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From development to evolution: the re-establishment of the "Alexander Kowalevsky Medal"

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ABSTRACT The Saint Petersburg Society of Naturalists has reinstated the Alexander O. Kowalevsky Medal. This article announces the winners of the first medals and briefly reviews the achievements of A.O. Kowalevsky, the Russian comparative embryologist whose studies on amphioxus, tunicates and germ layer homologies pioneered evolutionary embryology and confirmed the evolutionary continuity between invertebrates and vertebrates. In re-establishing this international award, the Society is pleased to recognize both the present awardees and the memory of Kowalevsky, whose work pointed to that we now call evolutionary developmental biology.

KEY WORDS: *evo-devo, comparative embryology, Kowalevsky Medal, amphioxus, tunicates*

"...In looking to the future, paradoxically we also look to the past."
(Morris, 2000)

The St. Petersburg Society of Naturalists has reinstated the Alexander Kowalevsky Medal for Comparative Embryology, an award originally cast in 1910 but which has never yet been presented (Fig. 1). In reinstating this award, the St. Petersburg Society of Naturalists honors both the present awardees and the memory of A.O. Kowalevsky, one of the world's foremost comparative and evolutionary embryologists whose work pioneered what we today call evolutionary developmental biology.

The idea that studying embryos could be useful for understanding evolution has a long history. The modern comparative embryology that would become evolutionary embryology can be said to have originated in the researches of four men, each of whom had ties to the St. Petersburg scientific community: Kaspar Wolff, Christian Pander, Martin Heinrich Rathke and Karl Ernst von Baer. They were distinguished morphologists and left accurate drawings and descriptions of embryos of many vertebrate and invertebrate species (see Churchill, 1991).

Darwin's work caused a major split among the Russian comparative embryologists. Indeed, despite the fact that his work became one of the principle supports for Darwinism and for modern evolutionary developmental biology, the St. Petersburg embryologist of German Estonian descent, von Baer (Fig. 2), never subscribed to the theory of natural selection (see Ospovat, 1981; Nyhart, 1995). Yet his principles of embryology, especially his "*law of embryonic similarity*", according to which different animal groups

share common stages in early embryonic development, allowed younger investigators to use the community of embryonic development as a means to discern phylogenetic relationships (see Kaavere, 1991; Mikhailov, 1997). As Peter Bowler (1996, p. 141) notes:

"Many older morphologists - Karl Ernst von Baer is a good example - simply refused to accept the cross-type homologies. But evolutionism made it possible - indeed inevitable, on the principle of a monophyletic origin for the animal kingdom - to seek the links between the types."

The homologies between phyla were what Kowalevsky sought. And he sought them in the early development of the embryo, precisely where Baer's laws would predict them to be found. Again, as Bowler (1996, p. 142) concludes in his dissection of the movement from comparative to evolutionary morphology:

"New methods were introduced in an effort to seek links that derived from the darkest depths of the evolutionary past. The most obvious of these was Alexander Kowalevsky's use of histological techniques in the study of the early embryo to determine homologies that might no longer be visible in the fully developed organism."

Kowalevsky is most well known for his two papers (Kowalevsky, 1867a, 1871) presented to the Imperial Academy of Sciences in St. Petersburg which provided a new way of looking at evolution

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and development - by studying the cellular patterning of the early embryo. One of these papers documented the early development of the cephalochordate amphioxus (*Branchiostoma*); the other paper documented the affinities of tunicate larvae to vertebrates and caused them to also be classified as chordates. But in addition to these seminal papers in the relationship of evolution to development, his pioneering work on the embryonic development of annelids, brachiopods and many other animals greatly contributed to our vision of relations between different branches of the Metazoan kingdom.

