакологии 19-го века. Несмотря на сравнительно короткий период научной активности в этой области, Миддендорф смог добиться большого прогресса в изучении малакофауны России, как морской, так и континентальной, и опубликовал более 15 работ по малакологии, включая ряд фундаментальных таксономических монографий. Рассмотрены взгляды Миддендорфа на систематику, изменчивость и зоогеографию моллюсков, а также проанализирована разработанная им исследовательская программа по развитию малакологии в России. В приложении к статье дан полный перечень таксонов моллюсков, описанных Миддендорфом.

Introduction

Alexander Theodor (In Russian, Александр Федорович) von Middendorff (1815–1894) was one the most eminent naturalists of the 19th century Russian Empire. He made substantial contributions to various branches of science, and his scientific interests varied from systematic zoology to ethnography and meteorology. One cannot name him a zoologist *par excellence*; similarly to other prominent naturalists of the day (Alexander von Humboldt, Karl Ernst von Baer, Charles Darwin), Middendorff was a widely educated polymath able to conduct research in a variety of scientific disciplines. However, his zoological works constitute one of the most important parts of his scientific legacy. Born in St. Petersburg, in a Baltic German family, Middendorff (Fig. 1) was a Russian citizen of German origin belonging to the so-called "Ostsee noblemen", a social group, from which many prominent naturalists (K. von Baer, K. von Eichwald, A. von Keyserling, Ch. Pander, L. von Schrenck) came [Kongo, 1987].

Most biographical works on Middendorff are published In Russian [Yurgenson, 1966; Leonov, 1967; Matvienko, 1970; Sokolov, Shishkin, 2005]; the most comprehensive of all is a recent book by Sukhova and Tammiksaar [2015], which is an excellent example of a naturalist's scientific biography. This book combines Middendorff's *curriculum vitae* with a detailed exposition of his works in various branches of science. Tammiksaar and Stone [2007]

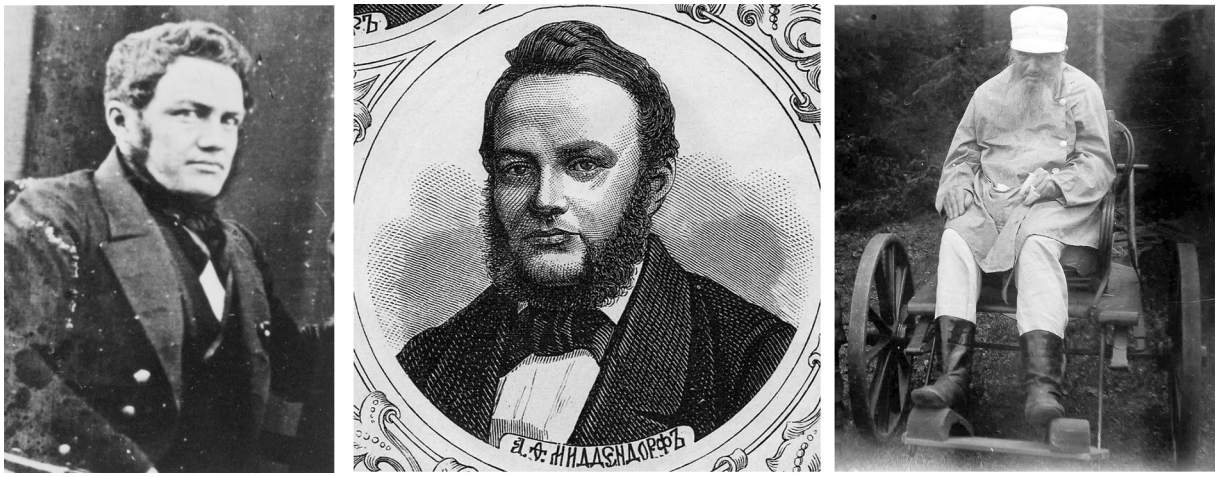

FIG. 1. Three ages of a zoologist: portraits of Alexander Middendorff, taken (left to right) in the 1840s, in 1868, and in the 1890s [after Sukhova, Tammiksaar, 2015].

РИС. 1. Три возраста зоолога: портреты Александра Миддендорфа, выполненные в 1840-е гг., в 1868 г. и в 1890е гг. [по: Сухова, Таммиксаар, 2015].

article is recommended to all readers not able to read Russian for a brief introduction into Middendorff's life and travels.

Recently, Sokolov and Shishkin [2005] summarized the contribution Middendorff made to mammalogy. However, the naturalist's malacological works, despite their significance, have never constituted a topic for a special publication. These works, although, are briefly mentioned in many papers devoted to the history of zoological and hydrobiological studies in Russia [Strauch, 1889; Zenkevich, 1951; Gorbunov, 1952; Fediakov, 1986; Vinarski, 2010; Vinarski *et al*., 2020]. The main goal of this paper is to sketch out the malacological works of Alexander von Middendorff and put them into the context of the historical development of malacology as a branch of zoology. The core material for this study was information taken from Middenforff's publications on molluscs; besides, I was able to examine some original specimens from his collection, kept in the Zoological Institute of the Russian Academy of Sciences (formerly the Zoological Museum of the Imperial Academy of Sciences of St. Petersburg; ZIN hereafter). A catalog of all molluscan taxa described by Middendorff, with remarks on their current taxonomic allocation and nomenclature, is represented as the appendix to this paper.

1837–1847: A malacologist's development

It is unknown, where and how Middendorff became interested in the study of molluscs. Born in 1815, he was the son of a Baltic German, an educated man, who taught the German in a gymnasium and later served as the head of the Main Pedagogical Institute in Saint-Petersburg. Young Middendorff chose a medical career and attended, in January of 1832, the medical faculty of the Dorpat (nowadays Tartu, Estonia) University. However, graduated in 1837, he did not become a practician physician and preferred instead to do research in natural sciences. His first professional appointment in the field was the chair of zoology in the St. Vladimir University in Kiev [Matveenko, 1970; Tammiksaar, Stone, 2007; Sukhova, Tammiksaar, 2015].

One may hypothesize that Middendorff's interest in malacology arose due to contacts with another Baltic German naturalist of Dorpat, Alexander von Schrenck (1816–1876), who studied terrestrial and freshwater Mollusca of the Baltic provinces of Russia and once published a large paper on this subject [A. Schrenck, 1848]. Remarkably, this article was prefaced by a letter "to my dear Middendorff", and the author explicitly stated that he made this faunal catalog due to the "promise" he once gave to Middendorff. Later on, von Schrenck collected continental molluscs of Southern Siberia and the so-called "Kirgizian steppe" [Vinarski, 2010].

In the mid-1840s Schrenck donated his malacological collection to the Zoological Museum of the Imperial St. Petersburg Academy of Sciences (ZMIA), nowadays – Zoological Institute of the Russian Academy of Sciences in St. Petersburg [Middendorff, 1848d; Strauch, 1889]. This collection included 560 specimens of snails and bivalves belonging to 60 species and varieties [Middendorff, 1848d].

However, the assumption of Schrenck's influence on Middendorff (or vice versa) is still not confirmed by any evidence; Middendorff himself never explained the reasons that prompted him to start his work with molluscs. Moreover, his earliest published

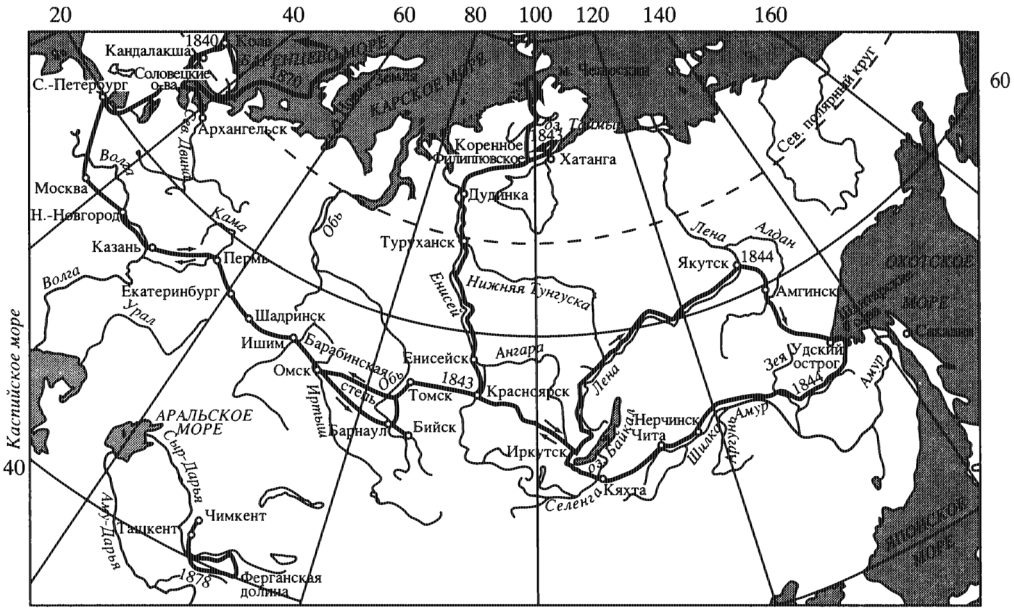

FIG. 2. The routes of Middendorff travels of the 1840s and 1878 [after Sokolov, Shishkin, 2005].

РИС. 2. Маршруты путешествий Миддендорфа по Сибири в 1840-е гг. и в 1878 г. [по: Соколов, Шишкин, 2005].

contributions in this field [Middendorff, 1847a, b] are so professionally written thus posing a question about where and when he made his first steps in malacology and who was (were) his mentor(s) in this branch of zoology. Perhaps, Middendorff fulfilled his malacological "apprenticeship" that took place between 1837 and 1839, when he had continued his education in foreign universities. In those years, he studied in Breslau (nowadays Wrocław, Poland), Halle, Königsberg (nowadays Kaliningrad), Prague, Vienna, and Berlin where he had a chance to work with several of the leading naturalists of the time [Tammiksaar, Stone, 2007].

Another key point in the development of Middendorff as a malacologist was his extensive travels. As a young man, he dreamed of explorations in remote lands and made serious tries to participate in a scientific expedition [Sukhova, Tammiksaar, 2015]. With the support of Academician von Baer, he was able to participate in the expedition to Russian Lapland, to the White Sea shores (May – October 1840), then almost unknown for naturalists. The head of this expedition became von Baer himself [Tammiksaar, Stone, 2007].

