

## Emil Godlewski, Jr. (1875-1944) pioneer of embryology at the Jagiellonian University of Krakow (Poland)

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**ABSTRACT** Emil Godlewski, Jr. (1875-1944) lived and worked in Krakow. He graduated from the Faculty of Medicine of the Jagiellonian University with the title of Doctor of Medical Science. He worked at the Faculty of Medicine, first in the Institute of Descriptive Anatomy and later as Professor of Biology and Embryology in the Department of Biology and Embryology, which he founded and led for many years. After early research on the development and histogenesis of muscles, professor Godlewski's scientific interests focused on regeneration and mechanisms regulating the process of fertilization, as well as early embryo development, blastulation and gastrulation. He was also interested in the origin of the primary differentiating cells in regenerates. He postulated the importance of epithelial tissue in this process and was the first to point out the change in the function, organization and role of the cells under the influence of external stimuli. Investigating fertilization and early development, he focused on the cooperation between the nucleus and the cytoplasm in the regulation of the early stages of development. Godlewski was also the author of the theory of migration of the inherited substances from the nucleus to the cytoplasm and, after their processing, from the cytoplasm to the nucleus. His works were never fragmentary, but always synthetical attempts at explaining important issues relating to the mechanisms of development. In 1936 Professor Godlewski was awarded the title of Member of the Pontificia Accademia delle Scienze. Apart from doing research and teaching, Emil Godlewski devoted a lot of time to social issues, especially those connected to medicine. When Poland regained independence after World War I, he actively participated in the reopening of the Jagiellonian University.

**KEY WORDS:** *Emil Godlewski, Jagiellonian University, embryology, fertilization, regeneration*

Emil Godlewski Jr., a son of Emil and Zofia, née Roszkowska, was born on August 12, 1875 in Holosk Wielki near Lwow. His father, Emil Godlewski Sr., was an eminent plant physiologist and coordinator of agricultural sciences in Poland. Godlewski Jr., completed his secondary school in Krakow, in 1893. Subsequently he enrolled in the Faculty of Philosophy of the Jagiellonian University. However, he became aware that the study of philosophy was not his vocation, therefore, after two years, he moved into the Faculty of Medicine at the Jagiellonian University. He graduated in 1899, obtaining the title of Doctor of Medical Sciences. It was already during his studies that he started to work as a volunteer in the Department of Descriptive Anatomy of the Jagiellonian University under the supervision of professor Kazimierz Kostanecki (1863-1940), a professor of anatomy and histology, who directed his interest to "development mechanics", a new approach to embryology, created by W. Roux. Kostanecki himself, was one of the first

biologists in Poland, who undertook experimental study of fertilization, parthenogenesis and mitotic divisions in embryos.

In 1901 Godlewski was appointed an assistant in the Department of Descriptive Anatomy of the Jagiellonian University. In 1902 he submitted his habilitation dissertation entitled: "Histogenesis of muscle tissue in skeletal muscles and heart in Mammals" (Godlewski, 1901a) and passed habilitation examination in front of the Council of the Faculty of Medicine of the Jagiellonian University, giving a lecture entitled: "Newest Outlooks on Regeneration". In the same year, Godlewski was nominated a docent of descriptive anatomy and embryology, and in 1911 he became professor in general biology and embryology. After the end of World War I when Poland regained independence in 1918, Godlewski, who still worked at Jagiellonian University, was nominated full professor of biology and embryology. From that moment, his academic, didactic and organizational activities were dedicated to Jagiellonian University.

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*Emil Godlewski*

**Fig. 1. Professor Emil Godlewski in 1935**, when he was Head of the Department of Biology of the Jagiellonian University, in Krakow, Poland.

Initially, Godlewski was involved in the studies of mitotic divisions during spermatogenesis of the snail (*Helix pomatia* L.). (Godlewski, 1897a, 1897b), and of muscle histogenesis (Godlewski, 1900, 1901a,b). Godlewski's numerous visits at the Zoological Station in Naples had a significant influence on his scientific development and resulted in long lasting personal contacts with the most prominent scientists involved in experimental embryology, such as Driesch, Herbst, Wilson, Morgan, Baltzer and many others.