A Biographical Memoir of Kowalevsky

The Making of an Embryologist

Alexander Onufrievich Kowalevsky (1840-1901) was born in the manor "Vorkovo" of the Daugapils district (Vitebsk Province, Russian Imperia) into a middle-class landowning family (see Adams, 1978). After his home education, he firstly enrolled at the School of Railway Engineers (1854) but then transferred to the St. Petersburg University as a student in the department of natural sciences at the Physical-Mathematical faculty (1858). Soon afterwards he traveled abroad to expand his scientific knowledge, visiting Heidelberg and Tübingen where he studied anatomy, histology and zoology under the direction of H.G. Bronn, H.A. Pagenstecher and K.R. Leuckart (1860-1862). For a short time Kowalevsky returned to St. Petersburg, and he graduated as a Candidate of natural sciences.

His embryological career started in 1863 in Naples where he began to investigate the embryonic development of amphioxus, tunicates, holothurians and other marine invertebrates. Here, he attempted to find developmental criteria for the phylogenetic "reconstruction" of these animals, first of all for amphioxus. It

seems likely that in selecting amphioxus as the first model object, Kowalevsky was influenced by Pagenstecher and Leuckart (see Vocinich, 1970). Scientific results of this work became the basis for his Magister's Dissertation ("*The Developmental History of Amphioxus lanceolatus* or *Branhiostoma lumbricum*") defended at St. Petersburg University in 1865 (see: List of the works of A.O. Kowalevsky, 1906). The main conclusions of the dissertation were as follows: (1) the lancelet that was previously considered a fish-like vertebrate actually belongs to cephalochordates and (2) at advanced stages of development, the lancelet embryo resembles the vertebrate. A large part of these conclusions continue to appear to be true today (see for instance, Holland, 2000; Holland and Chen, 2001; Arthur, 2002). At that time, the 73-year-old von Baer evaluated the Kowalevsky Dissertation as a "*first-class study*" (quoted in: Vocinich, 1970, p.110).

Kowalevsky then focused on the development of another controversial group of animals, the ascidians (Fig. 3). His attention was captured by peculiar characteristics of ascidian larvae that resemble those characteristics of lancelet and vertebrate embryos. He showed that ascidians, at that time classified as molluscs ("*soft-shelled clams*"), are characterized by certain developmental similarities with cephalochordates. He showed that ascidian larvae were certainly non-molluscan and, in fact, shared numerous traits with vertebrates. These characteristics included a neural canal similar to that of amphioxus, a brain, pharyngeal slits, and a notochord. By tracing these structures back to their origins in the embryonic germ layers, Kowalevsky demonstrated that these features were homologues, not merely analogues. He interpreted these as suggesting that the tunicate larva may have been the ancestor of the fish, and hence, of all vertebrates (see Beeson, 1978; Bowler, 1996).

This work became a major support for the evolutionary theory. Haeckel introduced it in his *Natürliche Schöpfungsgeschichte* of 1868, and Darwin himself, publicized Kowalevsky's research in the introduction to his *Descent of Man* (second edition, 1874, p. 160), stating that:

"We should be justified in believing that at an extremely remote period a group of animals existed resembling in many respects the larvae or our present Ascidians, which diverged into two great branches - the one retrogressing in development and producing the present class of Ascidians, the other rising to the crown and summit of the animal kingdom by giving birth to the Vertebrata."

Kowalevsky's work was featured in many reviews of biology (see Fig. 4), and the tunicate study became so well publicized that the opponents of evolution, especially morphologists such as Louis Agassiz, felt overwhelmed. Agassiz (1874) wrote, in an article published immediately after his death:

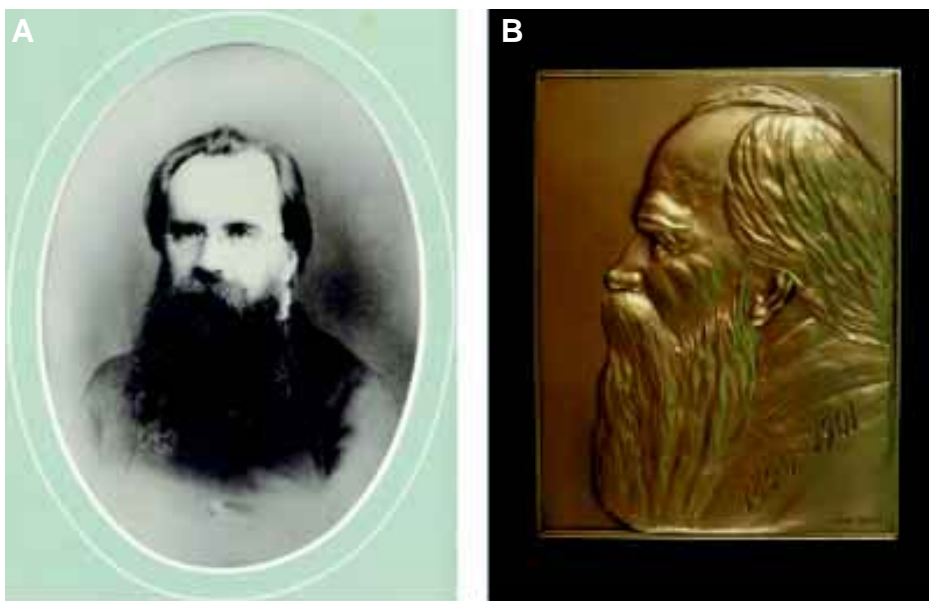


Fig. 1. Alexander Onufrievich Kowalevsky (1840-1901). (A) Kowalevsky's photograph taken in the middle of the eighties (from archives of the Department of Zoology of Invertebrates of St. Petersburg University). Other Romanizations of his family name include Kovalevskii (Vocinich, 1970) and Kovalevsky (Adams, 1978). The first name is sometimes spelled Alexandr. (B) The bronze medal with Kowalevsky's profile, designed by Petr Stadnitzky.



Fig. 2. Karl Ernst (Maksimovitch) von Baer (1792-1876), member of the Imperial Academy of Sciences (from Blyakher, 1962; modified).

"Kowalevsky describes, in the Ascidians, a formation of longitudinally arranged cells as representing an incipient backbone, running from the middle of the body into the tail, along a furrow of the germ of these animals in which the main nervous swelling is situated. This was hailed as a great discovery by the friends of the transmutation theory. At last the transition point was found between the lower and higher animals, and man himself was traced back to the Ascidians. One could hardly open a scientific journal or any popular essay on Natural History, without meeting some allusion to the Ascidians as our ancestors."

Agassiz then tried to counter these arguments, using data (largely from von Baer) suggesting that the ascidian neural tube is not dorsal at all, but, as is common in invertebrates, ventral. Scientific research has confirmed the dorsal neural tube and notochord of ascidian larvae as well as the affinities of these larvae with the vertebrates.

Further Research of A.O. Kowalevsky¹

Kowalevsky's motto was: "*In specialibus generalia quaerimus*" ("We seek the general in the specifics"). Following this dictum Kowalevsky attempted to reveal similar patterns of Metazoan development. His main field research on the development of marine animals was carried out at the Naples Zoological Research Station (see Fantini, 2000) and at various other sites in the Mediterranean, the Red Sea and the Black Sea, where he organized the Sevastopol Biological Station. These studies on numerous animal phyla expanded the germ-layer concept of Pander and von Baer to include the invertebrates, thus establishing another important embryological unity to the animal kingdom. In 1867, in his report on amphioxus, he also showed that invertebrates and vertebrates alike (*Psolinus*, *Amphioxus*, *Phoronis*, *Limnaeus*, *Echinus*, *Sagitta*, *Ascidia*, *Esclotzia*, as well as turtles, birds, and mammals) form from a bilaminar sac. "Thus the first formation of the embryo would be quite in agreement for all these different

animals; only in the further changes do we see the differences that characterize the individual type", Kowalevsky wrote (Kowalevsky, 1967a). The homologies of the germ layers between invertebrates and vertebrates was a theme that Kowalevsky would elaborate throughout his research (see Oppenheimer, 1967).