Though Middendorff held a position in Kiev, located in the southwestern part of the Empire, the Academy of Sciences commanded him to the White Sea hoping that "in the Polar seas he will find more prey for zoology than in the Black Sea" [Matveenko, 1970: 84]. The route of the expedition had run from Arkhangelsk westward to Norway. The travelers could visit the White Sea islands and explore the Barents Sea coast (Fig. 2). Apparently, during this travel Middendorff got his first experience in the study and sampling of marine molluscs. The zoological collections of these expeditions were divided between ZMIA and the St. Vladimir University; some specimens of molluscs collected by Middendorff are still extant (Fig. 3, A). However, according to Fediakov [1986: 5] Middendorff visited the White Sea "on the way", and the true scientific exploration of its molluscs started 40 years later. Tammiksaar and Stone [2007] state that the zoological interests of Middendorff in these years had been focused on birds, not molluscs. Perhaps, the main outcome of this first travel for Middendorff was that he was offered the opportunity of becoming the leader of an expedition to northern and eastern Siberia organized by the St. Petersburg Academy of Sciences with the participation of the Russian Geographical Society [Sukhova, Tammiksaar, 2015; Tammiksaar, Stone, 2007]. von Baer's support became crucial in this case as well.

The great Siberian travel (1842–1845) is the highest achievement of Middendorff as an explorer and traveler. It was an ambitious and bold enterprise that yielded considerable materials not only in zoology but also in botany, cartography, paleontology, physical geography, ethnography, and other fields of science. Most parts of Asiatic Russia remained unexplored by naturalists in that epoch, and Middendorff became the first zoologist to visit the Taimyr Peninsula, the Tugur Bay, and the Shantar Islands of the Sea of Okhotsk, and some other remote lands (see Fig. 2). The route of this expedition as well as its main results have been described in numerous publications [Sokolov, Shishkin, 2005; Tammiksaar, Stone, 2007; Sukhova, Tammiksaar, 2015], which allow me to omit the details of this travel and to focus on its

FIG. 3. Original specimens of Middendorff's malacological collection and their labels (ZIN). A. *Stagnicola atra* (Schrank, 1803) [= *S. palustris* (O.F. Müller, 1774). B. *Radix gebleri* (Middendorff, 1850). Scale bars 1 mm (A), 5 mm (B).

РИС. 3. Оригинальные экземпляры раковин, собранные Миддендорфом, и их этикетки (ЗИН). A. *Stagnicola atra* (Schrank, 1803) [= *S. palustris* (O.F. Müller, 1774). B. *Radix gebleri* (Middendorff, 1850). Масштабные линейки 2 мм (A), 5 мм (B).

significance for malacology. Middendorff returned to St. Petersburg with a rich collection of marine and continental molluscs, including some fossil ones. The latter were studied and described by the geologist A. von Keyserling [1845, 1848], who named a new species of cephalopods after its discoverer – *Ceratites middendorffi* Keyserling, 1845. In the current nomenclature, this species is accepted as *Olenekoceras middendorffi* [Dagis, Yermakova, 1988]. The fossil molluscs collected by Middendorff in Siberia were kept in the Geological Museum of the Academy of Sciences in St. Petersburg [Bodylevskiy, 1928].

The recent molluscs would become the object of Middendorff's studies of the late 1840s (see below). During his Siberian travel, he collected not only dried shells but also living animals and fixed them for the sake of further anatomical investigations. Besides, Middendorff made numerous observations on the distribution and ecology of marine and continental molluscs, for example, he traced the vertical distribution of snails and bivalves on the littoral zone of the Sea of Okhotsk [Middendorff, 1851a]. Another example of his zoogeographic observation is the finding of living freshwater snails of the family Physidae in the Taimyr Peninsula. The snails were found "under extremely unfavorable conditions, in the Taimyr land, at 73½° N, in a pool" [Middendorff, 1867] that very surprised the author himself, who did not expect to register any freshwater molluscs so far north. This finding remains the northernmost record for freshwater molluscs in the Northern Hemisphere [Vinarski *et al*., 2021].

It should be noted that Middendorff, as well as most marine zoologists of that epoch, was almost unable to explore the deep-sea malacofauna. Actually, his samplings were made "from the shore" [Zenkevich, 1951], i.e. in the intertidal zone, rarely from larger depths. Middendorff, however, fully acknowledged this shortcoming [see Middendorff, 1848d], though, it seems that he, following Forbes [Forbes, 1844; see Anderson, Rise, 2006 for details], believed that the deeper zones of the oceans may be totally devoid of organic life [Middendorff, 1851a]. The intensive study of the open ocean fauna started somewhat later, with the "Challenger" expedition, 1872–1876 [Zenkevich 1951; Kafanov, Kudriashov, 2000].

Since August 2, 1845, Middendorff was employed as an adjunct in zoology at the Academy of Sciences, and his main task was to prepare for publication the

materials of the Siberian expedition [Strauch, 1889; Tammiksaar, Stone, 2007]. Simultaneously, he had been involved in curating malacological collections of ZMIA. Not having an "official" working position in the Museum, he nevertheless served as the head of its "conchyliological department" from 1845 to 1855 [Strauch, 1889]. It allowed him to use the extensive collections of the Museum and its rich library. In 1846, Middendorff visited several natural history museums of Germany and the United Kingdom. As it may be assumed, the main focus of his research in 1845 and several subsequent years were molluscs. Within five years, 1847 to 1851, he published 13 papers on this subject, ranging from short notes with descriptions of new taxa [Middendorff, 1847a, 1848a, b, c, 1849c, 1850c] to voluminous monographs devoted to taxonomy, distribution, and ecology of Mollusca [Middendorff, 1847b, 1849a, b, 1851a]. Such incredible productivity presumes he devoted several years almost exclusively to malacological studies. The quality of these publications fitted the best malacological works of contemporary Western European zoologists, and Middendorff may be qualified as one of the most prominent students of molluscs of the 1840s–1850s.

The "conchyliological department" of ZMIA was much owed to Middendorff's curatorship, who organized an exchange of malacological materials between ZMIA and foreign museums, initiated the cataloging of the collection, and systematized specimens in accordance to classification accepted in those times [Strauch, 1889]. The materials, including type specimens of species new to science, collected by Middendorff himself were donated to ZMIA and became part of its malacological collections. Many of the type specimens described by Middendorff are extant and still available for examination.

Among museum innovations made by Middendorff, was the use of standard labels for mollusc collection lots (see Fig. 3 B). Later on, this practice was extended over other museum departments, having become thus a common standard in ZMIA.

In 1855, Middendorff was elected the permanent secretary of the St Petersburg Academy of Sciences which forced him to drop his activity in ZMIA [Strauch, 1889]. However, by this year he already ceased active work in malacology; his last publication devoted to Mollusca appeared in 1851 [Middendorff, 1851a]. During the second half of his life, Middendorff never returned to malacology. Though he continued to travel extensively, his expeditions brought almost no malacological results. For example, the account of the Middendorff expedition to the Baraba Steppe in Western Siberia (1868), contains no information of molluscs [Middendorff, 1870] though the Baraba steppe is rich in lakes and rivers, with a diverse malacofauna. Strauch [1889] mentioned samples of molluscs of the Cabo Verde Islands made by Middendorff and donated by him to ZMIA in 1868. However, these samples were not scientifically examined; Middendorff never published on molluscs collected in foreign countries. Some health problems forced Middendorff to resign from his position of permanent secretary of the Academy of Sciences in 1857. Two years later he left St. Petersburg and settled in his estate in Livonia (a part of nowadays Estonia) where he lived until his death [Sukhova, Tammiksaar, 2015]. It was almost impossible to continue zoological studies outside the capital of Empire, with its libraries and museum collections. Middendorff published some malacological materials in his "Siberian Fauna" [Middendorff, 1867], a monograph devoted chiefly to questions of zoogeography and ecology of animals. Though the author himself characterized this work as the "account of the life of Siberian vertebrates", he used some malacological observations made in Siberia to substantiate his conclusions. "Siberian Fauna" was the last contribution Middendorff made to the science of Mollusca.

1848: The "Agenda" for malacology in Russia

The article titled "Grundriss für eine Geschichte der Malacozoographie Russlands" ("Outline for a history of the malacozoography of Russia") published by Middendorff in 1848 [Middendorff, 1848d] is so remarkable and so indispensable for the proper understanding of his malacological research that, in my opinion, this paper needs to be discussed first. The scope of this relatively long article is much wider than its title. The history of the conchological and malacological explorations of the Russian Empire forms the main part of the study, whereas in the introductory paragraphs the author formulates an "Agenda" for the further development of the "domestic malacozoology" ("der Agenda unserer vaterländischer Malakozoologie"; Middendorff, 1848d: 431).

Having meticulously collected and discussed almost all preceding publications on the Russian molluscs, Middendorff became the first historian and bibliographer of this branch of zoology in our country. Though Middendorff (1848d, 1849a) had tirelessly stressed that the knowledge on the Russian Mollusca is very limited and that there is a need for extensive studies of taxonomy, anatomy, and distribution of species of the Empire's malacofauna, in this "Outline" he cited around 50 studies devoted to the topic, starting with Pallas works. Pallas was considered by him as the first "malacozoologist" of Russia; this naturalist made observations on molluscs during his long-term journey to the Urals and Siberia (1769–1774) and also described some species collected in the Caspian Sea and studied the samples made by the Russian naturalist Zuev in the White Sea.

Pallas [1788] described some marine molluscs of the Kurile Archipelago becoming thus a direct predecessor of Middendorff in the study of the North Asian malacofauna. Though Pallas initially intended to publish a special volume on molluscs and zoophytes as a part of his treatise "Zoographia Rosso-Asiatica", this plan remained undone.

Some observations of molluscs, as Middendorff [1848d] noted, were carried out even before Pallas, for example, those conducted by Steller in Kamchatka, in the 1740s. But materials of this explorer published many years after his death, contain only scattered, not systematized observations, mainly about the practical use of marine molluscs by the Kamchatka aborigines and about the presence of some cephalopods in the seas washing the peninsula. Samples of molluscs made by Steller were studied by Pallas [1788].

