# Alexander Onufrievich Kowalevsky (1840–1901)

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## Contents



**Abstract**

Alexander O. Kowalevsky (1840–1901), a founder of cellular and comparative evolutionary embryology, was one of the most prominent biologists of the nineteenth century. He worked at the intersection of zoology, embryology, and evolution. His studies on the lancelet, tunicates, insects, and germ layer homologies pioneered comparative embryology and confirmed the evolutionary continuity between invertebrates and vertebrates. In this chapter I present a short description of the life of A.O. Kowalevsky and his achievements and, with their help, illustrate the development of comparative evolutionary embryology in the last third of the nineteenth century. The chapter also presents the full bibliography of Kowalevsky.

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L. Nuño de la Rosa, G.B. Müller (eds.), *Evolutionary Developmental Biology*,
https://doi.org/10.1007/978-3-319-33038-9_9-1

**Keywords**

Alexander Kowalevsky · Comparative evolutionary embryology · Evo-devo

## Life

Alexander O. Kowalevsky was born on November 7, 1840, in the village of Vorkovo (Russia). His father, Onufriy I. Kowalevsky, owned a rural estate in Polessye (the Vitebsk Province, now Republic of Byelorussia). Another son, Vladimir (1842–1883), who was born two years later, would become a renowned evolutionary palaeontologist. Both brothers spent their childhood in the estate and were tutored at home until the age of 16. Their parents envisaged a practical career for the children, and their education was organized correspondingly (Dogiel 1945; Pilipchuk 2003; Fokin 2012).

In 1855 Alexander Kowalevsky entered the third year of the School of Railway Engineers in St. Petersburg. In 1858 he left it for the Department of Natural Sciences of the Physical-Mathematical Faculty of St. Petersburg University. A year later (1859) Kowalevsky left the university to continue his studies at Heidelberg University (Germany). Kowalevsky spent about two years in Heidelberg. At first he studied chemistry with Robert Wilhelm Bunsen (1811–1899) and Georg Ludwig Carius (1829–1875) and then anatomy, histology, and zoology under the supervision of Heinrich Georg Bronn (1800–1862) and Heinrich Alexander Pagenstecher (1825–1889). It was in Heidelberg that Kowalevsky began to work on the lancelet (*Branchiostoma lanceolatum*), which was to become his favorite research subject. It should be noted, however, that formally Kowalevsky was not a student at the university (Fokin 2012).

At the end of 1861 Kowalevsky moved to Tübingen University. His teachers were well-known scientists: Hubert von Luschka (1820–1875; anatomy), Friedrich Eduard Reusch (1812–1891; general physics), Hugo von Mohl (1805–1872; botany), Friedrich Quisted (1809–1889; geology), and Franz von Leydig (1821–1908; zoology and histology). In Tübingen Kowalevsky also improved his skills in microscopy (Fokin 2012).

In 1861 Kowalevsky briefly returned to St. Petersburg, where he became a Candidate of Natural Sciences for his research on the anatomy of the crustacean *Idothea entomon*. At the end of 1863 Kowalevsky returned to Tübingen and continued zoological studies under the supervision of F. von Leydig for several months. Then he moved to Naples and started his own scientific research. At that time Kowalevsky was already under a strong influence of Charles Darwin's (1809–1882) *The Origin of Species*, which he read in the early 1860s in the German translation (Dogiel 1945; Pilipchuk 2003).

Kowalevsky spent two years in Naples, completing his famous research, which became the basis for his Master dissertation "The Developmental History of the *Amphioxus lanceolatus* or *Branchiostoma lunbricum*" defended in St. Petersburg University in 1865 (Kowalevsky 1865). The main conclusions of the dissertation

**Fig. 1** Alexander Onufrievitch Kowalevsky. St. Petersburg, 1885. (From archives of the Department of Embryology of St. Petersburg State University)

were as follows: (1) the lancelet, previously considered a fish-like vertebrate, actually belongs to cephalochordates, and (2) its embryo and embryonic development resembles a vertebrate. Many of the conclusions still appear to be true (see for instance, Arthur 2002; Holland 2010). Karl Ernst von Baer (1792–1876), a famous embryologist who was 73 at that time, referred to the dissertation of Kowalevsky as a "first-class study."

