The Mexican Axolotl in Russia. The History of an Early Laboratory Animal as a Transnational Process, 1864–1940

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The Mexican axolotl has a long history as a laboratory animal. Going back 150 years, until 1864, this history offers insights into the beginnings of the use of laboratory animals in the life sciences and into the continuous dispersal of a foreign amphibian species across first Europe, then the rest of the world. This paper shows that Russia was part of a network in which an animal such as the Mexican axolotl could circulate and proliferate. Just like ideas, methods and people, these networks and spaces crossed national boundaries and tied together a transnational research community. While both laboratory practice and the necessary infrastructure were still fragile, they became more and more stable and axolotl turned from a curiosity that received considerable attention into a mundane research material. The case of Julius Schaxel shows that this research infrastructure became so standardized that it was possible for him to flee from Germany without bringing any equipment and to nevertheless be able to continue a specialized research program like Schaxel’s regeneration research.

Keywords: Axolotl, Julius Schaxel, research programs, laboratory practice.

Introduction

The Mexican axolotl (Ambystoma mexicanum) is one of the most widely used laboratory animals and a central organism in evo-devo research (Smith, Smith, 1971; Voss et al., 2009). But it is not a model organism in the narrow sense of the word (Ankeny and Leonelli, 2011). Even though there is an emerging infrastructure like the Ambystoma Genetic Stock Center at the University of Kentucky and sequence databases, the axolotl lacks the organized research community and coherent research agenda seen in model organisms. This is not least due to the fact that the axolotl has a much longer history as a laboratory animal than the model organism (Reiß, 2014). It is in fact the oldest self-sustaining laboratory animal population, celebrating its 150th anniversary in 2014. The axolotl came to science in the middle of the 19th century, at a time when the laboratory and the experiment were only about to emerge as the central place and method of the life sciences. When Thomas Hunt Morgan introduced Drosophila to the laboratory and developed his experimental system (Kohler, 1994) in the 1910s, axolotls were already mundane participants in laboratory life.

As we will show in this paper, in contrast to other model organisms, the distribution of the axolotl in Europe and its use as a laboratory animal were only loosely tied to specific research questions, research methods or research communities, if at all. Rather, it was distributed as a colonial curiosity, a pet for the aquarium and as a convenient and often supplementary material for research and teaching purposes in embryology. Nevertheless, the central questions, which are still investigated in the axolotl today, already occur in the animal’s early history as a laboratory animal.

“A Dust Sweeper”: Nikolai Leskov’s Writing and Public Hygiene

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The paper discusses N.S. Leskov’s ways of writing about the problematic matters of public hygiene. As a writer and a journalist N.S. Leskov took an interest in the matters of public hygiene early in his career as staff writer at Kiev’s newspaper “Sovremennaya Meditsina” (Contemporary Medicine) during the reforms of the 1860s and liberalization of the press. Leskov’s first feuilletons are presented as a characteristic feature of an early stage of the development of hygiene as a distinct medical discipline. The paper also discusses Leskov’s articles — especially those that have not been reprinted and his anonymous ones — in which he addressed the problems of hygiene. The author shows how the ‘hygienic’ topic slowly took hold of the writer’s artistic imagination. For example, in his late short novel “Product Prirody” (A Product of Nature) Leskov discussed hygiene in relation to his reflections on the concept of national character.

Keywords: N. S. Leskov, medical journalism, public hygiene, A. P. Walter, “Contemporary Medicine”, the reforms of the 1860s, Russian national character.
and connect its past, its present and its future. The distribution of animals, which are discussed in this paper, refers only to those documented in the sources. It is not excluded that more axolotls circulated along similar lines back and forth between the Russian empire and Central Europe.

The Mexican axolotl (*Ambystoma mexicanum*) is a neotenic salamander endemic to the lakes system in the Valley of Mexico (Illustration 1). Due to the growth of Mexico City, this formerly vast aquatic habitat today only consists of a set of artificial canals. Thus, the axolotl is close to extinction in the wild. At the same time, millions of individuals live in zoos, home aquaria and laboratories all over the world. This paradoxical situation began in the nineteenth century, when living axolotls were brought from Mexico to Paris and proliferated from there first all over Europe and then all over the world (Reiss, 2014; Reiss et al., 2014). Similar to the contemporary situation, the axolotls’ dichotomous existence as both an aquarium and a laboratory animal was crucial for its high levels of reproduction and subsequent dispersal (Reiss, 2012a; Reiss, 2012b; Reiss, Vennen, 2014).