Middendorff [1848d] also mentioned some works of foreign conchologists who described molluscs of the Russian fauna [e.g. Broderip and Sowerby, 1829; Hinds, 1845; Reeve, 1846].

Among the Russian authors, Middendorff [1848d] gave especially high esteem to three persons, whose works, in his opinion, had laid the foundation of systematic malacology in Russia. One of these authors, Eduard Eichwald studied the continental malacofauna of Lithuania, molluscs of the Caspian Sea, and worked extensively in the field of paleomalacology [e.g. Eichwald, 1830, 1838]. Julian Siemaschko, a zoologist and teacher, is well known as a compiler of a voluminous treatise "The Russian Fauna, being the Description and Illustration of Animals occurring in Russia", published in three volumes in 1850 and 1851. The minor publications of Siemaschko included several descriptive works on continental Mollusca of Russia [Siemaschko, 1847, 1848].

Ivan Krynicki, who was a professor at the Kharkov University, can be considered as a direct forerunner of Middendorff. He was a shell collector and exchanged specimens with the Western European naturalists [see Krynicki, 1837 for the catalog of his collection]. Most taxonomic works of this researcher were devoted to the description of continental molluscs of Southern Russia [Krynicki, 1833, 1836]; among taxa described by him, a number are accepted valid in the current nomenclature. Middendorff [1848d: 430] praised Krynicki's works as "excellent" ("trefflichen"). In 1832, Krynicki published a noteworthy paper titled "A plan of the undertaken description of slugs living within the Russian state "(notably it was published in Russian; "slugs" in these days was the vernacular Russian name for all shell-less gastropods) [Krynicki, 1832]. In this paper, Krynicki proposed a general plan of a monograph "Faunae Molluscorum Imperii Rossici Initia", which would contain illustrated descriptions of all species of Mollusca, both terrestrial and aquatic (marine and freshwater). In other words, Krynicki dreamed of something like an atlas of the Russian molluscs being an analog to illustrated books of animals published in Germany and other countries (Krynicki himself cited Sturm [1803] as a possible prototype of his edition). The author intended to write such a book in Russian, with short diagnoses in Latin. Unfortunately, Krynicki died relatively young and could not fulfill this ambitious plan.

However, the general conclusion Middendorff made after the review of the available literature was not encouraging. The knowledge of the Russian molluscs was extremely poor, especially if the great extent of the country and the diversity of its environmental conditions are taken into account. The study of molluscs had been "the most neglected branch of natural sciences within the boundaries of our Empire" ("die Malakozoologie so ziemlich der vernachlässigteste Theil naturhistorischer Untersuchungen in den Grenzen unseres Reiches ist"; Middendorff, 1848d: 425). Although the state of knowledge of the European Russia malacofauna can be characterized as "a mediocre, one can say; sometimes satisfactory" [Middendorff, 1848d: 430], the rest of the country area is virtually unknown from a malacological point of view. Even a simple checklist of the Russian malacofauna was lacking, and the distribution and ecology of molluscs of this country were next to totally unknown. In a later publication, the author wrote that "the great neglect of the study of malacozoology in Russia" forced him to make "a new building from the ground up" ("die grosse Vernachlässigung des Studiums der Malakozoologie in Russland, einen Neubau von Grunde aus aufzuführen zwingt"; Middendorff, 1849a: 330). He ended his description of the poor state of the Russian science of molluscs by an optimistic phrase: "Only he who is fully aware of his weaknesses may master them" («Der nur, der seiner Schwächen sich vollkommen bewusst ist, mag ihrer Herr werden»; Middendorff, 1848d: 426).

The "Agenda" for the "domestic malacozoology", as Middendorff [1848d, 1849a] designed it, can be seen as a deepened and much more advanced version of Krynicki's project. It was a comprehensive research program not restricted in its aims to publishing an illustrated atlas whatever voluminous it is. The research would start from detailed studies on anatomy and intraspecific variability in molluscs that would help to clarify the taxonomy and distinguish species from varieties. After the sound taxonomy is established, one is able to develop a zoogeographic zonation of the Empire's area based on the distribution of genera and species of molluscs. To achieve such a great goal, the efforts of a single researcher would be not enough. Middendorff planned that all scientific forces of the Russian Empire must be involved in this project. First of all, the Academy

of Sciences, with its rich resources and the research infrastructure (the Zoological Museum, extensive library) should participate in this initiative. The Empire's universities could contribute, for example, by publishing textbooks on malacology, so that the numerous amateur naturalists scattered across the country could effectively study the malacofauna of the regions in which they live. The same mission was entrusted to the learned societies, first of all, the Moscow Society of Naturalists, whose activities Middendorff highly esteemed.

The participation of the local naturalists, both professional and non-professional, Middendorff saw as a prerequisite for the success of the enterprise. Without their efforts, the Academy's capabilities would not have been enough. This project apparently corresponded to the Western European model of the organization of natural history studies. In many European countries the amateurs and regional learned societies, usually opened for non-professionals, played a huge role in the knowledge of national flora and fauna (see, for example, Allen, 1976). Middendorff suggested following this way in Russia since "the spirit of the times requires it" ("welche der Zeistgeist beansprucht"; Middendorff, 1848d: 432). He noted that collections of molluscs are relatively easy to form, so provincial amateur naturalists could compile such collections and send them to specialists for scientific studies.

However, the function of local scientists, according to Middendorff [1848d], is not to be limited to doing faunal surveys and sampling molluscs. These people could contribute to an important theoretical problem namely, to the revealing of the correlation between the variability of molluscs and their environment. The resolving of this problem will have clear implications for the practical taxonomy of molluscs. I would like to give here a rather long quotation from Middendorff precisely exposing his thoughts on this subject: "an unlimited field is open everywhere, as soon as one aims to delineate exactly the limits of the concept of species in nature; to determine the limits of their variability, in the different age stages and different sexes, [owed] to local influences, more or less accidental; to trace really hybrid forms in their distribution and origin... Such investigations, like those mentioned last, correspond mainly to the means which are always open to every local researcher, however much he is stripped of auxiliary means, indeed the solution of these questions can only be done by local researchers…" ("… ist ja überall ein noch unbegrenztes Feld offen, sobald man sich zur Zielscheibe stellt , die Grenzen des Begriffes der Arten in der Natur, genau abstecken zu wollen; die Grenzen der Abänderlichkeit derselben, je nach den verschiedenen Allerstadien und Sexualitätsverschiedenheiten, den örtlichen mehr oder minder zufälligen Einflüssen, zu bezeichnen; wirklich-hybride Formen in ihrer Ausdehnung und Entstehung zu verfolgen... Solche Untersuchungen, wie die zuletzt erwähnten entsprachen vorzugsweise den Mitteln, welche jedem Lokalforscher, sei er auch noch so sehr von Hülfsmitteln entblösst, stets offen stehen, ja die Lösung dieser Fragen kann nur von Lokalforschern…; Middendorff, 1848d: 469]. The sound taxonomy will allow one to make a sound zoogeographical analysis which critically depends on the availability of reliable lists of species of particular local faunas.

As I will try to show in the next section, Middendorff's own malacological research followed tidily this plan of the systematic description of the Russian Empire malacofauna.

1847-1851: Middendorff at the peak of his malacological career

The professional interests of Middendorff as a student of molluscs were focused on three main topics: morphology, taxonomy, and zoogeography. His morphological research covered both anatomical investigations of selected species of Mollusca and the study of shell variability, chiefly at the intraspecific level.

In 1847, Middendorff published the first part of his "Beiträge zu einer Malacozoologia Rossica" ("Contribution to Malacozoologia Rossica"), being a morphological and taxonomic monograph of the chitons (Polyplacophora) of the Russian fauna [Middendorff, 1847b], in which the author counted 21 species (10 of them were described by him as new for science). Interestingly, he classified chitons as belonging to the class Gastropoda (as a single genus *Chiton* of the family Cyclobranchiata). The next two parts of this serial [Middendorff, 1849a, b] dealt with the rest of the marine molluscs of the Russian seas, bivalves to cephalopods. Apparently, Middendorff published his revisions in the ascending systematic order, from the most primitive molluscs (chitons) to the most advanced ones (cephalopods). As a result, a reader had a three-part monographic study that summarized the available knowledge of the Russian seas molluscs. As the primary material for this study, Middendorff used all available collections, including the samples brought by him from Siberia. In the same years, he published a series of small papers, aimed mainly at describing new species of molluscs [Middendorff, 1847a, 1848a-c, 1849c, 1850c].

The monograph on chitons [Middendorff, 1847b] contained among other things, a very detailed account of the anatomical structure of a single species, *Chiton stelleri* Middendorff, 1847 (today placed in the genus *Cryptochiton* Middendorff, 1847). This account alone is 40 pages long (excluding tables and illustrations). The illustrations are very accurate showing the details of the anatomical structure (Fig. 4, A, B). In this publication, Middendorff [1847b:

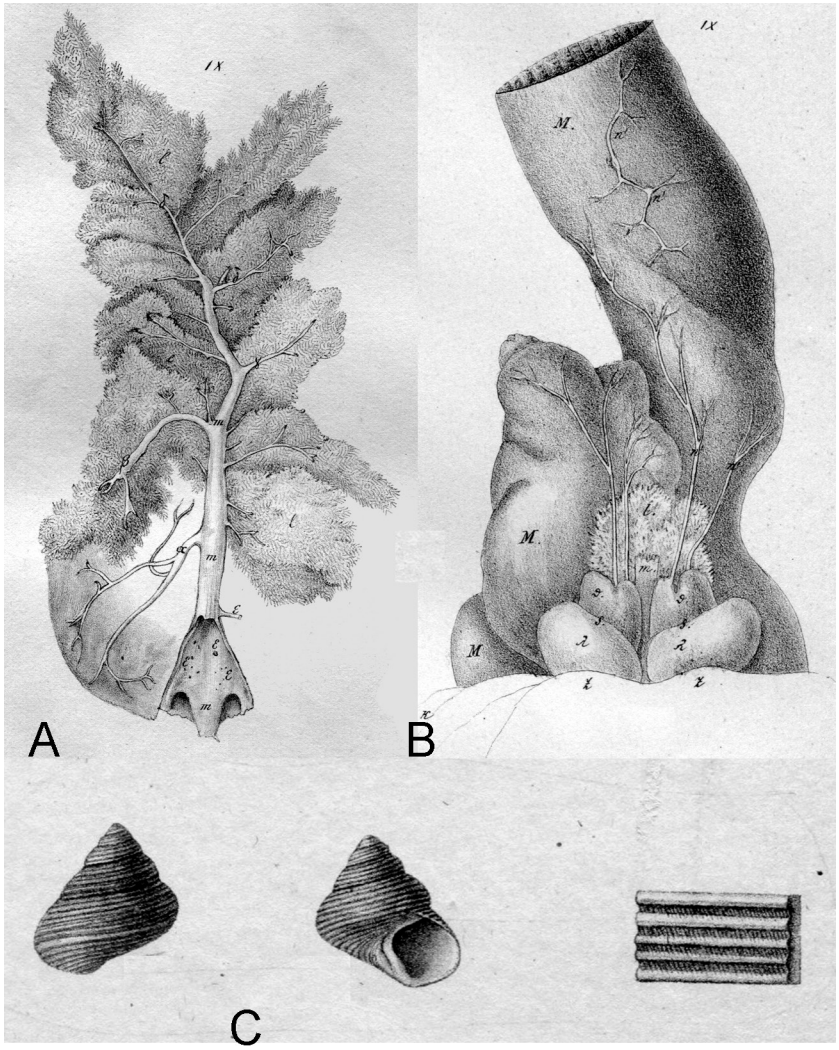

FIG. 4. Examples of illustrations of the shells and anatomical structures of molluscs in Middendorff's works. **A.** The circulatory system and the kidney of the chiton *Cryptochiton stelleri*. **B.** The anterior part of the stomach, throat sacks, and the stomach nerves (*nervi gastrici*) of the same species. **C.** The general view of shell and the shell surface sculpture of *Trochus modestus* Middendorff [A, B – after Middendorff, 1847b; C – after Middendorff, 1849b].

РИС. 4. Иллюстрации раковин и анатомических структур моллюсков из работ А.Ф. Миддендорфа. **A.** Кровеносная система и печень хитона *Chiton stelleri*. **B.** Передняя часть желудка, глоточные мешки (Schlundsäcke) и нервы желудка (*nervi gastrici*) того же вида. **C.** Общий вид раковины *Trochus modestus* Middendorff и её поверхностная скульптура [A, B – по: Middendorff, 1847b; C – по: Middendorff, 1849b].

118, 201, 205, etc.] coined a new morphological term – radula (or Reibplatte, in German), which would soon become ubiquitous in malacological literature.

Notably enough, Middendorff read before the Academy of Sciences his first communication about chitons on December 11, 1846. Considering that he returned from Siberia in March of 1845, the speed and vigor of his malacological studies look extraordinary. (One must remember that within the next years after the return, Middendorff was involved in numerous activities, including the organization of the Russian Geographical Society, and had no possibility to spare all his time to malacology). It was a heroic era when one talented person felt the strength to undertake the revision of all the marine molluscs of a huge country or all the molluscs of the whole subcontinent (Asiatic Russia)!

Modern authors evaluate Middendorff's anatomical study on chitons as "very important" (Kaas & Van Belle, 1985); however his taxonomic opinions, based, in part, on the anatomical data, are not so highly praised. According to Kaas & Van Belle (1985), the chiton taxa established by Middendorff, "being very heterogeneous, have not been retained by later workers, except for *Cryptochiton*". Anyway, the portion of species and genera of Mollusca described by Middendorff and accepted by modern taxonomists is rather high, being equal to 45 out of 87, i.e. a little more than 50% (see Appendix).

The total species richness of molluscs of the Russian marine fauna, in accordance with the three parts of "Contributions" [Middendorff, 1847b, 1894a, b], is equal to 225 (Table 1), which is much less than the currently accepted number [Kantor & Sysoev, 2005a, b] but exceeds considerably the earliest estimate made by Georgi [1801], who counted only 67 species in the Russian malacofauna.

The species accounts across all three parts of the "Contributions" were structured according to the same scheme, adopted in the conchology of that era: the Latin binomial name, synonymy, Latin diagnosis, description of morphology, ecology and distribution of the species, description of the varieties (if any), comments on diagnostics and nomenclature. In some cases, a differential diagnosis was also given. Black and white engravings with high-quality images of shells and some diagnostically significant features, for example, the surface sculpture and the hinge

structure (in bivalves) are provided (see Fig. 4 C). Measurements of entire shells (usually the shell height and width) and their parts are given, but, as a rule, without specifying the limits of variability, average values, and other quantitative characters that are now generally used. The same structure was adopted in the next taxonomic monograph by Middendorff [1851a], with adding an extensive zoogeographical part, lacking in the "Contributions": the latter formed a detailed systematic survey of the fauna, without analyzing it as a whole from a geographical or ecological point of view.

The three parts of the "Contributions", if one considers them as a whole, correspond to the best-quality analogous treatises on the marine Mollusca written by Middendorff's contemporaries (see, for example, Forbes & Hanley, 1848, 1849-1850). One of the peculiarities of Middendorff's work, which distinguishes it from most books authored by the Western European zoologists of the day, is the profound interest in the mollusc variability, which forced the Russian malacologist to spend many pages discussing the theoretical and practical issues related to this topic. He had high hopes that the studies of variability may become the key to the species problem, one of the most hotly debated, then and today, problems of taxonomy. The crossing experiments would provide another key.

To start with, I have to note that Middendorff may seem to adhere to a "subjectivist" view on the nature of species. At least, it can be concluded from his explicit statement that "the concept of species is just as much a subjective as that of the genus; albeit often to a lesser extent" ("dass der Begriff der Art eben so sehr ein subjectiver ist, als der des Geschlechts; wenn gleich häufig in geringerem Grade"; Middendorff, 1849a: 333). However, a closer examination of Middendorff's texts shows that, in his opinion, the "subjectivity" characterizes the procedure of species delineation, based on the subjective estimates of the taxonomic value of morphological similarities and differences, not the "nature of species" itself. Middendorff believed that one is able to delimit species objectively, following the reproductive isolation criterion. He wrote: "The concept of species would be invariably established if experience allowed us to agree with those scholars who believe that there are two naturally established species, unable to produce fertile bastards, just as starting from an axiom" ("Der Begriff der Art stände unveränderlich fest, wenn uns die Erfahrung denjenigen Gelehrten beizustimmen erlaubte, welche von der Annahme: dass zwei natürlich begründete Arten, keine fruchtbare Bastarde zu erzeugen vermögen, gleich wie von einem Axiome ausgehen"; Middendorff, 1849a: 333). Though the modern reader may regard it as a foreseeing of the 20th century "biological species concept", Middendorff's views were not pioneering. It was the perceived knowledge of those days; as summarized by Ellegård [1990: 206], in the middle of the 19th century "sterility was widely recognized as one of the most useful tests of species", and many naturalists believed that "God forbids hybrids to breed", which was seen as "a law of nature, designed and instituted by God" [Ellegård, 1990: 207-208].

Table 1. Taxonomic diversity of marine molluscs of the Russian Empire (including the northwest of North America) according to Middendorff [1847b; 1849a, b]*.

Таблица 1. Таксономическое разнообразие морских моллюсков Российской империи (включая северо-восток Северной Америки) по Миддендорфу [1847b; 1849a, b]*.

Class	Number of genera	Number of species
Polyplacophora	1	21
Gastropoda	35	144
Bivalvia	33	86
Scaphopoda	1	1
Cephalopoda	2	3
In total	**92**	**255**

*The distribution of species and genera among the classes made according to the current system.

What Middendorff [1849a: 334] actually proposed was a program of "experimental taxonomy". The author suggested that "only the experimental embryology (die experimentative Entwicklungsgeschichte)" can tell us "whether two species are still sharply separated in nature, i.e. show no transitions at all, or are able to produce really fertile hybrids". In another paper, discussing the methodological difficulties of the contemporary taxonomy, he complained that biologists "unlike physicists, are rarely able to do experimental work, i.e. [they] rarely can trace the action of living forces influenced by conditions…" [Middendorff, 1851b: 195]. Thus, he advocated the experimental approach to the problems of systematics though, simultaneously, fully realized that its efficacy is greatly constrained by inevitable circumstances. For example, it would be impossible for a museum taxonomist to subject *all* species of molluscs of the Russian seas to crossing experiments and, thus, reveal do they produce fertile hybrid offspring with closely related species or not. Hence the need for a thorough study of variability, which would give the indirect evidence of species' independence in doubtful cases. Middendorff advocated the "precise" study of variability based on numerical methods, both in his malacological [Middendorff, 1849a] and mammalogical [Middendorff, 1851b, 1867] publications. He argued that, theoretically, a numerical study of hundred specimens is required to reveal the internal taxonomic structure of a species (for example, of the brown bear, *Ursus arctos*; see Middendorff, 1851b) but his practical capacity to use statistical methods

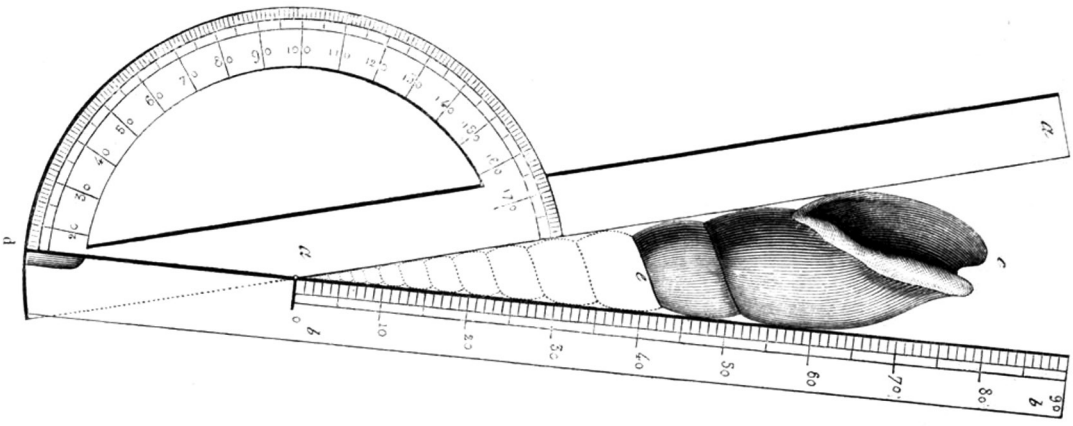

FIG. 5. The *Hélicometre*, or a device for the apical angle measurement [after d'Orbigny, 1851].