Between 1866 and 1867 Kowalevsky worked as a conservator of the Zoological Cabinet at St. Petersburg University. He took a special interest in the development of the bilateral, worm-like animals, which we now call phoronids. The results of these investigations provided the basis for his doctoral thesis presented publicly in 1867 under the title *Anatomy and Developmental History of Phoronis* (Kowalevsky 1867c). At the same time Kowalevsky published numerous articles on the embryology of worms, bryozoans, sea cucumbers, and ascidians. In the same year, Kowalevsky was awarded, together with Ilya Ilyich Mechnikov (1845–1916), the first Baer Prize from the Russian Imperial Academy of Sciences.

In 1868 Kowalevsky was elected professor at the Imperial Kazan University. At the end of 1869 he transferred to St. Vladimir Imperial Kiev University and was awarded the Baer Prize for the second time. He spent the money on two trips, first to Italy and then to the Red Sea, where he discovered the famous crawling ctenophoran *Coeloplana metschnikowii*. In 1871 Kowalevsky participated in the foundation of the Sevastopol Biological Station in the Crimea.

From 1873 to 1890 Kowalevsky worked as a full professor in Novorossiysk University (now Odessa, Ukraine) (Fig. 1). For him it was a relatively stable period of intense pedagogical and scientific work and established family life. However, he spent most of the summers in France, Switzerland, and Italy doing scientific research. Almost everywhere, Kowalevsky studied the embryology of various marine invertebrates. In the early 1880s he also participated in the research on the *Phylloxera*, a harmful vine pest that had appeared in southern Russian at that time.

In 1883, Kowalevsky was elected corresponding member of the Russian Imperial Academy of Sciences, and in 1890 he became a full academician. His interests were shifting toward physiology, in particular to excretion in different invertebrates. Kowalevsky made an outstanding achievement in the field of comparative physiology. Having modified and improved the technique of intravital injections, used to differentiate physiologically different parts of the excretory apparatus, Kowalevsky studied the effect of numerous substances on the excretory system of many invertebrates. As a result of the use of this new technique he managed to reveal the existence of different and diverse excretory apparatuses, many of which were previously unknown. The use of different substances also allowed him to identify the physiological significance of the discovered organs.

In 1890 Kowalevsky moved with his family to St. Petersburg. From 1890 until 1894 he was a professor at St. Petersburg University, where he was the head of the Anatomical-Histological Cabinet. In 1894 he founded a Special Zoological Laboratory in the Academy of Sciences, the first Russian center of experimental zoology. He worked there with his students, among them the embryologist Constantin Davydoff (1878–1960), the immunologist Sergei Metal'nikoff (1870–1946), the protistologist Vladimir Schewiakoff (1859–1930), and others (see Fokin 2000). He also supervised the construction of a special building for the Sevastopol Biological Station (1894–1897), the center for faunistic and morphological studies of the animals of the Black Sea and the Mediterranean basin (now Kowalevsky Institute of Marine Biological Research).

During this period, Kowalevsky became a recognized authority in evolutionary embryology and zoology. He was a member of the Society of Naturalists of Modena and the Cambridge Philosophical Society, a foreign member of the Royal Society, and a corresponding member of the Academies of Sciences of Brussels and Turin.

Kowalevsky died of cerebral hemorrhage on November 9, 1901, at the age of 61. He was buried at the Novo-Devichie Orthodox cemetery in St. Petersburg.

Kowalevsky was a tireless traveler. In total, he spent 12 years in expeditions and scientific missions. He undertook numerous expeditions and trips aimed at the exploration of marine animals at the Adriatic Sea (Trieste), the Mediterranean Sea (Naples, Messina, Villafranca, Marseille, Alger), the Caspian Sea, the Red Sea, in the English Channel (Roscoff), and other marine regions.

