

Experimental embryology in Soviet Russia: the case of Dmitrii P. Filatov (1876-1943)

T. A. DETTLAFF and S. G. VASSETZKY*

*Filatov¹ Laboratory of Experimental Embryology,
Kol'tsov Institute of Developmental Biology,
Russian Academy of Sciences, Moscow, Russia*

Dmitrii Petrovich Filatov was the founder of experimental embryology in our country, a great embryologist, the creator of an original comparative morphological trend in the mechanics of development, a naturalist and zoologist, and organizer and head of the school for experimental embryologists in Moscow.

Filatov's creative career can be shortly summed up as follows: from evolutionary comparative anatomy and embryology to experimentation as a method of explaining intrinsic patterns of development and, in experimental embryology, from a study of the interaction of parts in the individual organogeneses and in different animal species aimed at demonstrating the variability of ontogenetic interactions to analysis of the evolutionary significance of these interactions. This logically clear and, as seems now, quite obvious course was in fact revolutionary and novel. It was the result of pertinacious creative work and independent scientific thought. The overcoming of the restricted current scientific movement and the laying down of future routes is a destiny reserved for comparatively few really great scientists, among whom D. P. Filatov must undoubtedly be numbered.

During the years elapsed since the demise of Filatov, his science changed beyond recognition; there occurred a union of formerly dissociated sciences, namely experimental embryology (developmental mechanics), genetics and the molecular biology that arose during this period, a union conducive to enormous

progress in the study of patterns of development. The new methods of molecular biology and molecular genetics and the information gained by their use have revolutionized the science of development and have for some time relegated to the background many problems which had perplexed scientists in the past, though without detracting from their significance. The laws of inductive interactions, determination, and differentiation discovered before the advent of molecular biology require reappraisal at the new level of knowledge and mark out objects for molecular-genetic research.

On the other hand, the progress attained at the morphological level in understanding the integrity of the developing organism and the complexity and variability of ontogenetic correlations is still insufficiently taken into account when studying differentiation at the molecular level. The contribution made by Filatov in working out of these problems is very important and many scientific methodological and theoretical concepts developed by him were directed to the future. They still retain their importance today.

Several articles concerning Filatov's creative path have been published (Foreword to the sixth volume of the Transactions of the Institute of Experimental Morphogenesis, commemorating the 60th birthday and 35 years of scientific activity of D. P. Filatov; Malinovskli and Popov, 1943; Polezhaev, 1946).

Dmitrii Petrovich Filatov was born on January 31, 1876 in the village of Teplyi Stan in the Smolensk district. His father, Petr

*Address for reprints: Kol'tsov Institute of Developmental Biology, Russian Academy of Sciences, Ul. Vavilova 26, Moscow, 117808 Russia. FAX: (7-095) 1358012. e-mail: sqvas@ibrran.msk.su

Mikhailovich Filatov, a wealthy landowner, married when already elderly the serf peasant woman Klavdiya Vasil'evna Kazakova. Childhood impressions were apparently a source of the profound simplicity and democratic spirit of Filatov. Filatov's family was distinguished by undoubted natural gifts; his relatives were also outstanding scientists, such as the ship builder, mechanic and mathematician A.N. Krylov, member of the Russian Academy of Sciences, the ophthalmologist V.P. Filatov, member of the Russian Academy of Sciences, the zoologist Prof. B.M. Zhitkov, and the paediatrician Prof. N.F. Filatov. Filatov's childhood was spent in the family circle, in the village amidst nature, and, by the age of eight, he was already a keen hunter. His childhood impressions include meetings with the famous Russian physiologist I.M. Sechenov, who had come to stay at a neighboring farmstead with cousins and read to relatives and friends papers on physiology, which he illustrated by experiments on frogs from the Filatovs' pond. Conditions and life in Teplyi Stan were comprehensively described by Krylov in his memoirs.

Having graduated from high school in 1894, Filatov enrolled in the law faculty of the St. Petersburg University but soon transferred to the Department of Natural Science at Moscow University. In 1900, he graduated from Moscow University at the Department of Comparative Anatomy headed by Professor M.A. Menzbir. Then, from 1902 to 1907, Filatov worked as a supernumerary research worker at the Institute of Comparative Anatomy of Moscow University. At that time, Filatov learned and worked alongside the outstanding Russian morphologists, comparative anatomists, and embryologists. His first studies concern general and comparative embryology. After working as a student on development of the leech *Nepheleis* (Filatov 1898, 1900), Filatov carried out a serious comparative embryological investigation of development of the excretory system in amphibians (Filatov 1904, 1905) which demonstrated the great variability in development of the anterior and posterior canaliculi in *Anura* species and the homologous canaliculi in *Anura* and *Urodela*. He also studied their excretory functions using vital dyes.

A major place in Filatov's creative career was occupied by studies on the rudiment of the cartilaginous skull in some vertebrates (Filatov, 1906) and of the head metamerism (Filatov, 1907). Filatov pursued these studies also later, after a sojourn to Germany in 1906, where he worked in the laboratory of Prof. Furbringer, in the intervals between zoological expeditions to the Yamal peninsula in 1908, to the Caucasian Reserve during 1909-1912, and to the Commander Islands in 1913-1914, and in addition to teaching at the Petrovskii, now Timiryazev, Agricultural Academy.