РИС. 5. «Геликометр», или устройство для измерения апикального угла раковины [по d'Orbigny, 1851].

was extremely limited. The algorithms of biometrical analysis were not developed yet, and the author could base his judgments on the rank and status of particular species and varieties on examinations of limited samples, and he was unable to conduct even an elementary statistical analysis. Despite the theoretical demand that "hundreds of skulls" must be studied and measured [Middendorff, 1851b: 195], he delineated the varieties of *U. arctos* based on chiefly qualitative characters [Ibidem]. The same is characteristic of his studies of shell variability.

Nevertheless, Middendorff could foresee the significance that numerical taxonomy will gain in the future. He respected the first attempts to develop a mathematical model of a helicospiral shell coiling made by Moseley [1838] in England [see d'Arcy Thompson, 1942: 784-788 for a review of earlier studies of shell modeling]. The "laws" of shell variability are mainly of quantitative nature and can be formulated precisely, in mathematical terms [Middendorff, 1849a]. Taxonomy must become as "exact" as meteorology or some experimental fields of biology (e.g. physiology). To achieve it, Middendorff proposed to use a standard scheme of shell measurements, including the determination of the apical and sutural angles (the sutural angle is very rarely used in modern malacology, but see Korobkov, 1950). He recommended using some simple technical devices to make exact and repeatable measurements [Middendorff, 1849a]. One of such devices was the *helicometer* (a *Hélicometre*; Fig. 5) invented in France by Alcid d'Orbigny [1842, 1851]. «It may be possible to define out the constant angle of the logarithmic spiral characteristic of each particular species. If this were indeed possible, we should be able to exceed the limit of our wildest hopes, and this constant might save us from any further diagnosis» («es werde möglich sein, für jede besondre Art den für sie charakteristischen konstanten Winkel der logarithmischen Spirale festzusetzen. Wäre dieses in der That möglich, so würden wir die Grenze unsrer kühnsten Hoffnungen überschreiten können und diese Konstante könnte uns jeder ferneren Diagnose entheben»; Middendorff, 1849a: 348). Nonetheless, Middendorff himself doubted that the logarithmic spiral angle is so constant as one would desire.

Another aspect of shell variability extensively discussed in Middendorff's work is its "periodicity". It means that various species of marine gastropods exhibit similar series of intraspecific varieties which may be arranged in a sort of parallel "rows". For example, in respect of the general shell shape, most species include, besides the typical one, two varieties, the elongated (var. *elatior*) and depressed (var. *depressior*). The variability in the aperture height also produces three intraspecific varieties (var. *typica*, var. *altior*, and var. *brevior*) and so on. The overall variability of a particular gastropod species can be expressed by the use of a standard scheme of designations of the varieties which creates a nomenclature for the nomination of all theoretically possible phenotypic variants. For example, in the Littorinidae five independent characters (shell shape, coloration, sculpture, and so forth) may be presented by six alternative states each, which gives us an enormous number of possible combinations – 15625 [Middendorff, 1849a]. Certainly, not all of them are actually found in nature.

Middendorff hoped that the use of such a standard nomenclature will once enable malacologists to reveal the much desired but still unknown "laws" of variation and, thus, create the "natural" system of molluscs at the species level. At the first glance, it resembles Darwin's statement that "our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part differs, more or less, from the same part in the parents" [Darwin, 1859: 167]. However,

Middendorff's theoretical convictions were far from being evolutionary. Like his senior contemporary von Baer, Middendorff was rather skeptical of Darwin's theory of evolution and could not adhere to the transmutationist views. In 1867, he had an opportunity to express his views on Darwinism, and these turned out not to be sympathetic. Though acknowledging "the great merits of Darwin", Middendorff criticized his theory as being a too speculative and premature product of the "fantastic spirit of the day" [Middendorff, 1867: 797]. He stated that the "practitioners in zoology" cannot agree with Darwin's theorizing.

Though Middendorff [1849a] acknowledged the emergence of new varieties of marine molluscs, it was not a "evolutionary thinking" of any kind. His views well corresponded with an idea, commonly accepted in the pre-Darwinian epoch, that Ellegård [1990: 198-199] summarized in the following words: "Differences between species were looked upon as instituted by God, at the original Creation. Varieties, on the other hand, have not been directly formed by God. Varietal differences had arisen through the influence of various external conditions, such as food, climate or artificial selection, on the originally created specific form". In exactly this way the geographical varieties (or races) of marine molluscs arose. Middendorff [1849a: 336] dubbed them "the fruits of nature's experimentation" ("die Früchte des Experimentirens der Natur"), i.e. forms emerging as a result of the environmentally induced modifications. The differences in depth, wave action, salinity, and other external conditions induce phenotypic alterations that may be even heritable. It is not the evolution in the modern sense of the term; rather it is a recurring materialization of the potentially possible phenotypic variants. The transient forms between species, creating so many troubles for the practicing taxonomists, may emerge in this way (in addition to the hybridization). On Middendorff's own estimate, 20–25% of species of the boreal marine molluscs are linked by such forms about which even an experienced taxonomist is not able to say which species they belong to. The hybrid individuals are common, for instance, among the Buccinidae, which poses a doubt about the reality of many hitherto described species [Middendorff, 1849a; see also Trautschold, 1860, who discussed the transient forms in the fossil bivalves and cephalopods from the Darwinian point of view].

Some contemporary authors had criticized the species descriptions published by Middendorff as redundantly complicated. Thus, Carpenter [1857: 214], albeit being well-disposed towards Middendorff's work on molluscs, had found that his species descriptions are "very minute and complex, the remarks extremely diffuse…" As a rebuttal to Carpenter, Middendorff [1867] explained that such a detailing serves as a measure against the extreme species splitting adopted by some malacologists of those days. The neglect of the geographical variation leads to the careless production of new species based on slight differences, the "*Mihisucht*" as it was dubbed by some contemporary authors [see Evenhuis, 2008 for details]. Middendorff [1867] was a strong opponent of such a practice and protested against the elevation of geographical races (or subspecies, as we would say now) to the rank of full species. He polemized with "gentlemen" of a certain sort for whom "the assumption that the molluscs on the shores of Massachusetts *must* certainly be different from the molluscs on the shores of Oregon, is … something of a biblical authority, against which a precise scientific definition cannot resist" [Middendorff, 1867: 796, in a footnote]. Having compared some species of molluscs of the Sea of Okhotsk and the Atlantic Ocean, Middendorff became convinced of their identity. Therefore, climatic differences, as it was sometimes assumed at that time, do not always cause changes in the animal morphology [Middendorff, 1867].

Table 2. Taxonomic richness of the six marine faunal regions of the Russian Empire [after Middendorff, 1851a].

Табл. 2. Таксономическое богатство шести фаунистических регионов Российской Империи [по Middendorff, 1851a].

Faunal region	Number of genera	Number of species
Aralo-Caspian	3	11
Pontic	33	58
Baltic	7	9
Polar	36	108
Okhotskian	11	24
Northwest American	19	42

The factor of geography remained a recurrent theme for Middendorff throughout entire his malacological career. All practical difficulties and uncertainties the taxonomists had faced did not prevent him from developing the first zoogeographic zonation of the Russian Empire area on the basis of the malacofaunistic data [Middendorff, 1848d, 1851a]. He delineated six marine faunal regions (*Faunengebiete*) and provided the characteristics and the species lists for each of them [Middendorff, 1851a]. This zonation was more detailed than the subsequent zoogeographic schemes developed by the Western European authors [Woodward, 1856; Fischer, 1881]. The Baltic Sea malacofauna was revealed as the poorest of all, being the depleted version of the boreal European marine malacofauna (Table 2). The Black Sea (Pontic) fauna of molluscs is merely an impoverished variant of the Mediterranean fauna with the inclusion of some Caspian forms and no truly endemic taxa [Middendorff, 1848d, 1851a]. Middendorff called the Black Sea the "blind sack" of

the Mediterranean Sea and later on Sovinsky [1904] confirmed this conclusion estimating that the Black Sea harbors only 1/10 of the Mediterranean species. On the other hand, the Arctic seas of Russia turned out to maintain a relatively rich malacofauna. Based on apparently incomplete data available in the day, Middendorff [1851a] managed to list as many as 108 species of Mollusca in the Arctic seas.

The fauna of continental Mollusca of Russia, especially of its Asian part, is, according to the author, even poorer than the marine malacofauna. Middendorff tried to invoke the "observed meteorological peculiarities" of the country to explain this fact [Middendorff, 1848d: 460]. The largest part of Russia, excluding the North Black Sea region and the Transbaikalia, is inhabited by essentially the same fauna which is identical to the fauna of foreign Europe. Middendorff [1848d] speculated the center of its origin was located somewhere in Central Asia and proposed to designate this fauna as "Northwest Asiatic". The species richness of continental molluscs is decreasing in the northeastern direction and the Central Siberia maintains the poorest fauna of land and freshwater molluscs. Notably, Middendorff [1848d, 1851a, 1867] was not aware of the existence of species-rich and highly endemic malacofauna in Lake Baikal. The first scientific data on the Baikalian Mollusca were obtained several years after Middendorff completed the study of collections he brought from Siberia [Maack, 1854; Gerstfeldt, 1859; Dybowski, 1875].

However, the zoogeographic interests of Middendorff were not restricted to the Empire territory. He became probably the first author to formulate the concept of the "circumpolar" fauna of Mollusca [Middendorff, 1849a, 1851a, 1867] and conducted the first census of the Arctic malacofauna, which proved to be much richer than it was assumed before his study [see Vinarski *et al*., 2021 for details]. Middendorff [1851a, 1867] refuted the established opinion that the high latitude waterbodies can be completely devoid of molluscs, and could trace the northward distribution of freshwater molluscs to 73½º N (see above). Besides, he noted some evidence of geographic variation in the mollusc body size. Thus, the author reported that the freshwater pearl mussels in Transbaikalia are much larger than in other studied regions (possibly due to differences in the water chemistry); the same increase in body size was found by him in the Bering Sea molluscs as compared with the European ones [Middendorff, 1867]. However, he refused to explain these patterns since believed that science has no data enough to judge the factors which cause them.