During the 1860s and 1870s, Kowalevsky and his friend (and sometimes critic) I. I. Metchnikoff (later the Nobel laureate and founder of immunology) created a new biological discipline, comparative invertebrate embryology (Tauber and Chernyak, 1991). The two argued over the details of various organism's development. These arguments included the tunicates. Kowalevsky claimed the notochord originated from the dorsal portion of the endoderm, while Metchnikoff thought this region formed the ventral portion of the neural tube. Eventually Metchnikoff concurred with Kowalevsky. The two Russian embryologists also collaborated in working out a theory by which mesoderm formation might occur through invagination of the endoderm (Fig. 5).

Kowalevsky took special interest in the development of the bilateral, worm-like animals belonging to phylum *Phoronida*. The results of these investigations provided the basis for his Doctoral Thesis that was presented publicly in 1867 under the title: "*Anatomy and Developmental History of Phoronis*" (Kowalevsky, 1867b). At the same year, Kowalevsky (together with I.I. Mechnikoff) was awarded the K. von Baer Prize from the Russian Imperial Academy of Sciences.² Long after, re-esti-

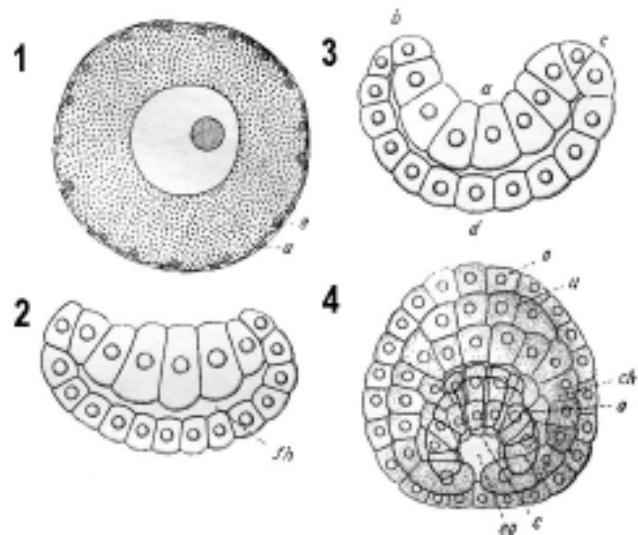


Fig. 3. Kowalevsky's drawing showing early stages of ascidian development (adapted from Kowalevsky, 1871). (1) Around the yolk, a tightly connected cell layer is generated by cells of the follicular epithelium (a) and the follicular cells invaded a yolk mass (e); magnification x550. (2) One wall (one-layer blastoderm) of developing egg is beginning to invaginate into the other; fh, cleavage cavity; magnification x290. (3) Advanced stages of invagination; bac, "lower" germ layer; bdc, "upper" germ layer; magnification x290. (4) Developing egg (embryo) at more advanced stages; eo, invagination orifice; ch, notochord cells originated from the "lower" germ layer; o, "upper" germ layer; magnification x290.

¹A detailed bibliography of Kowalevsky was beyond the scope of this article (for references see: Kowalevsky, 1951; Blyakher, 1959; Adams, 1978; Pilipchuk, 1990). His younger brother was the vertebrate evolutionary paleontologist, Vladimir O. Kowalevsky (the husband of Sonja Kowalevskaya).