In his paper of 1906, Filatov described the directional flows of mesenchyme and local accumulations of mesenchymal cells in the early skull anlage, at the stages preceding the cartilage formation. Filatov, not content with establishing this fact, also pondered over direct ontogenetic causes of this directional displacement (concentration) of the mesenchyme. He proposed that the displacements might be due to the influence of other nonmesenchymal rudiments of the head, which exert a mechanical pressure on the surrounding mesenchyme, with the result that the latter forms capsules around them or creates tensions which determine the direction of mesenchyme flows. In 1915, Filatov decided to test this suggestion. This in view, he removed the inner ear rudiment (auditory vesicle) of the toad embryo and transplanted it to another site. As narrated by A.V. Rummyantsev, initially, Filatov attached to this experiment the

limited value of an auxiliary method of investigation. In this experiment, he groped his way, incidentally evolving a microsurgery technique: he ground a standard needle to form a microknife and operated on the embryos under a simple dissection microscope using this knife and a drawn glass rod. This experiment gave an unexpected result: it was found that the auditory vesicle did not passively compress the surrounding mesenchyme, but actively attracted it; at the site of the ablated vesicle in the head, the auditory capsule was absent, while it developed on the abdominal side around the vesicle transplanted there. In this work, Filatov not only established a relationship between the auditory capsule development and the auditory vesicle, as had already been shown by Lewis (1907) (Lewis' work was unknown to Filatov at the time), but he also traced the routes of displacement of the mesenchyme during the laying down of the skull rudiment. He distinguished «fluctuating rudiments» forming the parachordal structures, trabeculae, and septa and mesenchyme accumulations which formed capsules. This work (Filatov, 1916) signified the birth of experimental embryology in Russia, called at that time developmental mechanics. Note that Filatov started these investigations entirely independently and only after the work of 1916 did he become interested in the literature on developmental mechanics. However he devoted himself to it only in 1922 after returning from a protracted field trip to the Aral Sea in 1919-1922.

In 1922, Filatov became a senior research worker at the Glubokoe Ozero Biological Station and in 1924, persuaded by N.K. Kol'tsov, he started to work at the Institute of Experimental Biology affiliated with the National Commissariat of Public Health of the RSFSR, where he organized the first laboratory of developmental mechanics in the USSR. Kol'tsov instantly recognized the value of Filatov's pioneer work and supported it in every possible way. Filatov was already an accomplished scientist when he set to work in the field of developmental mechanics.

Being a confirmed darwinist from his student days, Filatov was keenly interested in problems of variability and evolution of ontogenetic interactions. These interests determined his subsequent scientific career and led him to create a comparative-morphological trend in developmental mechanics. The main object of his research at this stage was the eye. Filatov took an interest in the discovery of differences in the relationship of lens formation to the influence of the eye rudiment between the common and green frogs (Spemann 1912, 1936). These differences consisted in the fact that after removal of the optic vesicle in the green frog, a lens developed from the locally remaining lens-forming epithelium, while the body epithelium, after the optic vesicle had been transplanted beneath it, was unable to produce a lens, whereas in the common frog at the same stages of development, the lens failed to form in the first experiment but did form in the second one.

Filatov was keenly interested in causes of these differences and soon published a series of articles (Filatov, 1925b, 1925c, 1925d, 1925e, 1925f, 1926), including three articles in «Archiv für Entwicklungsmechanik», which made him widely known. The studies in question were also interesting with respect to the experimental methods used. Here, Filatov was one of the first to use xenoplastic transplantation and explantation. He transplanted a piece of abdominal epithelium from the toad embryo to the site of the ablated lens-forming epithelium in the green frog embryo and showed that the eye rudiment of the green frog was able to induce a lens in the epithelium of the toad. Consequently, the differences

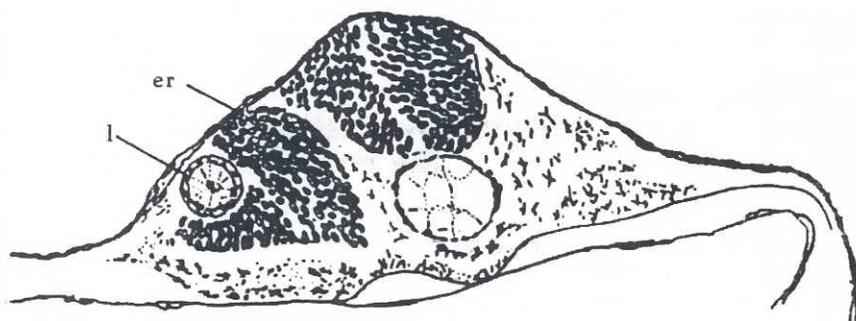


Fig. 1. Lens induction by the optical vesicle in the ectoderm of pike embryo (from Filatov, 1935b).

in results of experiments on transplantation of the eye rudiment under the body epithelium in the green and the common frogs are determined by those in the properties of the epithelium, rather than the eye rudiment. Already in his first studies on the eye development, Filatov proposed that the inductive processes might be of multistep type and other rudiments might determine the lens-forming material before the action of the eye in the green frog.

Later, in addition to his studies on the eye development (Filatov, 1934c) and estimation of the duration of the inductive action of the eye required for determination of the lens (Filatov, 1934d), Filatov also studied development of the limb and tried to elucidate the relative roles and interactions of the epithelium, mesenchyme and splanchnopleure in its determination (Filatov, 1927, 1928, 1930a,b, 1931, 1932, 1933). Note that the epithelio-mesenchymal interactions, which Filatov studied using the limb as a model, were recently shown to occur during development of the rudiments of many organs of both ectodermal and endodermal origin. Among the studies on the development of the limb, of special interest is the study in which Filatov first discovered the significance of the rudiment volume for initiation of differentiation of the organs (Filatov, 1931). Using the limb rudiment as an example, he showed that an artificial increase of the volume of cellular material in the limb bud accelerated its differentiation, whereas enlargement of the eye rudiment did not exert such an effect. On the basis of the study of the limb development, Filatov (1934a) formulated a hypothesis of nonspecificity of the initial stages of some organogeneses.