The influence of the geographic environment on molluscs, their communities, and the whole faunas is, according to Middendorff, enormous. He regarded the species content of a local marine fauna as a function of abiotic factors, the temperature and salinity being of the first importance. He believed that the marine molluscs act much better than the continental ones as the indicators of the abiotic regime of their environment, therefore one can use the "marine molluscs, at least most of the species, as living thermometers, salinity meters, bathometers, and the like" ["In diesem Sinne dürfen wir die Meeresmollusken, wenigstens die meisten Arten derselben, gleichsam als organische Thermometer, Halimeter, Bathometer u. d. m. betrachten"; Middendorff, 1851a: 351]. Therefore Middendorff's approach to the study of molluscs can be characterized as holistic; he tried to analyze the whole community or local fauna from the point of view of its relationships with the environment. In this respect, his works anticipate the later ecological explorations of the sea initiated in the 1870-s by Karl Möbius and some other authors [see Glaubrecht, 2008; Nyhart, 2009 and references therein].

1851 to the end of the century: In the wake of Middendorff

The 1851 monograph became the last of Middendorff's malacological papers. Since that year he published only a four-page appendix ("Zusatz") to Maack's [1854] article on continental Mollusca of Central Siberia, and, in 1867, the voluminous "Siberian fauna" translated into Russian two years later [Middendorff, 1867]. The latter book, albeit contained some data on the distribution and ecology of molluscs, cannot be treated as a malacological publication as the scope of this treatise was much broader.

However, the impetus Middendorff gave to the Russian malacology was rather strong. In 1867, Leopold von Schrenck, one more naturalist of the Baltic German origin, published a lengthy paper on the marine and continental molluscs sampled during his expedition to the Amur basin, a region not explored by Middendorff. Many of the collected species appeared to be new for science [L. Schrenck, 1867]. The structure and scope of Schrenck's treatise resemble that of Middendorff' [1851a]. The systematic part containing minute descriptions of particular species was continued by the second part, where various questions of zoogeography and ecology of molluscs were discussed [L. Schrenck, 1867]. Unluckily, later on, this talented naturalist decided to cease his studies on molluscs since his scientific interests shifted to ethnological studies.

Another example of the direct influence of Middendorff's malacology is a monograph on the White Sea Mollusca published by Solomon Herzenstein (1855–1894). The author acknowledged he was engaged in fulfilling research program developed by Middendorff and attempted to "reveal the general

morphological character of species of our fauna, determine their limits of distribution, and, to achieve these tasks, make a thorough comparison of our species with their closest relatives of other seas, etc." [Herzenstein, 1885: 636]. Like Middendorff and L. Schrenck, Herzenstein [1885] accompanied the systematic part of his work by a zoogeographic and ecological analysis of the studied malacofauna. The premature death prevented the author to continue his promising studies of the Russian marine molluscs.

Unfortunately, by the 1890s the peak of malacological research in Russia faded out, and the country almost totally lost experts in systematic malacology, save some prominent students of fossil molluscs (Ivan Sintsov, Nikolay Andrusov, and some others). However, the paleomalacological studies were beyond the scope of Middendorff's research, and this is not the place for a detailed discussion of this theme.

In the late 19th – first years of the 20th century, the foreign malacologists, primarily German and Swedish, dominated the field of study of Russian molluscs, especially the continental taxa. Several high latitude expeditions organized in Sweden brought back to Europe vast collections of molluscs which were studied by the Swedish conchologist Carl Agardh Westerlund [1877, 1887]. ZMIA had accumulated samples of molluscs made by prominent Russian explorers of Central Asia – Alexei Fedchenko, Nikolay Przhewalsky, Grigory Potanin, Sergei Korzhinsky but the Museum then lacked experts in systematic malacology, and these collections had been loaned to Western European malacologists to describe them [Martens, 1874, 1882; Westerlund, 1897; Simroth, 1902]. In 1896, Birulya complained that Russian zoologists are practically not interested in the study of molluscs and noted the poverty of Russian malacological literature [Birulya, 1896]. Non-professional malacology (rather conchology) was no better. As Krulikovsky [1889: 1] stated "[C]onchyliology, which has so many adepts in Western Europe that only some of the most popular branches of entomology could compete with it in this respect, is almost not developed in Russia". Gorbunov, who reviewed in retrospect the state of Russian malacology in the 19th century, noted that "[t]hose individual Russian scientists who devoted their time to the study of this issue, starting with A. Middendorff…, for the most part, either themselves interrupted work halfway, or, due to the shortness of their lives, did not have time to finish the work. In nearly 100 years, we have had only six or seven prominent experts in marine molluscs. Of these, A. Middendorff and L. Schrenck gave to some extent completed works, which, however, are now largely outdated and cover too little material" [Gorbunov, 1952: 216].

This situation had changed only during the first two decades of the 20th century when a new generation of Russia-born malacologists (Otto von Rosen, Wilhelm Lindholm, Konstantin Milashevich, Konstantin Deryugin) started to work actively [Vinarski, 2010, 2019].

The vast program of malacological research developed by Middendorff [1848d] was not, and could not be, completed during his lifetime. The lack of knowledge of the Russian malacofauna was realized by many authors long after Middendorff's death. For example, in the 1930s W.A. Lindholm wrote that the fauna of molluscs of "the [Soviet] Union, with the exception of the Crimea, the Caucasus, the White and Black Seas, has not been sufficiently studied" [Lindholm, 1936: 382]. The first more or less complete catalog of molluscs of the former USSR was published only in 2005 [Kantor, Sysoyev, 2005b], that is, one and a half hundred years after Middendorff.

Conclusion

As I tried to show in the preceding chapters, Middendorff's research program in malacology aimed at the systematic description of the entire Russian malacofauna, the zonation of the Empire territory based on the mollusc distribution data, and the revealing possible relationships between the taxonomic content of local malacofaunas and their environment. The study of anatomy and shell variability of molluscs was viewed as the prerequisite for achieving this ultimate goal. Middendorff made enormous efforts to fulfill this research plan.

Though Middendorff could devote to the study of molluscs only a relatively short period of his professional career, his malacological works constitute the largest and, perhaps, the highest achievement of this branch of science in 19th-century Russia. These works ushered in a (rather short) period of intense activity among Russian zoologists eager to do research on taxonomy, biogeography, and ecology of Mollusca of the domestic fauna. Middendorff's influence can be traced in the works of many later researchers, Leopold von Schrenck to Konstantin Milashevich. In the Soviet time, many prominent malacologists (G.P. Gorbunov, O.A. Scarlato, A.N. Golikov) highly praised Middendorff's contribution to the knowledge of marine molluscs, and the materials collected by him in the course of his Siberian travel are still studied by taxonomists [see, for instance, Golikov *et al*., 1987; Klishko *et al*., 2019].

Sukhova & Tammiksaar [2015] go so far that proclaim Middendorff the founder of Russian malacology that, however, is hardly absolutely true. Middendorf had praiseworthy predecessors in the study of molluscs of the Russian Empire, among which the giant figure of Peter Simon Pallas was. In the 19th century, although, Middendorff overshadowed all his contemporaries and the nearest followers, in terms of the fundamentality of his research, depth of analysis, and scientific significance. In many ways,

his work anticipates the future advancements of zoology, fully developed in the 20th century. I mean his interest in mathematical methods in taxonomy, attempts to give an ecological-faunistic analysis of local faunas, and, in general, a holistic approach to the study of molluscs, which is much higher than the plain description of new species and varieties. His efforts to reveal certain "periodicity" in shell variability forestall Nikolay Vavilov's "law of homologous series" [Vavilov, 1922] as well as repetitive attempts to build the "periodical systems" of various animal taxa [Preobrazhensky, 1982; Popov, 2008].

The universal nature of Middendorff's research is also emphasized by the fact that he was able to make a significant contribution to the knowledge of all groups of molluscs of the Russian fauna – marine, freshwater and terrestrial.

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Appendix

List of molluscan taxa introduced by Middendorff, with remarks on their current taxonomic status

The current taxonomic allocation of the taxa described by Middendorff is given following some recent catalogs and databases (Kantor & Sysoev, 2006; Vinarski & Kantor, 2016; MolluscaBase, 2020).

aeruginosa [*Patella* (*Acmaea*)] Middendorff, 1848b: 318. Type locality – USA, California, Fort Ross, Sonoma County. Current taxonomic allocation is uncertain. [Gastropoda: ? Acmaeidae].

Ametrogephyrus (as a subsection of the section *Dichachiton* Middendorff, 1847) Middendorff, 1847b: 97. Type species – *Chiton fasciatus* Quoy et Gaimard, 1835 (subsequent designation). = *Cryptoplax* Blainville, 1818. [Polyplacophora: Cryptoplacidae].

ampullacea (*Bullia*) Middendorff, 1848c: 245. Type locality – Russia, Sea of Okhotsk, Shantar Islands. = *Volutharpa ampullacea* (Middendorff, 1848). [Gastropoda: Buccinidae].

ancyloides [*Patella* (*Acmaea*)] Middendorff, 1848b: 317. Type locality – USA, Alaska, Kenai Bay near Sitka Island. Current taxonomic allocation is uncertain, junior homonym of *Patella ancyloides* Forbes, 1840. [Gastropoda: ? Acmaeidae].

angulato-carinata [*Tritonium* (*Fusus*) *antiquum* var.] Middendorff, 1849a: 463. Type locality – Russia, the White Sea, and Taimyr Peninsula (subfossil). = *Neptunea communis* (Middendorff, 1849). [Gastropoda: Buccinidae],

antiquata [*Tritonium* (*Fusus*) *despectum* var.] Middendorff, 1849a: 464. Type locality – not stated. = *Neptunea despecta* (Linnaeus, 1758). [Gastropoda: Buccinidae].

arctica (*Cancellaria*) Middendorff, 1849a: 441. Type locality – The Bering Strait. = *Neoiphinoe arctica* (Middendorff, 1849). [Gastropoda: Capulidae].