Russia was one of the countries which were part of this process. The Russian part of the history of the axolotl demonstrates two points. First, it shows that not only scientists, students, concepts and practices traveled back and forth between scientific communities in Russia and central Europe, but also organisms of scientific importance. Second, the history of the axolotl makes visible a heterogeneous field of animal husbandry and breeding in Russia that allowed for the development of a stable axolotl population.

First steps: from Paris (1864) to the Russian Empire

The first living axolotls came to Europe in 1864. These 34 animals were a rather insignificant part of a huge collection of natural and cultural artifacts gathered by a scientific expedition, which the French government had sent to Mexico to systematically explore the country and its resources. In the 1860s, Mexico was occupied by France and the expedition had the mission to explore and sample the natural and cultural resources of the country. The recipient of the animals was the *Société impériale d’acclimatation*, the French acclimatization society and the central hub for the animals that circulated in the colonial networks. While most axolotls were brought to the society’s zoo, the *Jardin zoologique d’acclimatation*, six individuals, five males and one female, were given to the zoologist Auguste Duméril, professor of herpetology and ichthyology at the famous *Muséum d’Histoire Naturelle* known first of all due to the names of Lamarck, Cuvier and Saint-Hilaire. Duméril was also responsible for the *collection des reptiles*, the part of the museum’s Ménagerie, where fish, reptiles and amphibians were kept and exhibited.

Due to the long tradition and the collective experience in keeping unknown animals from all over the world, Duméril and the staff of the *collection des reptiles* within one year managed to bring the axolotls to reproduction. A few months later, some of the newly born animals transformed into a land-living form. The axolotls’ reproduction and the mysterious transformation caught a lot of attention among scientists all over Europe (Illustration 2). At the same time, the animals’ high reproductivity in the *collection* — Duméril reports 3300 new individuals between 1865 and 1867 — became the foundation for the first wave of distribution of axolotls over Europe.
The first period (1860s and 1870s): The first wave of distribution

The first wave of axolotls is directly linked to Auguste Duméril (1812–1870) in Paris. Taking advantage of the high reproductivity of the axolotls in the collection des reptiles, he gave animals to interested persons and institutions all over Europe. While he also experimented with sending fertilized eggs or very young individuals by train or mail, most of the animals were picked up in Paris by traveling scientists.

Russia was part of Duméril’s network of distribution. In 1867, the Baltic naturalist Karl Eduard von Eichwald (1795–1876) travelled to Paris and came back to St. Petersburg with ten animals (Eichwald, 1867; Geinitz, 1888). The Moscow Acclimatization Society (Société d’acclimatation de Moscou) put several animals on display at an exhibition (Duméril, 1869).

Russian naturalists and scientists did not only bring animals to Russia, but were also instrumental in distributing the animals further across Europe. When the Russian experimental zoologist Aleksandr O. Kowalewski (1840–1901) visited Paris in the late 1860s, he brought axolotls to Kasan, where he held a professorship at the Imperial University (Panceri, 1867). At some point, he gave animals to his friend and colleague Elias I. Metschnikoff, who at that moment worked in Odessa (Metschnikoff, 1876). On his way home, Kowalewski stopped in Naples for research purposes and gave some animals to Paolo Panceri (1833–1877), professor of comparative anatomy at Naples university (Panceri, 1867). Panceri in turn bred the axolotls successfully and distributes them in Italy (Sanctis, 1870).

In the late 1860s, Aleksandr Ivanovic Babuchin (1827–1891), professor of histology and physiology in Moscow, owned several animals, which he had obtained directly from Duméril. He gave several axolotls to his student Jacques von Bedriaga (1854–1906) (Bedriaga, 1877). Bedriaga continued his studies in Germany, first with Ernst Haeckel (1834–1919) in Jena and then with Carl Gegenbaur (1826–1903) in Heidelberg. He took his axolotls with him.

It is characteristic for this first wave of distribution, that these axolotls did not initiate substantial research. Rather, they were exemplars for the events in the collection in Paris. Some researchers attempted to reproduce and investigate the transformation. In Russia, only Metschnikoff and Bedriaga published on their experiments, as did Bedriaga in the 1870s, after he had already moved to Germany. Also in the 1870s, Ludwig Stieda (1837–1918), associate professor (Extraordinarius) of anatomy at the university of Dorpat (later Jurchev, now Tartu, Estonia), published his research on the central nervous system of the axolotl (Stieda, 1875). He had acquired the material for this study in Würzburg, where the German anatomist Albert Kölliker (1817–1905) had a large axolotl colony. Although Stieda made his tissue preparations in Würzburg, he also brought eight living axolotls to Dorpat and presented them to the Dorpater naturforschenden Gesellschaft (Stieda, 1874).