## Work

Evolutionary developmental biology (evo-devo) compares developmental processes of different organisms to infer their ancestral relationships and the evolution of developmental processes. In its present form, evo-devo emerged in the 1970s.

However, its origins date back to the evolutionary embryology of the second half of the nineteenth century, and Kowalevsky was one of its pioneers. He used new histological techniques to determine homologies that were no longer visible in the adult organism (Mikhailov and Gilbert 2002). His studies using cell lineage to show the homologies of the notochord in tunicates, the lancelet, and vertebrates became a major argument in support of the theory of evolution and contributed to the transformation of descriptive embryology into evolutionary embryology, one of the bases of modern evo-devo.

## The State of Comparative Animal Embryology Before Alexander Kowalevsky

Between 1828 and 1837 von Baer suggested the doctrine of the two main embryonic layers: the upper layer and the lower layer (renamed ectoderm and endoderm, respectively, by George James Allman (1812–1898) in 1853), and Robert Remak (1815–1865) (in 1855) added a third, middle, germinal layer – the modern mesoderm (Hall 1998).

Although von Baer himself was only involved with the embryology of various classes of vertebrates, he tried to build the entire system of the animal kingdom based on not only comparative anatomy but the development of different animal groups. He recognized four types of development: radial (in coelenterates), spiral (in mollusks), symmetrical (in articulates), and bisymmetrical (in vertebrates). These four types approximately coincide with the four types of anatomical structure of animals according to Georges Cuvier (1769–1832), and von Baer, similarly to Cuvier, considered the types of development as independent and unrelated.

In the first edition of *The Origin of Species* Darwin emphasized the importance of embryology as one of the "three pillars" of evolutionary theory (morphology, embryology, and palaeontology). However, he lacked the substantial evidence confirming such a statement. It was based only on Fritz Müller's (1821–1897) research on the history of the development of various crustacean groups and on his own studies of development in barnacles. It is Alexander Kowalevsky who should be considered as one of the first scientists who empirically proved the importance of embryology as a pillar of evolutionary theory.

By the time when Kowalevsky began his research on marine zoological material, Darwin's general principles of the theory of evolution were widely confirmed by evidence from comparative anatomy in the practice of breeding domestic animals and cultivated plants. Phylogenetic relationships within such well-defined groups as vertebrates or arthropods were not in doubt. One of the major aims of the evolutionists of the second half of the nineteenth century was to detect the relationship between vertebrates and invertebrates and then to establish a taxonomic position, and thus a phylogenetic relationship, of certain artificial groups such as worms and other questionable groups such as acrania, tunicates, bryozoans, brachiopods, and chaetognaths with the rest of the animal world. These forms later attracted Kowalevsky's attention.

When Kowalevsky and his friend I. Mechnikov (who was to become a Nobel Prize winner and the founder of immunology) began their embryological research, evolutionary embryology as a distinct field of science did not seem to exist. They decided to assess relationships across the animal kingdom on the basis of the identification of developmental similarities between the embryos of different phyla. Under a strong influence of *The Origin of Species*, Kowalevsky and Metchnikoff made comparative embryological studies on a huge number of invertebrate and vertebrate species, pioneering evolutionary embryology (see Mikhailov 2012; Mikhailov and Gilbert 2002; Levit 2007).

The most frustrating aspect of marine invertebrate research at that time was its episodic character. Field studies could only be pursued during inter-semester breaks. This was exacerbated by the problem that the animals, once collected, had to be kept alive and taken to laboratories for developmental studies and histological analysis, often over long distances. However, the scientific activity of Kowalevsky coincided with a surge of organization of marine biological stations throughout Europe. A permanent experimental marine station with an aquarium, preferably near invertebrate-rich waters, made it possible for zoologists not only to study the life history of various marine animals in detail but also to work with model organisms. This switch to the study of model organisms was an extremely important factor in the development of a new research direction, experimental embryology, which later became a major component of evo-devo.