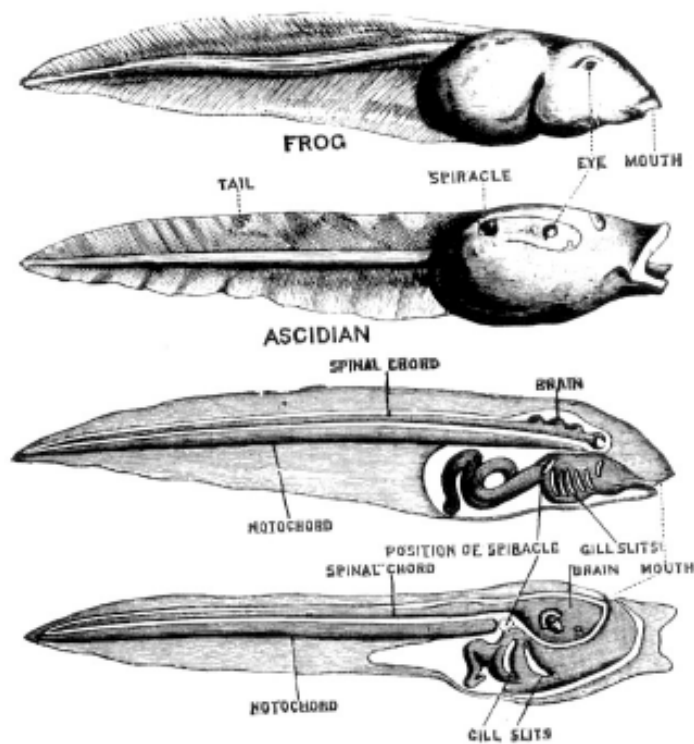


Fig. 4. Tadpole of a frog and an ascidian (from Lankester et al., 1891).

mating this period of Kowalevsky's research, Brian Hall (1998, p.138) notes:

"Between 1866 and 1871, Kowalevsky laid the foundations of our knowledge of the fundamental, shared features of vertebrate embryos....Our understanding that vertebrates develop from a bilayered gastrula can be traced to this fundamental work, which revolutionized embryology and zoology".

The work on the embryonic development of lancelets, tunicates, ctenophores, coelenterates, worms, echinoderms, and brachiopods was notable for careful attention to methodological details. Here, Kowalevsky succeeded in maintaining in laboratory conditions several marine species and their embryos that had been cultured previously. Thanks to his excellent experimental skills, he was able to perform a large-scale screening of developmental patterns in many animal species. Kowalevsky's work was not confined to the early stages of embryonic development but was also extended to the patterns of organogenesis and growth as well as to different aspects of taxonomy and morphology of the species studied.

Although Kowalevsky's experimental success was considerable, he did not make much effort to synthesize his observations and theories into a coherent treatise on evolution. Nonetheless, Kowalevsky's ideas have fared well over the past thirteen decades. At present, it is generally accepted that the vertebrates evolved from protochordates by modifications of the developmental programs. Moreover, it seems to be likely that many characteristics that were previously associated with vertebrates only can be also

traced in chordates (Cameron et al., 2000; Graham, 2000; Murakami et al., 2001; Satoh, 2001). For instance, it has been suggested that the evolution of the vertebrates could involve the acquisition of the so-called "new head" (Gans and Northcutt, 1983). The data about *Hox* gene expression in cephalochordates suggest that the vertebrate head is actually homologous to the anterior part of the lancelet. At present, the amphioxus – the most primitive of living chordates, is considered as an example of the so-called "vertebrate in waiting" (see Holland and Holland, 1999). Ascidian embryos are also beginning to gain popularity as a model organisms for comparative expression studies of highly conserved developmental genes that control a body patterning in vertebrates (see Satou and Satoh, 1999; Cunliffe and Ingham, 1999). Moreover, there are experimental evidences for the conservation of cis-regulatory mechanisms controlling *Hox* gene expression in the neural tube of amphioxus, mouse and chick embryos (Manzanares et al., 2000; Holland and Chen, 2001). While the absolute specificity of the germ-layers is not as fixed as Kowalevsky had hypothesized, the similarities between the genetic mechanisms underlying invertebrate and vertebrate development has become a major feature of evolutionary developmental biology (see Raff, 1996; Gilbert et al., 1996; Wilkins, 2001).