asmi [*Patella* (*Acmaea*)] Middendorff, 1848b: 318. Type locality – USA, Alaska, Sitka Island. = *Lottia asmi* (Middendorff, 1848). [Gastropoda: Lottiidae].

astartoides "Beck" (*Venus*) Middendorff, 1849c: 572. Type locality – South coast of the Sea of Okhotsk; Espenberg Cape of the Bering Sea. = *Liocyma fluctuosa* (Gould, 1841). [Bivalvia: Veneridae].

baerii [*Tritonium* (*Fusus*)] Middendorff, 1848c: 243. Type locality – the Bering Sea (without a precise location). = *Buccinum baerii* (Middendorff, 1848). [Gastropoda: Buccinidae].

behringii [*Tritonium* (*Fusus*)] Middendorff, 1848c: 243. Type locality – the Bering Sea (without a precise location). = *Beringius behringii* (Middendorff, 1848). [Gastropoda: Buccinidae].

behringiana [*Tritonium* (*Fusus*) *antiquum* var.] Middendorff, 1848c: 243. Type locality – Russia, Sea of Okhotsk, Shantar Islands, and Tugur Bay. = *Neptunea behringiana* (Middendorff, 1848). [Gastropoda: Buccinidae].

behringiana (*Pecten islandicus* var.) Middendorff, 1849b: 528. Type locality – the Bering Sea (without a precise location). = *Chlamys behringiana* (Middendorff, 1849). [Bivalvia: Pectinidae].

beringiana (*Anodonta cellensis* var.) Middendorff, 1851: 284, pl. 29, figs. 1-3. Type locality – the USA, Aleutian Islands, Unalashka Island, Lake Kenai. = *Beringiana beringiana* (Middendorff, 1851). [Bivalvia: Unionidae].

brandtii (*Chiton*) Middendorff, 1847a: 117. Type locality – Russia, Sea of Okhotsk, Shantar Islands and Tugur Bay; USA, Alaska, Sitka Island. = *Schizoplax brandtii* (Middendorff, 1847). [Polyplacophora: Schizoplacidae].

carinata [*Tritonium* (*Fusus*) *despectum* var.] Middendorff, 1849a: 465. Type locality – European coast of the Arctic Ocean (without a precise locality). = *Neptunea despecta* (Linnaeus, 1758). [Gastropoda: Buccinidae].

cingulata (*Paludinella*) Middendorff, 1849a: 376. Type locality – Russia, Sea of Okhotsk, the larger Shantar Island. = *Onoba cingulata* (Middendorff, 1849). [Gastropoda: Rissoidae].

commodum (*Pilidium*) Middendorff, 1851: 214, pl. 17, figs. 1-4. Type locality – Russia, Sea of Okhotsk, south coast. = *Piliscus commodus* (Middendorff, 1851). [Gastropoda: Velutinidae].

communis [*Tritonium* (*Fusus*) *antiquum* var.] Middendorff, 1849a: 460. Type locality – The Arctic Ocean, many localities. = *Neptunea communis* (Middendorff, 1849). [Gastropoda: Buccinidae].

compressa (*Cyclas calyculata* var.) Middendorff, 1851: 288, pl. 29, figs. 9-10. Type locality – Russia, south of Kamchatka Peninsula. = *Musculium compressum* (Middendorff, 1851). [Bivalvia: Sphaeriidae].

concentrica (*Patella caeca* var.) Middendorff, 1848b: 319. Type locality – Russia, Sea of Okhotsk, Shantar Islands, and Tugur Bay. = *Lepeta concentrica* (Middendorff, 1848). [Gastropoda: Patellidae].

Cryptobranchia (as a subgenus of the genus *Patella* Linnaeus, 1758) Middendorff, 1851: 183. Type species – *Patella caeca* O.F. Müller, 1776. = *Lepeta* Gray, 1842. [Gastropoda: Patellidae].

Cryptochiton (as a subgenus of the genus *Chiton* Linnaeus, 1758) Middendorff, 1847b: 97. Type species – *Chiton stelleri* Middendorff, 1847. = *Cryptochiton* Middendorff, 1847. [Polyplacophora: Cryptochitonidae].

cryptospira (*Velutina*) Middendorff, 1849a: 435; 1849c: 18. Type locality – Russia, Sea of Okhotsk, Shantar Islands. = *Velutina cryptospira* Middendorff, 1849. [Gastropoda: Velutinidae].

dahuricus [*Unio* (*Alasmodon*)] Middendorff, 1850: 109. Type locality – Transbaikalia (without a precise localition). = *Margaritifera dahurica* (Middendorff, 1850). [Bivalvia: Margaritiferidae].

decemcostata (*Purpura*) Middendorff, 1849a: 445, pl. 9, figs. 1-3; 1849c: 18. Type locality – The Bering Strait. = *Nucella canaliculata* (Duclos, 1832). [Gastropoda: Muricidae].

depressior (*Physa hypnorum* var.) Middendorff, 1851: 298, pl. 30, figs. 18-19. Type locality – Russia, near Falchudda Lake, Taimyr Peninsula, and Barnaul. = *Sibirenauta elongata* (Say, 1821). [Gastropoda: Physidae].

Dichachiton (as a section of the subgenus *Phaenochiton* Middendorff, 1847) Middendorff, 1847b: 97. Type species – *Chiton larvaeformis* Burrows, 1815 (subsequent designation). = *Cryptoplax* Blainville, 1818. [Polyplacophora: Cryptoplacidae].

eschrichtii (*Turritella*) Middendorff, 1849a: 396, pl. 11, fig. 1. Type locality – USA, Alsaka, Sitka Island. = *Neostylidium eschrichtii* (Middendorff, 1849). [Gastropoda: Turritellidae].

eschscholtzii (*Chiton*) Middendorff, 1847a: 118. Type locality – USA, Alaska, Sitka Island. = *Mopalia lignosa* (Gould, 1846). [Polyplacophora: Mopaliidae].

gebleri [*Limnaeus* (*Gulnaria*)] Middendorff, 1850: 110. Type locality – Russia, Altai Mts., the northern slope (most probably – Zaisan Lake in Kazakhstan). = *Radix gebleri* (Middendorff, 1850). [Gastropoda: Lymnaeidae].

genuina (*Patella caeca* var.) Middendorff, 1848b: 319. Type locality – Norway, Greenland, and Massachusetts. = *Lepeta caeca* (O.F. Müller, 1776). [Gastropoda: Patellidae].

gibba (*Petricola*) Middendorff, 1849c: 573, pl. 18, figs. 5-7; Type locality – USA, Alaska, Sitka Island. = *Petricola carditoides* (Conrad, 1837). [Bivalvia: Veneridae].

grandis (*Crepidula*) Middendorff, 1849a: 429, pl. 11, figs. 8-10; 1849c: 19. Type locality – USA, Alaska, Sitka Island. = *Grandicrepidula grandis* (Middendorff, 1849). [Gastropoda: Calyptraeidae].

grandis (*Littorina*) Middendorff, 1848c: 241. Type locality – Bering Sea, St. Paul Island. = *Littorina squalida* Broderip et G.B. Sowerby I, 1829. [Gastropoda: Littorinidae].

Hamachiton (as a section of the subgenus *Phaenochiton* Middendorff, 1847) Middendorff, 1847b: 97. Type species – *Chiton fascicularis* Linnaeus, 1767 (subsequent designation). = *Acanthochitona* Gray, 1821. [Polyplacophora: Acanthochitonidae].

herculea [*Anodonta* (*Dipsas*)] Middendorff, 1848a: 303. Type locality – Russia, Transbaikalia, Onon River. = *Cristaria plicata* (Leach, 1814). [Bivalvia: Unionidae].

herculea (*Natica*) Middendorff, 1848c: 246. Type locality – the USA, north California (without a precise locality). Current taxonomic allocation is uncertain. [Gastropoda: Naticidae].

inflatum (*Cyclas calyculata* var.) Middendorff, 1851: 287-288. Type locality – Russia, Barnaul (the sampling site of the lectotype; see Vinarski & Kantor, 2016 for details). = *Musculium inflatum* (Middendorff, 1851). [Bivalvia: Sphaeriidae].

insignis (*Trichotropis*) Middendorff, 1849a: 436, pl. 10, figs. 7-9; 1849c: 18. Type locality – Bering Sea, without a precise locality. = *Ariadnaria insignis* (Middendorff, 1849). [Gastropoda: Capulidae].

kamtschatica (*Onychoteuthis*) Middendorff, 1849a: 515, pl. 12, figs. 1-6. Type locality – Russia, Kurile Archipelago, Shumshu Island. = *Gonatus kamtschaticus* (Middendorff, 1849). [Cephalopoda: Gonatidae].

kamtschaticus (*Limnaeus*) Middendorff, 1850: 110. Type locality – Russia, Kamchatka Peninsula (without a precise locality). = *Kamtschaticana kamtschatica* (Middendorff, 1850). [Gastropoda: Lymnaeidae].

kurila (*Littorina*) Middendorff, 1848c: 242. Type locality – Russia, Sea of Okhotsk, Kurile Islands. = *Littorina sitkana* Philippi, 1846. [Gastropoda: Littorinidae].

lividus (*Chiton*) Middendorff, 1847a: 120. Type locality – USA, Alaska, Sitka Island. = *Chaetopleura angulata* (Spengler, 1797). [Polyplacophora: Chitonidae].

luridum [*Tritonium* (*Fusus*)] Middendorff, 1848c: 244. Type locality – USA, Alaska, Sitka Island. = *Paciocinebrina luridum* (Middendorff, 1848). [Gastropoda: Muricidae].

major (*Margarita arctica* var.] Middendorff, 1848c: 246. Type locality – Russia, Sea of Okhotsk (coast), and Shantar Island. = *Margarites helicinus* (Phipps, 1774). [Gastropoda: Margaritidae].

maxima (*Lutraria*) Middendorff, 1849c: 582, pl. 19, figs. 1-4; Type locality – USA, Alaska, Sitka Island. = *Tresus capax* (Gould, 1850). [Bivalvia: Mactridae].

merckii (*Chiton*) Middendorff, 1847a: 120. Type locality – USA, Alaska, Sitka Island. = *Mopalia lignosa* (Gould, 1846). [Polyplacophora: Mopaliidae].