## The Works of Alexander Kowalevsky and the Foundation of Evolutionary Comparative Embryology

The fact that Kowalevsky turned to the study of the *Amphioxus* does not mean that he just came across an interesting object among the rich Mediterranean fauna. He consciously sought to investigate it, setting it as his task even before his arrival in Naples. At that time, *Amphioxus* was attributed to vertebrates, and Kowalevsky himself called it "a wonderful fish." He hoped to find in its embryology common developmental features of invertebrates and vertebrates, a foresight was brilliantly justified (Dogiel 1945).

Kowalevsky used *Amphioxus* as a model system in his studies in Naples in 1866 (Fig. 2). He identified in its embryos the principal features common to all chordates such as the notochord, the dorsal nerve cord, and metameric muscles. He also showed that embryonic development in *Amphioxus* was that of a typical vertebrate, with a notochord, multiple gill slits, and medullary folds fusing to form a neural canal (Fig. 2c, d) (1867b). A remarkable discovery made by Kowalevsky in his work on *Amphioxus* development was the description of a two-layered embryo arising through typical invagination type gastrulation, which later turned out to be common for many invertebrates. Kowalevsky established the presence of the two main germ layers, the upper and the lower one, in *Amphioxus* and later in tunicates and ctenophores. Until that time the presence of the two germ layers was considered an exclusive feature of vertebrates (1867b).