The second period (1880s–1914): A former curiosity becomes standard

After this phase, it took until the 1880s for the axolotl to reappear in science. While during the initial phase of distribution the focus of interest lay clearly on the animal itself and its transformation, axolotls were now used as mundane research material (Illustration 3).

In 1884 and 1886 Vladimir Weliky, assistant in the physiological laboratory of the Imperial Academy of Sciences in St. Petersburg published two papers on the anatomy of the lymphangion in the axolotl and the fire salamander (Weliky, 1884; Weliky 1886). In 1884, the histologist M. Lavdowsky used axolotls to study haematopoiesis (Lavdowsky, 1884).

Dietrich Barfurth (1849–1927), professor of comparative anatomy, histology and embryology at the Dorpat University, used axolotls as well as other species to study the process of regeneration in amphibians, on which he published in 1891 and 1894 (Barfurth, 1891; Barfurth, 1894).

In 1892, a graduate of Kharkiv University working at the Chair of Histology of the Moscow University Alexander Kolossov did a histological investigation of endothelia in a range of vertebrate species (Kolossov, 1892). A year later, a histologist and embryologist from Moscow University Basilius Lwoff published his study of the development of the germ layers in fish, amphibians and reptiles with the axolotl being the sole representative of the order Amphibia (Lwoff, 1893). At the same time, a zoologist from the Moscow University Wladimir Zykov investigated the relation between cartilage and notochord in the axolotl (Zykov, 1893). Nikolai Ivanzoff (Moscow University) published a comparative anatomy of the bones of the middle ear in amphibians and reptiles in 1894 (Iwanzoff, 1894).

Again in Dorpat Hermann Adolphi, prossector (an anatomist preparing dissections) at the Anatomical Institute of the university, published an embryological study of the nerve plexus of the limbs and the sacrum in 1898 (Adolphi, 1898). In the same year, Nikolai Bogdanoff (Moscow) studied eosinophilic granulation in various vertebrate species. In 1900, a zoologist Evgenij Mikhailovich Stepansow, who worked under J. K. Ogneff in Moscow, developed a new method to embed microtome preparations using axolotl tissue (Stepanow, 1900). Victor Faussek in St. Petersburg published a study on the histology of the gills in fish and amphibians in 1902 (Faussek, 1902). In 1905, J. K. Ogneff (Moscow) investigated the influence of darkness on the axolotl and the goldfish (Ogneff, 1905). A year later, Alexander A. Maximow (1874–1928) in St. Petersburg published a study of the development of new connective tissue under the influence of inflammations in the axolotl (Maximow, 1906). In the same year, Nikolai K. Koltzsoff (1872–1940) (Moscow) described the cytoskeleton of the spermatozoon of animals (Koltzsoff, 1906). Alexei E. von Smirnow (1859–1910), a histologist at the Tomsk University, developed a method to prepare permanent preparations of red blood cells in 1907.
German developmental biologist Julius Schaxel (1887–1943), after fleeing from Germany from prosecution by the national socialists in 1933, could effortlessly continue his experimental research with axolotls at his new position in the Laboratory for Evolutionary Morphology at the Academy of Sciences of the USSR in Leningrad (Reiss, 2007; Reiss et al., 2007). Schaxel was the last student of Ernst Haeckel and, as many of Haeckel’s most prominent students, built his academic career on the experimental study of developmental phenomena. In 1918, Schaxel received a grant from the Carl Zeiss Foundation in Jena to establish his own laboratory for experimental research, the Anstalt für experimentelle Zoologie. Albeit much broader in scope, Schaxel mainly did experimental research on axolotls, studying regeneration as a means to better understand basic ontogenetic phenomena (e.g. Schaxel, 1921).

In his new position in Leningrad, Schaxel could directly continue his axolotl-based research. While his first publications in Russian journals were probably the results of experiments from his time in Jena (Schaxel, 1934a; Schaxel, 1934b), he started to publish new research in the late 1930s (Schaxel, Ivanova, 1939; Schaxel, Schneider, 1939; Schaxel, 1940). Due to the history of the Mexican axolotl as a laboratory animal, it was no problem for Schaxel to follow up on his research practice with an animal that in nature was endemic to a small region in Mexico.