In order to compare the variability of interactions between the parts of the embryo at the early stages of development in a wider range of objects, Filatov experimentally removed the auditory vesicle in embryos of the Russian and stellate sturgeons (Filatov, 1930c) and pike (Filatov, 1935a) and also transplanted the eye rudiment of the pike to a foreign site (Filatov, 1935b).

Since the late 1930s, Filatov's first pupils N.A. Manuilov, V.V. Popov, and M.N. Kislov were working under his guidance. From 1931 until 1941, Filatov was also in charge of the Laboratory of Developmental Mechanics at the State Research Institute of Experimental Morphogenesis affiliated with the National Commissariat of People's Education, while in 1940 he organized and headed the Department of Embryology at the Moscow State University. The number of his pupils and coworkers increased; among his pupils are T.A. Bednyakova, M.N. Gosteeva, T.A. Dettlaff, R.E. Kogan, F.N. Kucherova, N.I. Lazarev, D.A. Potemkina, O.A. Sidorov, and A.P. Sheina. At the Institute of Experimental

Biology, B.L. Astaurov, G.V. Lopashov, A.A. Malinovskii, and L.V. Polezhaev had close working contacts with Filatov.

In these years, D.P. Filatov thought and wrote extensively on general theoretical topics. His first theoretical article was devoted to defining the concept of determination (Filatov, 1934b). It ranked high in importance inasmuch as it appeared during the period of extreme confusion among scientists, some of whom believed this fundamental concept of developmental mechanics to be untenable. Filatov removed the criterion of irreversibility from the definition of determination and introduced a correction for the experimental conditions. He wrote: «We can define the

determinational process in the epigenetic part of development as that influence of some parts of the developing organism on its other parts due to which the latter, under certain conditions, pass through some stages of their development» (Filatov, 1934b).

In a special article, D. P. Filatov (1937b) discussed the importance of the experiment for morphological characterization of the organs and establishment of their homology. Evolutionary morphologists generally begin a study of the development of an organ from the appearance of a morphologically discernible rudiment. They explain similarities of the position and of the modes of development of the rudiment of two compared organs in different animals by the inheritance of morphogenetic processes of the organ from their common ancestor. The historical morphology does not approach closer than this to a causal analysis of morphogenesis, writes Filatov. Meanwhile, experiments on the developmental mechanics made it possible to extend the history of development of the organs to stages preceding the appearance of their rudiments: They revealed the sources of cellular material involved in formation of the rudiment and interactions of parts of the embryo preceding its appearance.

The question of significance of these data for homology of the organs did not have an unequivocal solution at that time. In the light of results of his own studies on various sources of capsule-forming mesenchyme in fish and amphibians and on the basis of the published data, Filatov drew a significant conclusion, namely that in ontogenesis, «the original structures may arise by different routes and the final result (i.e., the formation of a certain rudiment) is more conservative than the construction of the apparatus which leads to it.» In this article, Filatov subscribes to the view, expressed earlier by Kol'tsov (1934), about the causes of recapitulation of the features observed in the embryogenesis of higher vertebrate animals, which they are losing in the adult state (notochord, gill slits, etc.): Recapitulation was due to the fact that the rudiments of these organs exert an inductive influence and play a morphogenetic role. Filatov believed that although the data of developmental mechanics provide new materials for morphological characterization of the organ, in some cases only, they can be accepted by comparative morphology as arguments in favor of homology, while on the whole, they question the very bases of the so-called "homologization" of the organs according to the data of embryology.

In the following years, D.P. Filatov steadily proceeded to formulate the tasks of the comparative-morphological trend in developmental mechanics. With the aid of pupils and coworkers,

Filatov pioneered a systematic comparative-morphological study of the similar organogeneses in different groups of animals and different organogeneses in the same species. In each organogenesis, he was concerned with the very first stage, i.e., formative interactions of parts at the stages preceding the appearance of visible rudiments of the organs. To standardize these investigations, Filatov introduced the concept of morphogenetic apparatus. For example, the morphogenetic apparatus consists of two parts of the embryo (a source of formative action and a source of morphogenetic reaction) interacting during a short period of determination, which temporarily binds them into one system. The purpose of comparative studies of different morphogenetic apparatuses was to classify them, to reveal the features typifying their evolution, and to elucidate the connections between individual morphogenetic apparatuses in ontogenesis, that provide for integrity of the developing organism. In order to plan and organize these investigations, Filatov introduced the concept of main and secondary experiment. The main experiment establishes the existence of a morphogenetic apparatus, while secondary experiments ascertain the properties of this apparatus. The performance of experiments according to a standard plan and by identical methods makes it easier to obtain comparable characteristics for different apparatuses.

Filatov put forward all these propositions in a series of lectures which he read at the Institute of Morphogenesis in 1936. Later, they were published as a book entitled «The Comparative-Morphological Trend In Developmental Mechanics» (Filatov, 1939b). The subsequent development of Filatov's theoretical concepts was reflected in a series of articles (Filatov, 1939a, 1940, 1941a, 1941b, 1943a).

Instead of a random accumulation of isolated facts, Filatov pursued his research systematically on a definite object of investigation (the morphogenetic apparatus).