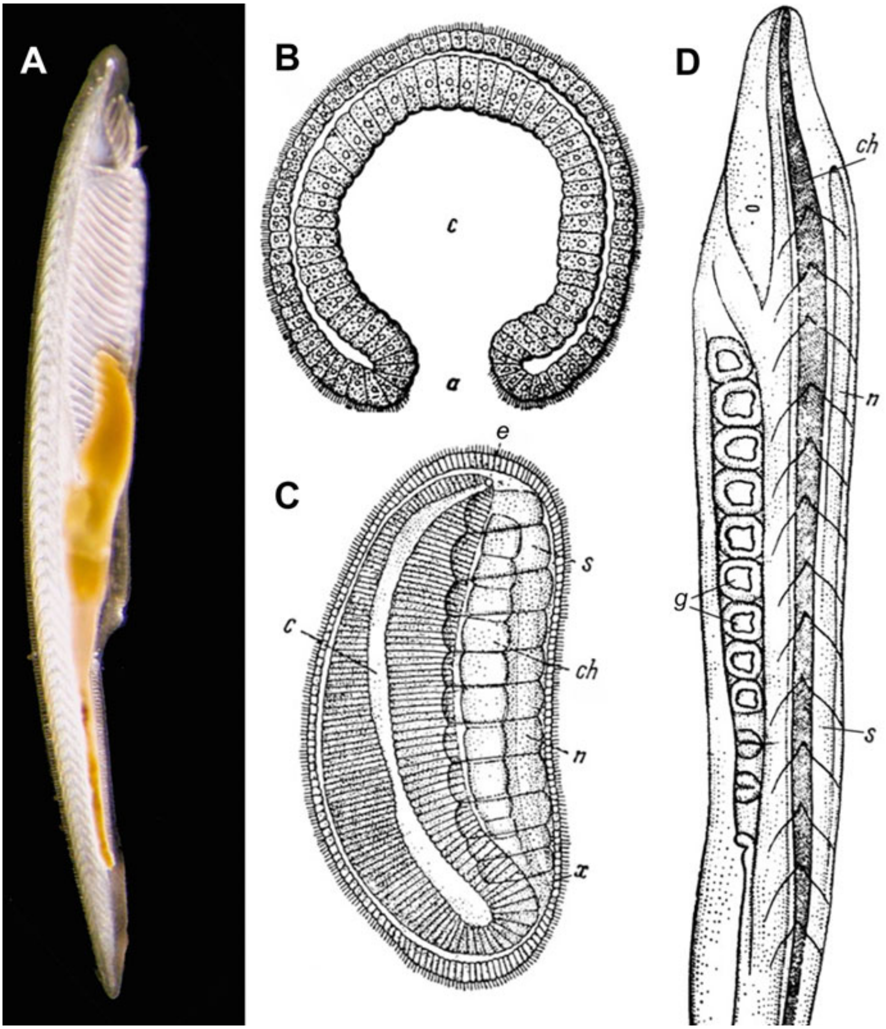


**Fig. 2** (**a**) Adult lancelet *Branchiostoma lanceolatum*. B-D. Kowalevsky's drawing showing early stages of lancelet development (adapted from Kowalevsky 1865). (**b**) Mid-to-late gastrula; (**c**) newly hatched embryo with 11 somite pairs; (**d**) free larva with 11 gill slits. a – blastopore; c – archenteron; ch – notochord; e – ciliated ectoderm; g – gill slits; n – nerve cord; s – somites; x – neuropor

Concurrently with the study of *Amphioxus*, Kowalevsky studied the development of tunicates, ctenophores, and holothurians. Tunicates attracted him by the uncertainty of their taxonomic position. They are now recognized as the most basal group of chordates, but a century and a half ago, they were classified as mollusks related to shipworms, a group of wood-boring clams (Fig. 3a). The result of Kowalevsky's research was unexpected even for its author: according to the type of cleavage,

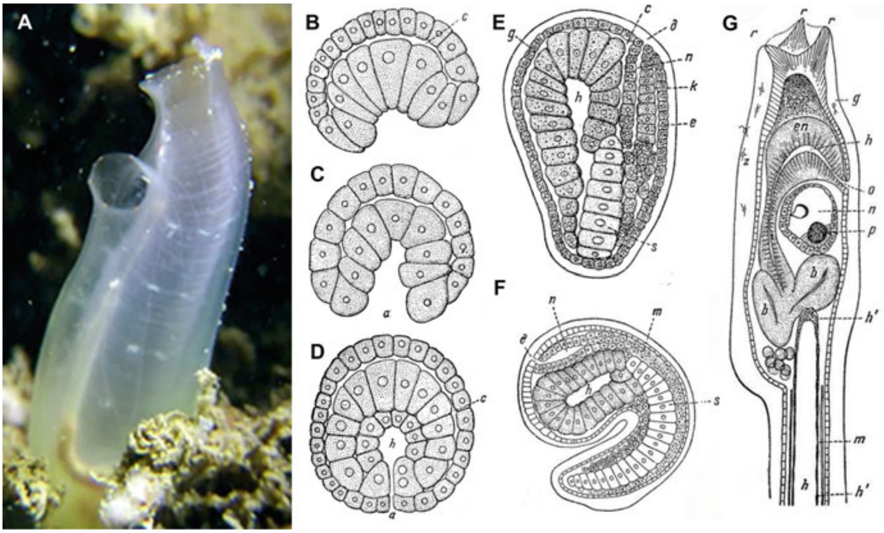


**Fig. 3** (**a**) Adult ascidia *Ciona intestinalis*. (**b–g**) Kowalevsky's drawing showing embryonic development of ascidia *Ciona intestinalis.* (Aadapted from Kowalevsky 1866d). (**b**) Beginning of gastrulation by invagination; (**c**) advanced stage of invagination; (**d**) developing embryo at the stage of neurulation and notochord formation; (**e**, **f**) lateral view of later embryo, showing first appearance of neural tube and arrangement of notochord cells into a single column, and with short tail (**f**). a – blastopore; c – cleavage cavity; d – neuropor; e, g – ectoderm; h – archenteron; m – presumptive muscle cells; n – neural canal; s – notochord cells originated from the "lower" germ layer. (**g**) Anterior part of larva (tadpole). g – mantle; b – intestine; o – oral aperture; en – endostyle; n – cerebral vesicle; p – ocellus; h – notochord; m – muscle band; r – adhesive papillae

gastrulation, and other features of embryonic development, the tunicates turned out to be closely related to *Amphioxus* (Fig. 3b–g). He discovered an affinity between ascidian tadpoles and vertebrates and suggested that ascidians might have been vertebrate ancestors (Kowalevsky 1866d, 1868b, 1871b).