During the later period, the research of professor Godlewski concentrated on two important embryological processes: regeneration of the lost parts of an organism, and fertilization. Research on the regeneration was carried out on the classical model organisms: marine colonial hydroid *Tubularia mesembryathemum* (Godlewski, 1904a) and amphibians. His study of tail regeneration in common newt led to one of the most spectacular discoveries, namely, the significance of the nervous tissue in post-amputation regeneration (Godlewski, 1904b). He believed that the nerves are necessary for proper regeneration of a lost organ, and showed that the critical number of nerve fibers in the amputation stump is necessary for the proper regeneration, whereas the type of these fibers is not important. This pioneering discovery paved the direction for further studies and for many years it was widely quoted by other authors studying the role of nerve cells in the initiation of regenerative processes. In his further studies of the role of nerves in regeneration, Godlewski took a special interest in the mechanisms of stimulation and inhibition of regeneration. His discovery that covering of the post-operative wound with a skin flap prevents the initiation of regeneration, whereas

partial covering allows the regeneration only in the uncovered part (Godlewski, 1928), played a key role in the development of the research on mechanisms of regeneration and was widely quoted by other researchers.

Godlewski also tried to find the source of undifferentiated cells from which regeneration blastema is built and which, after differentiation, are capable to restore the lost organ (Godlewski, 1910). He assumed, that these cells are of epithelial origin and they are capable of de-differentiation, i.e. they are able to return to the stem cell state. Subsequently, under the influence of proper stimuli, they may undergo metaplasia, and ultimately change into cells of other tissues. This idea, although erroneous, directed further research into the origin and manner of differentiation of blastematic cells.

Another field of Godlewski's interests covered various aspect of fertilization (Godlewski, 1906), and parthenogenesis (Godlewski, 1901b, 1911). His research of cross fertilization, and artificial parthenogenesis in invertebrates were particularly interesting. Although the process of fertilization is usually species specific, he proved that under experimental conditions (under the influence of factors normally inducing parthenogenesis) gametes of different species are able to fuse. Using this approach he was able to produce early embryos from Echinoidea eggs fertilized with sperms of other Echinoideans, snails or worms. He observed that these hybrid embryos, which most frequently developed only to the larval stage, experienced a plethora of chromosomal anomalies including the elimination of chromosomes. As a rule, there was an early elimination of maternal or paternal (depending on the model of experiment) chromosomes. Thus the development was directed solely by a genome of one species only.

These studies were also addressing the issue of the significance of ooplasm, egg cell nucleus and the sperm nucleus for the proper development and differentiation of the embryo (Godlewski, 1908). In order to clarify the role of the ooplasm, Godlewski improved the techniques of fertilization of the fragments of enucleated eggs of Echinoidea. Embryos that he produced by fertilization of enucleated Echinoidea eggs with sperm of Crinoidea, were able to develop to the gastrula stage. Contrary to the expectations, however, these embryos, did not have the traits of Crinoideans, i.e. they were developing according to the maternal program of differentiation, imposed by the egg cytoplasm of Echinoidea. This was a proof that the egg cytoplasm contains some kind of determinants that play a significant role in development. Godlewski suggested that, in the Echinoideans, the egg cytoplasm directs an early differentiation, and embryo development until the gastrulation stage (Godlewski, 1918, 1924a). These pioneering experiments were very innovative and sometimes were regarded as controversial, but later appreciated and widely accepted by other scientists.

The observations of the behavior of cell nuclei in the maturing oocyte and dividing blastomeres resulted in the hypothesis of migration of genetic material between the nucleus and cytoplasm (Godlewski, 1908, 1921), as a basis for proper differentiation. According to this theory, during oocyte maturation certain material migrates from the nucleus to the ooplasm where it is stored until fertilization. After sperm penetration, this material moves in opposite direction, i.e. from the cytoplasm to the zygotic nucleus where it influences developmental program, causing for example an intensive replication of chromosomes necessary for fast mi-

otic divisions during cleavage. Godlewski also thought that at the beginning of gastrulation, the nuclei supply the inheritance particles necessary for cell differentiation.

In recognition of his academic achievements, professor Godlewski was elected a member of the Polish Academy of Arts and Sciences and was granted the title of *honoris causa* doctor of the University in Lwow. He was an active member of the Warsaw Scientific Society and was an honorary member of many medical societies in Poland. Yet the greatest honour was his election, in 1936, to the Pontifica Accademia delle Scienze, an international society, operating under direct auspices of Pope Pius XI. Before World War II professor Godlewski was the only Polish scientist who was given the honour to be a member of this distinguished academic group.

The effects of scientific activity of Godlewski were not only numerous publications in leading scientific journals, but also reviews and monographic articles (Godlewski, 1909, 1923, 1925). Apart from this activity, in 1924 he wrote an excellent textbook of embryology, which was used by the students of medicine, biology and agricultural sciences (Godlewski, 1924b). The book was reprinted many times, and its updated versions were published after the end of World War II, already after Godlewski's death.

Neither research activity nor organizational and community service of professor Godlewski were obstacles to his didactic work with students. He conducted very interesting and up to date lectures of biology and embryology which were attended not only by students of the Faculty of Medicine but also by students of other Faculties of the Jagiellonian University, such as Faculty of Philosophy which included Natural Sciences, as well as Professor's colleagues and University authorities.