Filatov marked out the comparative morphological method for use in the new trend of research. He attached much greater value to the comparative method than W. Roux and most other experimental embryologists. Unlike W. Roux, who, when making comparison, sought only to confirm a fact previously established on another object, Filatov was concerned mainly with the differences, and he saw in the comparative method a means for detecting variability in morphogenetic apparatuses. Filatov defined the comparative method as «a method of putting the static into motion and thus revealing its hidden properties» (Filatov, 1934b). "In a comparative morphological investigation, the approach to the object," states Filatov, "is largely determined by the evolutionary concept and rests upon the fact that every morphological phenomenon has not only the present but also the past and the future" (Filatov, 1941a). The historical method sheds light on those sides of a phenomenon which otherwise would have remained in obscurity and Filatov equates this method with the third dimension. Filatov wrote that whereas in embryology, the historical comparative-morphological method has long lost its novelty, in developmental mechanics, during experimental study of phenomena preceding the formation of rudiments of the organs, it would be «novel to a considerable degree» (Filatov, 1941a, p. 3). Filatov was one of the first and most consistent darwinists in developmental mechanics and the comparative-morphological trend that he set was indeed new for developmental mechanics.

The main conclusion drawn by Filatov on the basis of a comparative-morphological study of the morphogenetic apparatuses

of the lens and supporting filaments was that in various amphibians, there are series of parallel variability in the capacity of the covering epithelium to produce lens and supporting filaments in the presence of the appropriate formative factors. Proceeding from the premise that during evolution, the dispersed state of organs (or their multiple formation) precedes the concentrated state (formation of individual organs), Filatov believed that this concentration of organs depends on the evolutionary changes in the morphogenetic apparatuses and may be accompanied (or result from) by the concentration, first, of a source of formative influence (e.g., eye) and later of a source of morphogenetic reaction.

Filatov distinguished four stages in evolution of the morphogenetic apparatuses of lens and supporting filaments. The first is a hypothetical stage, when both the source of formative influence (visible organ) and the source of morphogenetic reaction are in a dispersed state. The second stage is a condition common to the majority of living amphibian species, where a part of the morphogenetic apparatus, which is the source of formative influence, is concentrated, while the lens- and filament-forming properties are widely dispersed in the covering epithelium. At the third stage, these properties begin to concentrate in the region of normal location of these organs. This state of the material of supporting filaments, theoretically predicted by Filatov, was found by him in the Spanish newt (Filatov, 1943b). At the fourth stage, the filament-forming properties of the epithelium completely disappear, although the source of formative influence persists. In the latter case, e.g., in the axolotl, the supporting filaments are usually absent under the normal conditions, but can be produced experimentally if the epithelium of the axolotl, which is incapable of forming filaments, is substituted for the newt epithelium (experiment of O. Mangold). For the lens, this state was not demonstrated, but it may be assumed to occur in the blind cave-dwelling amphibians. The last stage, reduction of the organ, is possible under the conditions, when the variability for the particular feature is not restricted by the effect of natural selection.

The term «concentration» (or centralization) of the formative capacity of the epithelium is used by Filatov to designate the process as a result of which during normal development, when the eye exerts an inducing influence on the epithelium, the lens-forming material alone is capable of forming a lens, while the remaining epithelium no longer possesses this capacity, although it possessed it at an earlier stage. This was shown for the green frog in the experiments of Filatov's student Sheina (1940). Filatov wrote (1943a, p. 57) that «evolution of the morphogenetic apparatuses of the supporting filaments and lens is a function of a more general process, namely the progressive differentiation of epithelium,» which proceeds in different species at varying speed and is under the control of natural selection.

The dispersed condition of the formative capacity or capacity to produce additional organs (lenses, supporting filaments, etc.) is, according to Filatov, the result of some past multiple state of this organ in remote ancestors. However, possible formation of additional rudiments by the covering epithelium in a foreign site at the early developmental stages may be explained by similar genotypes of its component cells and does not need to rely upon assumptions about original multiplicity of organs, i.e., a historically determined directional transition from the dispersed state of formative capacities to the concentrated one.

Aside from a concentration of morphogenetic properties, Filatov's law can be defined as a coordinated shift of the capacity of the

covering epithelium in different amphibians to form lenses and supporting filaments at a relatively earlier or later developmental stage (Dettlaff, 1948; Ginsburg, 1950b). This objectively established law would not be discovered without a comparative-morphological study of correlations between various morphogenetic apparatuses in each species and their comparison in different animal species, i.e., beyond the comparative-morphological research trend created by D. P. Filatov.

Filatov's hypothesis (1939b) about complex morphogenetic reactions and formative influences still retains great validity. In order to compare and classify different morphogenetic processes, it is necessary, wherever possible, to determine their components. Noting the need to break the morphogenetic apparatus up to its constituent elements, Filatov at the same time indicated the limit beyond which he thought such breakdown pointless. He wrote, «As regards the comparative method, I was interested in the fact that the compared should reflect as fully as possible the specificity of the whole. We endeavor not to carry our analysis to the limit at which morphogenesis and integrity of the organized phenomenon disappear» (1939b, pp. 21-22). Thus, Filatov does not include the study of the physicochemical bases of development in the comparative-morphological trend of developmental mechanics. It should be borne in mind that when Filatov spoke about that topic, molecular biology did not yet exist and only first experiments with dead inducers were carried out. Nonetheless, Filatov saw prospects in studying the chemical nature of the formative effect, but only after the complex morphogenetic process is broken up to its constituent parts, i.e., after analysis of its complexity (Filatov, 1936, 1939b).