The tunicate larva, whose formation Kowalevsky traced in remarkable detail, resembles a vertebrate embryo. Its nervous system looks like a tube arising from the longitudinal depression of the upper germ layer, the chord passes along the tail of the larva, and there are gill slits in the anterior part of the alimentary canal (Fig. 3g). The discoveries of Kowalevsky concerning the development of *Amphioxus* and especially tunicates were so striking that at first they were met with suspicion. Our present understanding that vertebrates develop from a two-layered gastrula can be traced to this fundamental work, which revolutionized embryology and zoology (Hall 1998). Kowalevsky suggested that vertebrates, including the cephalochordate *Amphioxus*, might have evolved from tunicate-like ancestors. This idea was endorsed by Darwin (1874) and Ernst Haeckel (1834–1919) (1874), who considered tunicates as "connecting intermediate forms between the lower worms on the one hand and vertebrates on the other" (Holland and Gibson-Brown 2003).

Kowalevsky's findings and conclusions were quickly accepted by other prominent evolutionists such as Karl Gegenbaur (1826–1903). The origin of vertebrates from an ascidian tadpole-like ancestor became a favored theory. In 1894, Arthur Willey (1867–1942) reviewed the information on the embryology of amphioxus and ascidians in an influential book "*Amphioxus* and the Ancestry of the Vertebrates" (Hall 1999).

The famous English zoologist Sir Edwin Ray Lankester (1847–1929) emphasized that although Albert Kölliker (1817–1905) and Remak had studied the development of some tissues from embryonic cells earlier, it was Kowalevsky who "in small transparent embryos (such as those of Ascidia, *Amphioxus*, *Sagitta* and *Argiope*) traced the history of adult organs cell by cell to the original egg-cell" (Lankester 1902).

Darwin delighted in the discovery that the tunicate was actually a chordate. Kowalevsky's research suggested to Darwin that the argument from embryonic recapitulation could be carried back beyond the vertebrates to non-vertebrates. The ascidians might then be considered in their earliest form the ancestor of the vertebrates (including man), while their present form showed a regression to a non-vertebrate character. Darwin believed that, should Kowalevsky's research be confirmed by other scientists, "the whole will form a discovery of the very greatest value" (Darwin 1874. Cited in Bljacher 1959).

Another important work of Kowalevsky in the 1860s was his research on the embryology of ctenophores (1866c, 1873). Kowalevsky described very accurately the peculiar cleavage of their eggs and for the first time discovered a cross-shaped cell anlage between ecto- and endoderm, giving rise to tentacle muscles. In other words, he found the mesoderm absent in the rest of the coelenterates, to which Ctenophora and Cnidaria then belonged.

Kowalevsky made the first embryological studies on several other invertebrate groups such as coral polyps, echiurids, phoronids, camptozoas, and acrania. In case of some other groups, his work was preceded only by superficial and incomplete studies (comb jelly, amphineura, scaphopods, chaetognaths, brachiopods, echinoderms, and tunicates). In the study of the development of annelids, insects, and arachnids, Kowalevsky had several predecessors, but his research provided so much fundamentally new data that Kowalevsky's works continue to be cited in modern works devoted to these subjects.

The technique of making histological sections used by Kowalevsky (1871a, 1886b, c, d, 1887) started a new era in insect embryology (Fig. 4). These studies were also of great significance for general embryology since they formed the basis of the classical germline theory. Kowalevsky (1885, 1887) made the first strictly scientific descriptions of internal processes during insect metamorphosis and organogenesis. These works were made under the influence of phagocytic theory, founded shortly before by a friend of Kowalevsky, I. Metchnikoff. Henri Viallanes (1856–1893) and August Weismann (1834–1914) noticed before Kowalevsky that the organogenesis of definitive organs during the metamorphosis of flies was accompanied by the destruction of most larval organs (Bljacher 1959) but did not describe this process in detail. Professor Mitrophan Ganin (1839–1894) in Warsaw