The third period, after 1914

The delay between the arrival of the first living axolotls in Russia during the first wave of distribution by Duméril and the use of axolotls as research material for anatomical, embryological and later experimental studies can be explained by the fact that the animals did not disperse due to conceptual or methodological considerations in the first place. Their distribution was initially driven by other interests. Instrumental was the aquarium as the space in which the animals could spread. In fact, the axolotl was the first exotic aquarium animal, which was successfully bred in Europe and thus available in large numbers and at a low price (Illustration 4). As also the proliferation of the axolotls in Russia shows, the acclimatization movement with its societies and public exhibitions was an important context, in which the aquarium and with it the axolotls dispersed.

Characteristic for the appearance of the axolotl as research material is the fact, that the animals’ origin and identity became less important. During the first wave, references to Duméril and the Parisian axolotls was always highlighted in the publication. This changed in the second wave, as the animals had lost their status as a rare and extraordinary curiosity. While Stieda still names Albert Kölliker as the origin for his tissue material and of the living animals he brought to Dorpat/Jurjew, from the 1880s onwards, this kind of reference disappears entirely from publications. This shows that the axolotls had become so ubiquitous in Russia, that no further reference or address of gratitude had to be given.

As in the rest of Europe, the usage of axolotls as research material increases massively after the First World War (Illustration 5). The animals had become part of more elaborate experimental systems, namely research on the physiology of thyroxin (e.g. Zawadowsky, Bessmertnaja, 1927; Vorontsova, 1928) and developmental biology/regeneration research (e.g. Filatow, 1928; Morosov, 1930). They became so widespread and common that the

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A home aquarium-terrarium combination from the late 19th century (Bade, 1899, p. 15)

Conclusions

Starting in the 1860s, zoology became an academic discipline of its own. Especially prevalent in Germany, this increased both the research output and the teaching load for the newly founded institutes and professorships (Nyhart, 1995). Significant for this development, the laboratory was introduced as both the new mode and the new place where research and teaching were practiced conjointly. As axolotls were easily available, they were used to supplement the domestic amphibian species commonly applied in this context. The developments in Russia
have, in principle, paralleled those in Germany due to especially strong scientific connections and the widespread of German language in Russian academic circles.

The history of the Mexican axolotl in Russia shows the existence of networks and spaces in which animals could circulate and proliferate all over Europe. Just like ideas, methods and people, these networks and spaces crossed national boundaries and tied together a transnational research community. While both this practice and the necessary infrastructure were still fragile, they became more and more stable and the axolotl turned from a curiosity that received considerable attention into a mundane research material. The case of Julius Schaxel shows that this research infrastructure became so standardized that it was possible to flee from Germany without bringing any equipment and to nevertheless be able to continue a specialized research program like Schaxel’s regeneration research.

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Мексиканский аксолотль в России. История лабораторного животного как международный процесс, 1864–1940

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Мексиканский аксолотль (Ambystoma mexicanum) как лабораторный объект имеет долгую историю. Уходящая на 150 лет назад к 1864 г., эта история открывает новые горизонты в деле исследований лабораторных животных в науках о жизни, а также позволяет проследить распространение аксолотля в Европе и в мире. Цель данной статьи — показать, что российские лаборатории были частью международной взаимосвязанной системы, в которой они занимали важное место. Мексиканский аксолотль превратился из диковинки в полноценный исследовательский материал. Случай Шакселя и его аксолотля привлек внимание многих исследователей, а он стал важным элементом международного аксолотльного сообщества. Однако, несмотря на его широкое распространение, интерес к аксолотлю в России был относительно низким. Затем, в 1870-х гг., интерес к аксолотлю в России начал возрастать, и этот интерес был связан с открытием новых возможностей для изучения процессов развития и регенерации у этого вида.

Ключевые слова: аксолотль, Юлиус Шаксель, исследовательские программы, лабораторные практики, лабораторные животные.

Улитки в гербарии: малакологическая коллекция академика С. И. Коржинского и её судьба

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Академик С. И. Коржинский (1861–1900) был одним из крупнейших русских ботаников второй половины XIX в. В его наследии фиксируется процесс создания собственной коллекции континентальных моллюсков (пресноводных и наземных) Среднего Предуралья. Собранные им коллекции моллюсков были использованы для изучения видового разнообразия и экологии вида. С. И. Коржинский был одним из первых русских исследователей, который начал активное использование моллюсков в качестве индикаторов состояния экосистем в прошлом. В статье показано, что С. И. Коржинский успешно использовал данные о моллюсках для реконструкции прошлого соотношения степного и лесного биомов в Восточной Европе. В их числе могут быть названы такие крупные исследователи, как К. фон Бэр и В. В. Докучаев в России, А. Неринг в Германии.

Ключевые слова: С. И. Коржинский, степной биом, геоботаника, континентальные моллюски, малакологические коллекции, флора Восточной Европы.