The problem of integrity of the developing organism and the role of gradient systems and morphogenetic apparatuses in its realization remained constantly in Filatov's field of vision. He already showed in his article «Organ Formation without Gastrulation» (Filatov, 1937a, 1937c) the absence of direct causal relationship between the sequentially arising morphogenetic apparatuses and, hence, the completeness of development is ensured by other factors. Systematic approaches to analysis of integrity of the developing organism are discussed by Filatov, as mentioned above, in his last works.

In the present article, we have constantly spoken about Filatov the embryologist. However, while the study of cytogenetic patterns of development and evolution of the causal mechanisms of development was the main, it was not the only concern of Filatov. The zoological and applied studies of Filatov (1910, 1912, 1913, 1925a; Filatov and Duplakov, 1926, 1927) are of interest to specialists even today.

Dmitrii Petrovich Filatov died on January 13, 1943 while still creatively active, soon after his major article «Developmental Mechanics as a Method of Studying Some Problems of Evolution» was published (Filatov, 1943a).

The Second World War held up the work of Filatov's pupils for a long time. When the war was over, the comparative-morphological trend of research was resumed and developed actively both in the Laboratory of Developmental Mechanics at the Institute of Cytology, Histology and Embryology of the USSR Academy of Sciences, which after Filatov's death was headed by his pupil V.V. Popov, and in the Laboratory of Organogenesis (headed by Prof. N.I. Dragomirov) at the Severtsov Institute of Evolutionary Morphology (director academician I.I. Schmalhausen). In 1948, after the notorious session of the Lenin All-Union Academy of Agricultural Sciences, these studies were stopped completely.

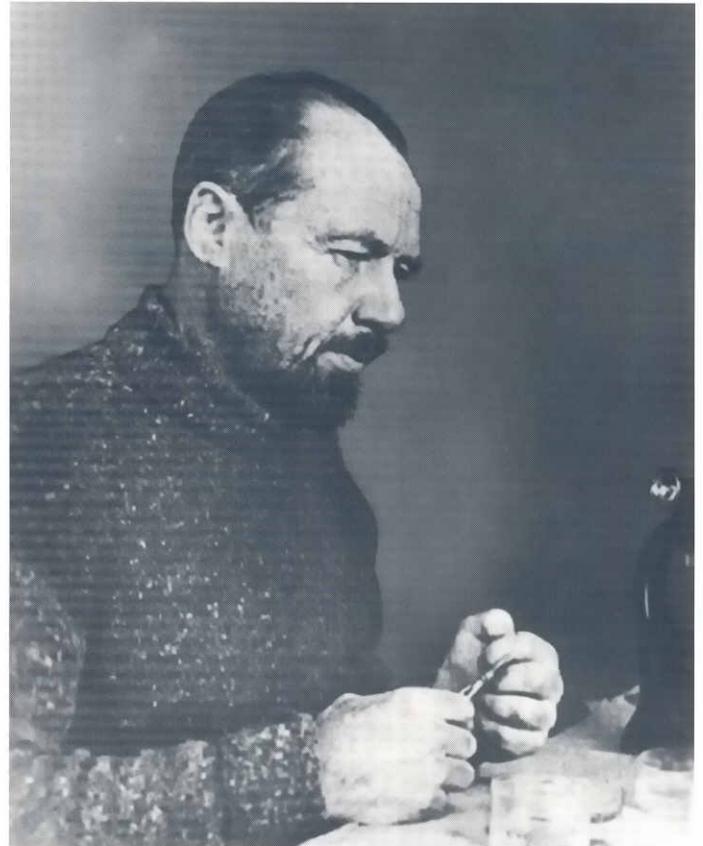


Fig. 2. Prof. Dmitrii P. Filatov (1876-1943) in his laboratory

Up to the stopping of this research, the work both of the immediate pupils of D.P. Filatov and of other Soviet embryologists (A.S. Ginsburg, G.P. Gorbunova, N.I. Dragomirov, G.V. Lopashov, O.G. Stroeveva, and O.I. Schmalhausen) yielded new valuable data which confirmed and extended the laws established by Filatov, and corrections were made to some of his postulates. It was found that in diverse species of Amphibia there was a parallel change in the ability of the ectoderm not only to produce lenses, supporting filaments, and covering epithelium, but also its other derivatives, namely the material of the labyrinth, olfactory organ, and eye. Ginsburg (1950b) proposed, on the strength of her own findings and published data, an extended formulation of the law earlier established by Filatov. She wrote: «Species-specific features of development of various ectodermal rudiments are based on species-specific features of development of the ectoderm as a whole: more or less early latent differentiation of the ectoderm, accompanied by segregation of the areas possessing a stable organogenic specificity.» It was found that apart from the parallelism observed by Filatov in changes of the rate of differentiation of the covering epithelium in series of various Anura and Urodela species, these species could be arranged in one continuous series according to this feature: the ectodermal epithelium differentiated earlier in all studied species of the Anura than in the Urodela (Ginsburg, 1950b).

These differences in the time of latent differentiation of the ectodermal epithelium and its derivatives in the Anura and Urodela are matched by those in the time of determination of the polarity of

the ectoderm and chordamesoderm, as well as in the time of their dissociation into layers. It was also found that the earlier latent differentiation of ectodermal derivatives in the Anura embryos as compared with the Urodela embryos is matched by the differences in time of onset of gastrulation: gastrulation starts at later stages of segmentation in the Anura than in the Urodela, with the result that at the identical stages of gastrulation and subsequent development, the Anura embryos are older than the Urodela embryos, and their ectodermal epithelium contains cells belonging to later generations (Dettlaff, 1948, 1956).