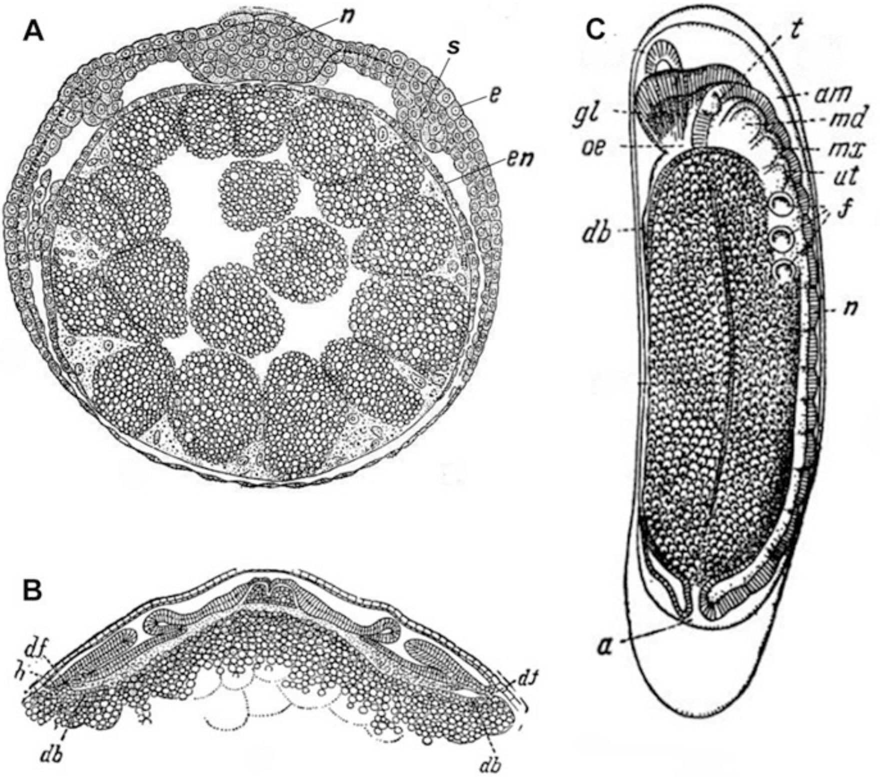


**Fig. 4** Kowalevsky's drawing showing embryonic development of annelids and insects (adapted from Kowalevsky 1871a). (**a**) Development of *Euaxes* sp. (Annelida, Clitellata). Cross section of the anterior end of the embryo at the germ band stage. (**b**) The water beetle *Hydrophilus piceus* (Insecta, Coleoptera): Cross section of the ventral side of the embryo at the stage when germ band covers the entire ventral side. db – visceral mesoderm; df – somatic mesoderm. (**c**) Honey bee *Apis mellifica* (Insecta, Hymenoptera): longitudinal section of the embryo at the stage of dorsal closure of germ layers. a – anus; e – ectoderm, en – endoderm; f – anlage of legs; gl – brain lobe; md – mandibles; mx – maxilla; n – anlage of ventral nerve cord, t – antenna; s – anlage of somites

established the significance of the so-called germinal discs, from which the organs of an adult fly developed, but the process of destruction of the larval organs still remained obscure (Bljacher 1959). Kowalevsky was the one to solve the riddle by discovering the phenomenon of histolysis in the metamorphosis of flies, that is, the digestion of decaying tissues by phagocytes.

At the same time (in the late 1860s) Kowalevsky was much attracted by vertebrate development. He studied embryonic development of sharks and teleosts, amphibians, turtles, birds, and mammals (1869, 1870f, i). He identified the basic principles of fish development, in this way introducing "fish to the general theory of the development of vertebrates" (Poljanskij 1955, p. 40).