University Commitments

Besides the preoccupation on research, Kowalevsky had many other commitments (teaching, administration, and etc.). From the beginning of his professional life, Kowalevsky had permanent relationships with Russian universities. In 1866 Kowalevsky became a conservator of the Zoological Cabinet at the St. Petersburg University and he met for the first time with Karl Fredrik (Fedorovitch) Kessler, who was a director of its Zoological Department. Kessler organized a department-sponsored research trip of Kowalevsky to the Mediterranean Sea where Kowalevsky not only performed his experiments but also collected a judge number of marine animals. A number of his collections, still in existence and carefully keeping, laid the basis of the Museum of Invertebrates.

In 1868, after his extremely productive period of experimental research, Kowalevsky, at the age of 28, was appointed ordinary (full) Professor at the Kazan' University. Later he taught as a professor at the Saint Vladimir (Kiev, 1869-1873), Novo-Russian (Odessa, the former Novorossiysk, 1873-1890) and finally at the St. Petersburg (1891) University at which he was the director of the Anatomical Histological Cabinet (1891-1894). Up to that time, Kowalevsky was a member of the Society of Naturalists of Modena and the Cambridge Philosophical Society, a foreign member of the Royal Society, a corresponding member of the Academy of Sciences of Brussels and Turin. In 1890 he was elected as a member of the Russian Imperial Academy of Sciences.

Kowalevsky continued pursuing his research after he had earned all these honors. In addition, he devoted much time and effort to help biological research in Russia. Under the supervision of Kowalevsky, a new department named the Special Zoological Laboratory was founded in the Imperial Academy. At this laboratory, Kowalevsky worked with his students, among them embryologist Constantin Davydoff, immunologist Sergei Metal'nikoff, protistologist Vladimir Schewiakoff and others (see Fokin, 2000). Despite his numerous commitments and administrative duties at that time, Kowalevsky was in the prime of his scientific life. In a fall of 1901, he was busy with

²The Prize was instituted by the Academy in 1864 in commemoration of the 50th jubilee of a Baer' professional activity. The Baer Prize was awarded by the St. Petersburg Academy up to 1906. Once again, Kowalevsky (besides with Metchnikoff) was awarded the Prize in 1870.

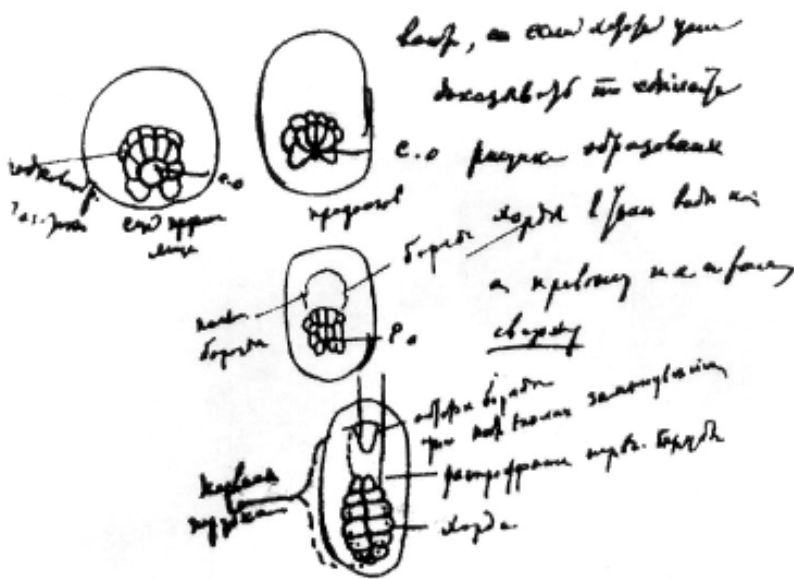


Fig. 5. Ingression of the vegetal plate to form mesoderm illustrated in a letter sent by A. O. Kowalevsky to I. I. Metchnikoff (from Tauber and Chernyak, 1991).

arrangements of his future long-time scientific voyage to Java, but a sudden hemorrhage of the brain ended his life at the age of 61.