Many new facts were obtained that confirm and extend Filatov's postulate about the complexity of morphogenetic apparatuses. More precise data were obtained about the relative role of the chordamesoderm underlayer and sense organs in determination of the labyrinth material (Kogan, 1944, Ginsburg, 1950a) and of the olfactory organ (Schmalhausen, 1950) in various amphibian species. The complexity of morphogenetic processes in the development of the olfactory organ (Schmalhausen, 1951), eye (Lopashov, 1960), and excretory system (Potemkina, 1953) was established. A method was evolved for the relative characterization of the duration of development (Dettlaff and Dettlaff, 1960; Dettlaff, 1965; Ignatieva, 1979), which extended the possibilities of comparative studies researches and enabled a unit of the duration of development comparable for various species to be introduced.

There has recently been a substantial change in the aims and methods of embryological research all over the world, and the range of objects of research has widened. The Laboratory of Developmental Mechanics founded by Filatov in 1924 at the Institute of Experimental Biology, later renamed as the Laboratory of Experimental Embryology, was repeatedly restructured. It was successively incorporated within the Institute of Cytology, Histology and Embryology of the USSR Academy of Sciences, Severtsov Institute of Animal Morphology of the USSR Academy of Sciences, and, finally, Kol'tsov Institute of Developmental Biology, of the USSR Academy of Sciences (now Russian Academy of Sciences). In 1947, the name of Dmitrii Petrovich Filatov was conferred on the Laboratory of Experimental Embryology at the Institute of Cytology, Histology and Embryology of the USSR Academy of Sciences.

Following Filatov's death, the laboratory was in charge of V.V. Popov in 1943-1954 and of B.L. Astaurov during 1954-1967. In 1967, with the organization of the Institute of Developmental Biology, the laboratory was split into three independent laboratories, viz., Laboratory of the Developmental Cytogenetics headed by B.L. Astaurov, Laboratory of Organogenesis headed by G.V. Lopashov, and Filatov Laboratory of Experimental Embryology headed by T.A. Dettlaff.

At present there are several laboratories at the Kol'tsov Institute stemming up from the Filatov Laboratory which are now headed by pupils of Filatov's pupils or of his colleagues: Filatov Laboratory of Experimental Embryology (head-S.G. Vassetzky), Laboratory of Cell Differentiation (head-O.G. Stroeve), Laboratory of Developmental Biophysics (head-N.D. Ozernyuk), Laboratory of Organogenesis (head-A.T. Mikhailov), Laboratory for Problems of Regeneration (head-V.I. Mitashov), Laboratory of Developmental Cytogenetics (head-V.A. Strunnikov).

In recent years, work has been carried out at the Filatov Laboratory of Experimental Embryology on the patterns of organization of the mature egg in oogenesis, fertilization, and early

embryogenesis, with specific emphasis on the role of cytoskeleton and hormonal control in these processes; in all these studies, the methods and approaches of the comparative-morphological trend of research evolved by Filatov are widely used for analyzing the patterns of development not only at the morphological level but also at the submicroscopic and molecular-biological levels.

It is impossible in a short article to adequately elucidate the contents of scientific research of D.P. Filatov, and, in particular, to put over Filatov's individual style of scientific thinking and his profound and original philosophic and analytic approach to the phenomena of development. Reading the works of Filatov will acquaint one not only with scientific facts but also with the rationale of research, reflections and deliberations of interest to all embryologists following an independent research path.

The pupils and comrades of Dmitrii Petrovich Filatov will gratefully remember him as an exceptional man, teacher and comrade.

References

- DETTLAFF, T.A. (1948). A Comparative-experimental Study of the Evolution of Ectoderm, Chordamesoderm and Their Derivatives in Anamnia. Doctoral Dissertation, Moscow.
- DETTLAFF, T.A. (1956). Species-specific differences in morphogenetic properties of embryonic material and shifting of gastrulation in relation to cleavage stages: Importance of correlation of developmental stages and cell populations. *Trans. (Doklady) USSR Acad. Sci.* 111: 1149-1152.
- DETTLAFF, T.A. (1965). Duration of interkinetic states of cells, cell divisions and differentiation. In *Cell Differentiation and Inductive Mechanisms*, Nauka, Moscow, pp. 147-159.
- DETTLAFF, T.A. and DETTLAFF, A.A. (1960). Dimensionless characteristics of developmental duration in embryology. *Trans. (Doklady) USSR Acad. Sci.* 134: 199-202. (Russian).
- FILATOV, D.P. (Filatov, D.) (1898). Einige Beobachtungen über die Entwicklungsvorgänge bei *Nephelis vulgaris* M. *Zool. Anz.* 21: 645-647.
- FILATOV, D.P. (1900). History of the development of *Nephelis vulgaris*. In *Transactions of the Department of Ichthyology of the Russian Imperial Society for Acclimatization of Animals and Plants*, Vol. 3, Studies of the Hydrobiological Station Established on the Glubokoe Lake by the Department of Ichthyology, pp. 42-71. (Russian).
- FILATOV, D.P. (Filatov, D.) (1904). Entwicklungsgeschichte des Exkretionssystems bei den Amphibien. *Anat. Anz.* 25 (2-3): 33-47.
- FILATOV, D.P. (1905). History of the development of the excretory system in Amphibia. *Transactions of Comparative-Anatomical Institute of the Moscow University* 1: 1-64. (Russian)
- FILATOV, D.P. (Filatov, D.) (1906). «Zur Frage über die Anlage des Knorpelschädels bei einigen Wirbeltieren.» *Anat. Anz.* 29.
- FILATOV, D.P. (Filatov, D.) (1907). Über die Metamerie des Kopfes von *Emys lutaria*. *Morphol. Jahrb., Ser. B* 37: 289-296.
- FILATOV, D.P. (1910). Summer and winter trips in Northwest Caucasus in 1909 for description of the Caucasian bison. *Yearbook of the Zoological Museum of the Imperial Academy of Sciences* 15: 171-217. (Russian).
- FILATOV, D.P. (1912). The Caucasian bison. *Transactions of the Academy of Sciences, Ser. VIII* 30 (8): 1-40.
- FILATOV, D.P. (1913). An account of a tour to the Commander islands in summer 1913. *Materials to the Knowledge of Russian Fishery* 3 (5): 1-112. (Russian).
- FILATOV, D.P. (1914). An account of a tour in summer 1914 to the Commander Islands. *Materials to the Knowledge of Russian Fishery* 4 (5): 1-18. (Russian).
- FILATOV, D.P. (1916). Ablation and transplantation of auditory vesicles in embryos of *Bufo*. *Russ. Zool. J.* 1: 27-54.
- FILATOV, D.P. (1925a). Biology and morphology of Aral Sea fish: Preliminary communication. *Russ. Zool. J.* 5: 36-52. (Russian).
- FILATOV, D.P. (1925b). Significance of early stages of some organogeneses. *J. Exp. Biol. Ser. B* 1 (1-2): 145-163. (Russian)