## Homology of the Germ Layers

Homology of the germ layers as a universal principle that applies beyond separate individual "phyla" of animals was formulated by Kowalevsky in 1871. It was part of the empirical basis for the Darwinian monophyletic view of evolution. In the introduction and in the concluding remarks to his most extensive work "Embryological studies of worms and arthropods" (1871a), Kowalevsky states with utmost clarity the principles of the theory of germ layers as an anlage, the homology of which should be limited only to representatives within a phylum but also when comparing animals from different phyla. According to Kowalevsky, germ layer homology "speaks of the relationship of types, for which we find evidence in invertebrates at every step" (Kowalevsky 1871a, p. 19). Haeckel appreciated Kowalevsky's work, writing in his *Anthropogenie*: "The most significant embryo histories in the recent time were those of Kowalevsky" (Haeckel 1874, p. XX).

Kowalevsky did not doubt the true relationship between different animal phyla, based on the similarity of the early stages of their embryonic development. In this regard, he homologized the developmental stages, germ layers, and various organs. However, it is not quite clear what the homologization criteria were for Kowalevsky. Apparently, he relied on the similarity of the developmental processes and their corresponding stages, the topography of the germ layers and their further fate, that is, their derivatives, those parts of the body and organs that originate from different layers.

## Legacy

In the literature devoted to the scientific legacy of Kowalevsky, it has often been discussed why there were no definitive phylogenetic conclusions and broad morphological generalizations in his works. The authors of the necrologies and memoirs, who knew Kowalevsky closely, answered this question in more or less the same manner, writing about Kowalevsky's adherence to well-established facts, his dislike for speculations, and his exceptional scientific sensitivity and caution (see Dogiel 1945; Pilipchuk 2003). His aim was not schematization but a detailed study of specific ontogenetic phenomena that undergo change in the course of the historical development of the animal world. From the beginning to the end of his scientific activities, Kowalevsky found explanations of these changes in Darwin's theory.

The largest contribution to science made by Alexander Kowalevsky was the proof of the unity of the laws governing the development of the entire animal world. In his famous "History of the development of the *Amphioxus*" (1865, 1867b, 1870h, 1876) and in a series of subsequent works on the development of ascidians, coelenterates, echinoderms, polychaetes and arthropods, Kowalevsky proved the universal prevalence of the same early larval stages (blastula, gastrula, and some others) in different animal phyla. He proved the homology of the germ layers throughout the animal world and the correspondence of the main types of cavities (gastral, primary and secondary) in different animals.


**Fig. 5** The Alexander Kowalevsky bronze medal award of the Saint-Petersburg Society of Naturalists for extraordinary achievements in evolutionary developmental biology and comparative zoology. (**a**) – front face; (**b**) – reverse side

Many researchers wrote about accounting of how Kowalevsky fits into a history of evo-devo (see Mikhailov and Gilbert 2002; Raff and Love 2004; Mikhailov 2012). The main conclusion is that the widespread focus on the molecular biological techniques that have allowed the discovery of homologous regulatory genes, homologous developmental pathways, and changing patterns of homeotic gene expression over the past three decades confirmed many of the discoveries made by Kovalevsky in animal development (Satoh et al. 2012; Holland 2015; Stolfi and Brown 2015).

An international prize, the Alexander Kowalevsky Medal, has been established to honor Kowalevsky's discoveries in embryology (Fig. 5). It is awarded by the St. Petersburg Society of Naturalists in Russia for outstanding contributions to the understanding of evolutionary relationships among major groups in the animal kingdom, to evolutionary developmental biology, and to comparative zoology (see Mikhailov and Gilbert 2002; Ereskovsky 2012).

## Cross-References

- ▶ Developmental Homology
- ▶ Ernst Haeckel (1834–1919)
- ▶ Evo-Devo and Phylogenetics
- ▶ Evo-devo's Contributions to the Extended Evolutionary Synthesis
- ▶ Macroevolution

**Acknowledgments** Author gratefully thanks Natalia Lentsman for English correction. This work was supported by the Russian Science Foundation grant no. 17-14-01089.

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