The International Award: The “Alexander Kowalevsky Medal” by the St. Petersburg Society of Naturalists

The St. Petersburg Society of Naturalists is one of the oldest scientific societies in Russia. The foundation of the Society was laid in 1868. Its founder and first president (1868-1882) was a famous Russian zoologist, K. F. Kessler. Historically the Society has strong ties with the St. Petersburg University and for many years it survived as a part of the University. The Society had among its presidents such academic figures as geologist and paleontologist Alexander Inostrantzev, geologist and philosopher Vladimir Vernadsky, physiologist Alexander Ukhomskii, zoologists Valentin Dogiel and Yuri (George) Polyansky. Among honorary members the Society elected Karl von Baer, Rudolf Virchow, Charles Darwin, Ernst Haeckel, Louis Pasteur, Ilya Metchnikoff and Alexander Kowalevsky. The Society supported many expeditions and founded in 1882 the Solovetsk (later Murmansk) Marine Biological Station (see Fig. 6) and in 1896 the Borodin Freshwater Biological Station.

In 1910, the St. Petersburg Society of Naturalists had established an international award in commemoration of Alexander Kowalevsky and his legacy. The award included a modest sum of 250 gold rubles and a bronze medal with Kowalevsky’s profile designed by Petr Stadnitzky (see Fig. 1B). According to its statute, the award was to be given for original works in the comparative anatomy and embryology of invertebrates. Professors V.V.Zalensky, V.M. Shimkevich and A.S. Dogiel (father of V.A. Dogiel) were elected the members of the International Award Committee in 1913 (A.K. Dondua, personal communication).

Unfortunately, the First World War followed by the Russian Revolution and Civil War undercut the traditional international ties of the St. Petersburg Society of Naturalists, and interrupted the inauguration of this project. Luckily, the original medal was saved in the Hermitage collections and in the State Mint, where it was first produced in the 1910s and where even the original casting mold was preserved. The St. Petersburg Society of Naturalists recently discovered the existence of the original casting mold and decided to reinstate the international award with the original medal designed over 90 years ago. The decision of the Society was to re-establish the international award “Alexander Kowalevsky Medal” which would include a diploma and bronze medal in its original form. The Kowalevsky’ Medal will be awarded for achievements in comparative and evolutionary embryology to the scientists who have contributed greatly to the understanding of evolutionary relations between major groups of animal kingdom.

At the end of 2001, the Society awarded several medals to honor the distinguished scientists in the field of comparative and evolutionary embryology whose life and work spanned over many years of the 20th century. The Society selected these researchers based on the recommendation letters obtained from the nominators (over 30 persons) from different countries. The final selection for the award was based on a full list of names ranked according the number of nominations. From the year 2002, the Society will intend to make this award the annual, giving every year one medal to a scientist who has made outstanding contributions to comparative and evolutionary developmental biology. Again, selection will be based on the international nominations.

The winners of the first Kowalevsky Medals were announced at the December meeting of the St. Petersburg Society of Naturalists. They are: D. Anderson (Australia), G. Freeman (USA), B. Hall



Fig. 6. Post card entitled “General View on the Murmansk’ Biological Station” with personal note by Valentin Dogiel (from the fund of V.A. Dogiel in Archives of the Russian Academy of Sciences, Russia). Comparative embryology, anatomy and systematic zoology of marine organisms were the prevailing fields of the Station activity. The animal supply and studying was guaranteed by an efficient fishing-fleet. A research boat shown on the card goes under the name of Alexander Kowalevsky.

(Canada), O. Ivanova-Kazas (Russia), C. Nielsen (Denmark), R. Raff (USA), R. Riedl (Austria), and K. Sander (Germany).

While comparative embryology is different from today's evolutionary developmental biology, this earlier science proved to be an appropriate basis for the advancement of evolutionary developmental biology, and studies on the diversity of developmental patterns and strategies are still an essential component of *evo-devo* research (see Raff, 2000). Hence the importance of international awards such as the "Alexander Kowalevsky Medal", which help demonstrate the significance and place of comparative developmental biology in modern evolutionary science.

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