- FILATOV, D.P. (Filatow, D.). (1925c). Über die unabhängige Entstehung (Selbstdifferenzierung) der Linse bei *Rana esculenta*. *W. Roux Arch. Entwmech. Org.* 104 (1-2): 50-71.
- FILATOV, D.P. (Filatow, D.) (1925d). Ersatz des linsenbildenden Epithels von *Rana esculenta* durch Bauchepithel von *Bufo vulgaris*. *W. Roux Arch. Entwmech. Org.* 105 (3): 475-482.
- FILATOV, D.P. (1925e). The fate of transplanted lens in newt larvae and the reaction of the epithelium to the transplant. *Russ. Zool. J.* 4 (3-4): 3-13. (Russian).
- FILATOV, D.P. (1925f). Mechanism of development of the lens. *Proceedings of the Hydrobiological Station at the Glubokoe Lake* 6 (2-3): 68-72. (Russian).
- FILATOV, D.P. (Filatow, D.) (1926). Über die Entwicklung des Augenkeimes einiger Amphibien in vitro. *W. Roux Arch. Entwmech. Org.* 107 (3): 575-582.
- FILATOV, D.P. (Filatow, D.) (1927). Aktivierung des Mesenchyms durch eine Ohrblase und einen Fremdkörper bei Amphibien. *W. Roux Arch. Entwmech. Org.* 110: 1-32.
- FILATOV, D. P. (Filatow, D.) (1928). Über die Verpflanzung des Epithels und des Mesenchyms einer vorderen Extremitätenknospe bei Embryonen von Axolotl. *Roux' Arch. W. Roux Arch. Entwmech. Org.* 113: 240-244.
- FILATOV, D.P. (Filatow, D.) (1930a). Die Beeinflussung der Extremitätenanlage von Anuren durch in ihrer Nähe angebrachte Transplantate. *W. Roux Arch. Entwmech. Org.* 121: 272-287.
- FILATOV, D. P. (Filatow, D.) (1930b). Über die Wechselbeziehungen des Epithels und des Mesenchyms einer vorderen Extremitätenknospe beim Axolotl. *W. Roux Arch. Entwmech. Org.* 121 (1-2): 288-311.
- FILATOV, D.P. (Filatow, D.) (1930c). Entwicklungsmechanische Untersuchungen an Embryonen von *Acipenser guldens* und *A. stellatus*. *W. Roux Arch. Entwmech. Org.* 122 (3): 546-583.
- FILATOV, D.P. (1931). Importance of the size factor in acceleration of some morphogenetic processes. *J. Exp. Biol.* 1(2): 137-162. (Russian).
- FILATOV, D.P. (Filatow, D.) (1932). Entwicklungsbeschleunigung in Abhängigkeit von einer künstlichen Vergrößerung der Anlage. *Zool. Jahrb. Allg. Zool., Pt. 1:* 1-8.
- FILATOV, D.P. (Filatow, D.) (1933). Über die Bildung des Anfangsstadiums bei der Extremitätenentwicklung. *W. Roux Arch. Entwmech. Org.* 124.
- FILATOV, D.P. (1934a). Heterogenous induction of limbs and its importance for the theory of organogenesis. *Proc. Res. Inst. Exp. Morphogenesis* 1: 26-37. (Russian).
- FILATOV, D.P. (1934b). Determinational processes in ontogenesis. *Adv. Mod. Biol.* 3 (4): 440-456. (Russian).
- FILATOV, D.P. (1934c). Morphogenetic effect of the rudiment of the eye cup on the body epithelium in the common frog. *Biol. J.* 3 (2): 261-268. (Russian).
- FILATOV, D.P. (Filatow, D.) (1934d). Wie lange muss bei *Rana temporaria* die Augenbecheranlage auf das Korperepithel wirken, damit sich nach Entfernung des Bechers eine freie Linse entwickle. *Zool. Jahrb. Allg. Zool., Pt. I* 54(2): 224-236.
- FILATOV, D.P. (1935a). Ablation of auditory vesicle in pike embryos. *Proc. Dev. Dynamics* 10: 333-336. (Russian).
- FILATOV, D.P. (1935b). Removal and transplantation of eye rudiment in pike embryo. *Arch. Anat. Histol. Embryol.* 14 (1): 45-50. (Russian).
- FILATOV, D.P. (1936). Foreword. In *Experimental Zoology* (Eds. Huxley, E. and De Beer, G.R.), Biomedgiz, Moscow, pp. 1-15. (Russian translation).
- FILATOV, D.P. (1937a). Organ formation without the gastrulation process. *Biol. J.* 6 (2): 385-391. (Russian).
- FILATOV, D.P. (1937b). Importance of morphological characterization of the organs and their homologization. *Proc. USSR Acad. Sci., Proc. USSR Acad. Sci. (Sokl. Akad. Nauk. SSSR) Ser. Biol.* 3: 955-976. (Russian).
- FILATOV, D.P. (Filatow, D.) (1937c). Über die Linseninduzierung nach Entfernung des chordamesoderm bei *Rana temporaria*. *Zool. Jahrb. Allg. Zool., Pt. I* 58 (1): 1-10.