mertensii (*Chiton*) Middendorff, 1847a: 118. Type locality – USA, California (without a precise locality). Most probably, the type locality is Fort Ross, Sonoma County, California. = *Lepidozona mertensii* (Middendorff, 1847). [Polyplacophora: Ischnochitonidae].

minuta (*Crepidula*) Middendorff, 1849a: 428, pl. 11, figs. 3-5; 1849c: 17. Type locality – USA, Alaska, Sitka Island. = *Crepidula nummaria* Gould, 1846. [Gastropoda: Calyptraeidae].

modestus (*Trochus*) Middendorff, 1849a: 318. Type locality – USA, Alaska, Sitka Island. Current taxonomic allocation is uncertain. This name is in-

valid being a junior homonym of *Trochus modestus* Reeve, 1843. [Gastropoda: ? Trochidae].

mongolicus (*Unio*) Middendorff, 1850: 109. Type locality – Russia, Transbaikalia (without a precise localition). = *Middendorffinaia mongolica* (Middendorff, 1850). [Bivalvia: Unionidae].

ochotense [*Tritonium* (*Buccinum*)] Middendorff, 1848c: 244. Type locality – Russia, Sea of Okhotsk, without a precise locality. = *Buccinum ochotense* (Middendorff, 1848). [Gastropoda: Buccinidae].

ochotense (*Scalaria*) Middendorff, 1849c: 17. Type locality – Russia, Sea of Okhotsk, Nikhta Bay. = *Acirsa ochotensis* (Middendorff, 1849). [Gastropoda: Epitoniidae].

ooides [*Tritonium* (*Buccinum*)] Middendorff, 1848c: 245 (renamed *Tritonium ovoides* in Middendorff, 1851). Type locality – Russia, Sea of Okhotsk, Tugur Bay. = *Pseudoliomesus ooides* (Middendorff, 1848). [Gastropoda: Buccinidae].

originalis [*Tritonium* (*Fusus*) *antiquum* var.] Middendorff, 1849a: 459. Type locality – not stated. = *Neptunea antiqua* (Linnaeus, 1758). [Gastropoda: Buccinidae].

pallasii (*Chiton*) Middendorff, 1847a: 117. Type locality – Russia, Sea of Okhotsk, Shantar Islands, and Tugur Bay. = *Amicula vestita* (Broderip et Sowerby, 1829). [Polyplacophora: Mopaliidae].

personoides [*Patella* (*Acmaea*)] Middendorff, 1849a: 365, pl. I, fig. 2. Type locality – USA, Alaska, Kenai Bay near Sitka Island. Current taxonomic allocation is uncertain. A replacement name for *Patella ancyloides* Middendorff, 1848, non Forbes, 1840. [Gastropoda:? Acmaeidae].

Phaenochiton (as a subgenus of the genus *Chiton* Linnaeus, 1758) Middendorff, 1847b: 97. Type species – *Chiton larvaeformis* Burrows, 1815 (subsequent designation). = *Cryptoplax* Blainville, 1818. [Polyplacophora: Cryptoplacidae].

pileolus [*Patella* (*Acmaea*)] Middendorff, 1848b: 318. Type locality – USA, Alaska, Sitka Island. Current taxonomic allocation is uncertain. [Gastropoda: ? Acmaeidae].

Pilidium Middendorff, 1851: 214 (non Forbes et Hanley, 1849). Type species – *Pilidium commodum* Middendorff, 1851. = *Piliscus* Lovén, 1859. [Gastropoda: Velutinidae].

Platysemus (as a subsection of the section *Hamachiton* Middendorff, 1847) Middendorff, 1847b: 98. Type species – *Chiton fascicularis* Linnaeus, 1767 (subsequent designation). = *Acanthochitona* Gray, 1821. [Polyplacophora: Acanthochitonidae].

schantaricum (*Pleurotoma*) Middendorff, 1849a: 447-448; 1849c: 19. Type locality – Russia, Southern coast of the Sea of Okhotsk and Shantar Islands. = *Oenopota schantaricum* (Middendorff, 1849). [Gastropoda: Turridae].

schantaricum [*Tritonium* (*Buccinum*) *undatum* var.] Middendorff, 1848c: 245. Type locality – Russia, Sea of Okhotsk, Shantar Island. = *Buccinum schantaricum* (Middendorff, 1848). [Gastropoda: Buccinidae].

schantaricum [*Tritonium* (*Fusus*)] Middendorff, 1849a: 475. Type locality – The Sea of Okhotsk, Shantar Islands; the Bering Sea, St. Paul Island. = *Aulacofusus brevicauda* (Deshayes, 1832). [Gastropoda: Buccinidae].

schantaricus (*Trochus*) Middendorff, 1849a: 413. Type locality – Russia, Sea of Okhotsk, Shantar Islands. = *Margarites schantaricus* (Middendorff, 1849). [Gastropoda: Margaritidae].

schrenkii (*Helix*) Middendorff, 1850: 110. Type locality – North Asia, without a precise locality. = *Fruticicola schrenkii* (Middendorff, 1850). [Gastropoda: Camaenidae].

scrobiculatus (*Chiton*) Middendorff, 1847a: 121. Type locality – USA, California (without a precise locality). According to Clark (2004). the type locality should be restricted to Fort Ross, Sonoma County, California. = *Lepidozona scrobiculata* (Middendorff, 1847). [Polyplacophora: Ischnochitonidae].

septentrionalis (*Pectunculus*) Middendorff, 1849c: 583, pl. 21, figs. 1-3; Type locality – North-west coast of North America, Ukamok Island. = *Glycymeris septentrionalis* (Middendorff, 1849). [Bivalvia: Glycymeridae].

sibirica (*Valvata cristata* var.) Middendorff, 1851: 299. Type locality – Russia, Siberia, from three localities – Barnaul, Berezovo, and Kamchatka. = *Valvata sibirica* (Middendorff, 1851). [Gastropoda: Valvatidae].

simplex (*Pleurotoma*) Middendorff, 1849a: 448; 1849c: 19. Type locality – Russia, Sea of Okhotsk, southern coast. = *Obesotoma simplex* (Middendorff, 1849). [Gastropoda: Mangeliidae].

simplex [*Tritonium* (*Buccinum*)] Middendorff, 1848c: 244. Type locality – Russia, Sea of Okhotsk, Shantar Islands. = *Buccinum simplex* (Middendorff, 1848). [Gastropoda: Buccinidae].

sitchana (*Crepidula*) Middendorff, 1849a: 428, pl. 11, figs. 3-5; 1849c: 17. Type locality – USA, Alaska, Sitka Island. Current taxonomic allocation is uncertain. [Gastropoda: ? Calyptraeidae].

sitchensis (*Chiton*) Middendorff, 1847a: 121. Type locality – USA, Alaska, Sitka Island. In the opinion of Clark (2004: 50), this is wrong, and the type specimens "came from Kamchatka, or the Okhotsk Sea". = *Mopalia lignosa* (Gould, 1846). [Polyplacophora: Mopaliidae].

sitchense [*Tritonium* (*Fusus*)] Middendorff, 1848c: 244. Type locality – USA, Alaska, Sitka Island. Current taxonomic allocation is uncertain. [Gastropoda: ? Buccinidae].

spongiosa (*Velutina*) Middendorff, 1850: 108. Type locality – Russia, Kamchatka Peninsula, at its southern tip (Lopatka). = *Velutina coryacea* (Pallas, 1778). [Gastropoda: Velutinidae].

stelleri (*Chiton*) Middendorff, 1847a: 116. Type locality – Russia, Kamchatka, near Petropavlovsk. =

Cryptochiton stelleri (Middendorff, 1847). [Polyplacophora: Cryptochitonidae].

striata [*Tritonium* (*Fusus*) *islandicum* var.] Middendorff, 1849a: 472, pl. 4, fig. 14. Type locality – "Russian Lappland", the Arctic Ocean coast; the Bering Sea. = *Colus islandicus* (Mohr, 1786). [Gastropoda: Buccinidae].

subpersonata (*Helix*) Middendorff, 1850: 110. Type locality – Russia, vicinities of Udskoe (near the Okhotsk Sea coast). = *Triodopsis subpersonatum* (Middendorff, 1850). [Gastropoda: Polygyridae].

subtenebrosa (*Littorina*) Middendorff, 1848c: 242. Type locality – Russia, Kurile Islands, Urup Island. = *Littorina sitkana* Philippi, 1846. [Gastropoda: Littorinidae].

sulcata [*Tritonium* (*Fusus*) *islandicum* var.] Middendorff, 1849a: 471, pl. 4, fig. 13. Type locality – "Russian Lappland", the Arctic Ocean coast. = *Colus islandicus* (Mohr, 1786). [Gastropoda: Buccinidae].

Platysemus (as a subsection of the section *Hamachiton* Middendorff, 1847) Middendorff, 1847b: 98. Type species – *Chiton albus* Linnaeus, 1767 (subsequent designation). = *Stenosemus* Middendorff, 1847. [Polyplacophora: Ischnochitonidae].

Symmetrogephyrus (as a subsection of the section *Dichachiton* Middendorff, 1847) Middendorff, 1847b: 97. Type species – *Chiton pallasii* Middendorff, 1847 (subsequent designation). = *Amicula* Gray, 1847. [Polyplacophora: Mopaliidae].

varicoso-carinata [*Tritonium* (*Fusus*) *despectum* var.] Middendorff, 1849a: 467. Type locality – not stated. = *Neptunea despecta* (Linnaeus, 1758). [Gastropoda: Buccinidae].

ventricosior (*Paludinella stagnalis* var.) Middendorff, 1851: 194-195, pl. 25, figs. 3-4. Type locality – Russia, Sea of Okhotsk, south coast. = *Falsicingula ventricosior* (Middendorff, 1851). [Gastropoda: Falsicingulidae].

vernicosa (*Modiolaria*) Middendorff, 1849c: 536. Type locality – Sea of Okhotsk; Alaska, Kadiak and Ugak islands. = *Vilasina vernicosa* (Middendorff, 1849). [Bivalvia: Mytilidae].

wosnessenskii (*Chiton*) Middendorff, 1847a: 119. Type locality – USA, Alaska, Acha, and Sitka islands. = *Mopalia ciliata* (G.B. Sowerby II, 1840). [Polyplacophora: Mopaliidae].

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