- FILATOV, D.P. (1939a). Some current topics of developmental mechanics. *Arch. Anat. Histol. Embryol.* 21 (1): 3-18. (Russian).
- FILATOV, D.P. (1939b). *The Comparative-Morphological Trend in Developmental Mechanics, Its Object, Aims and Methods*, USSR Acad. Sci. Press, Moscow. (Russian).
- FILATOV, D.P. (1940). Specific features of a new trend in developmental mechanics. *Proc. Moscow State University* 43: 7-13. (Russian).
- FILATOV, D.P. (1941a). The historical approach to the phenomena of developmental mechanics and its significance. *J. Gen. Biol.* 2 (1): 3-16. (Russian).
- FILATOV, D.P. (1941b). Some types of connections between developmental mechanics and comparative descriptive morphology. *Proceedings of the Institute of Cytology, Histology and Embryology*, USSR Academy of Sciences 1: 59-65. (Russian).
- FILATOV, D.P. (1943a). Developmental mechanics as a method of studying some problems of evolution. *J. Gen. Biol.* 4 (1): 28-64. (Russian).
- FILATOV, D.P. (1943b). Some features of the formation of supporting filaments in larvae of the Spanish newt. *Trans. (Doklady) USSR Acad. Sci.* 41(7): 324-326. (Russian).
- FILATOV, D.P. and DUPLAKOV, S.N. (1926). Results of study of the Aral Sea fish. *Bulletin of the Middleasian State University* 14: 203-230. (Russian).
- FILATOV, D.P. and DUPLAKOV, S.N. (1927). Results of study of the Aral Sea. *Bulletin of the Middleasian State University* 15: 339-383. (Russian).
- GINSBURG, A.S. (1950a). Age-related changes in the ectoderm of the auditory region in the frog. *Trans. (Doklady) USSR Acad. Sci.* 11(6): 1195-1196. (Russian).
- GINSBURG, A.S. (1950b). Species-specific features of early stages of development of the labyrinth in Amphibia. *Trans. (Doklady) USSR Acad. Sci.* 13(1): 229-232. (Russian).
- IGNATIEVA, G.M. (1979). *Fish and amphibian early embryogenesis. Comparative Analysis of the temporal regularities of development*. "Nauka" Press, Moscow, pp. 176.
- KOGAN, R.E. (1944). Chordamesoderm as inducer of auditory vesicles. *Trans. (Doklady) USSR Acad. Sci.* 45: 42-45. (Russian).
- KOLT'SOV, N.K. (1934). Genetics and the physiology of development. *Biol. J.* 3 (2): 420-456. (Russian).
- LEWIS, W.H. (1907). Experiments on the origin and differentiation of the optic vesicle in Amphibia. *Am. J. Anat.* 1: 259-278.
- LOPASHOV, G.V. (1960). *Mechanics of Development of Eye Rudiments in Embryogenesis of Vertebrates*. USSR Academy of Sciences Press, Moscow. (Russian).
- MALINOVSKII, A.A. and POPOV, V.V. (1943). D.P. Filatov: obituary. *J. Gen. Biol.* 4 (3): 129-133. (Russian).
- POLEZHAEV, L.V. (1946). D.P. Filatov (1876-1943) as a scientist and his role in developmental mechanics. *J. Gen. Biol.* 7 (5): 313-343. (Russian).
- POTEMKINA, D.A. (1953). Interactions between the mesonephros and the wolffian duct in Amphibia during formation of the excretory system. *Trans. (Doklady) USSR Acad. Sci.* 89(3): 577-580.
- SHEINA, A.P. (1940). Comparative study of the lens-forming properties of the body epithelium at the early stages of development of *Rana temporaria*, *Rana esculenta* and *Rana arvalis*. *Trans. (Doklady) USSR Acad. Sci.* 42: 72-74.
- SCHMALHAUSEN, O.I. (1950). Comparative experimental study of the early stages of development of the olfactory rudiments in Amphibia. *Trans. (Doklady) USSR Acad. Sci.* 74(4): 863-865.
- SCHMALHAUSEN, O.I. (1951). Conditions of formation and differentiation of olfactory organs during embryonic development. *Trans. (Doklady) USSR Acad. Sci.* 76(3): 469-471.
- SPEMANN, H. (1912). Zur Entwicklung des Wirbeltierauges. *Zool. Jahrb. Allg. Zool., Pt. I* 32: 1-98.
- SPEMANN, H. (1936). *Experimentelle Beiträge zu einer Theorie der Entwicklung*, Springer, Berlin.