Apart from an intensive research and numerous teaching responsibilities at the Jagiellonian University, Godlewski took an active part in the community life. A particularly significant moment in his biography is marked by the period of World War I and immediately afterwards, where Poland's statehood was being reborn in the difficult post-war years in the ruined country. During the war he worked as a doctor in one of the military hospitals in Krakow. In 1914 in response to the call of the bishop of Krakow, Adam Sapieha, Godlewski joined the Bishop Committee gathering distinguished representatives of the community, including numerous professors of the Jagiellonian University, which was created to provide assistance for the poor, diseased, expatriated and those who suffered during the war. Professor Godlewski was the head of the sanitary section of the committee, whose aim was the establishment of mobile sanitary units and provisional hospitals. In recognition of his achievements in this field he was appointed, in 1920, the National Chief Commissary for the struggle with epidemics. He fulfilled all community, medical and organizational tasks with great commitment and diligence, without sparing his time or health.

The outbreak of World War II in 1939, occupation of Krakow by the Germans, and the closure of the Jagiellonian University by the occupants, combined with detention and expulsion to concentration camps of the majority of university professors and staff put an end to didactic and scientific activity of the Professor. Godlewski managed to avoid arrest and from the first days of the war, he tried to work for the welfare of the community. However, later the Nazis took over the Healthcare Department of the Jagiellonian University, which deprived Godlewski of any chance of carrying out his

activities. Moreover, he was forced, together with his family, to abandon his living place and was expatriated. The experience of war completely ruined the Professor's health – he fell seriously ill and died on April 25, 1944 in the result of an extensive cerebral hemorrhage.

Professor Godlewski was the founder and, for many years (1918-1939) the head of the Department of Biology and Embryology of the Jagiellonian University in Krakow. As the Head of the research group, he left a lot of freedom to his staff and students in choosing the field and subjects of their research. He educated many scientists who became later professors of the Jagiellonian and other universities in many branches of biology, not only embryology, but also histology, histochemistry, physiology, genetics or even biochemistry. Professor Godlewski's follower and successor in the Department of Biology and Embryology of the Jagiellonian University was Professor Stanislaw Skowron (1900-1976), his student, and later a co-worker. Skowron was granted the title of a professor already in 1938, yet his career was interrupted by the outbreak of World War II and his arrest, together with other professors of the Jagiellonian University. After being released from the concentration camp, upon return to Krakow, he started teaching in the underground Jagiellonian University, where he lectured on many biological topics, including embryology. After the war, he became the head of the Department of Biology and Embryology, which after re-organization of medical universities in 1950 and subsequent separation from the Jagiellonian University, was included into the Medical Academy. His scientific interests concentrated on embryology, genetics, evolution and medical biology. He was particularly interested in the regeneration process: he developed the concepts initiated by Godlewski on the role of nervous system in the process of regeneration and the origin of cells in the blastema. Skowron was interested also in

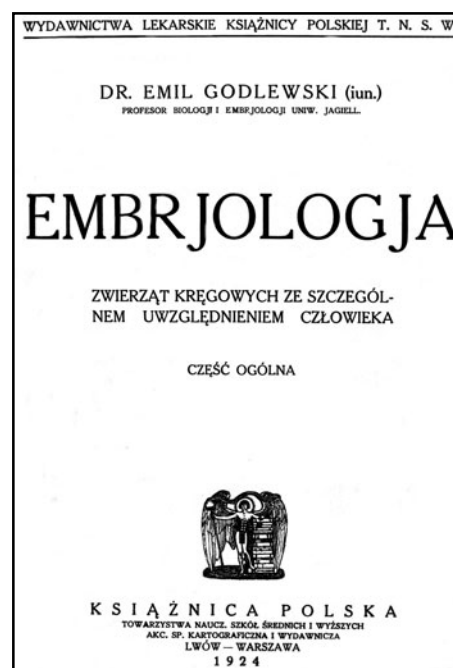


Fig. 2. The front page of the first edition (1924) of Emil Godlewski's book on embryology.

various aspects of early embryogenesis, such as the role of sperm in the generation of cleavage furrows, the mechanism of their formation, and the role of karyokinetic spindle in this process.

In 1965 Skowron resigned from the post of the head of Department of Biology and Embryology of the Medical Academy, and was replaced by professor Zbigniew Srebro (b. 1931). Under his supervision, the academic and didactic activities in embryology focused on the early stage of embryonic development and regeneration. While professor Srebro was the Department's head, another reorganization of Krakow Universities took place: the Department of Biology and Embryology was, in 1993, incorporated together with the entire Medical Academy into the Jagiellonian University. Currently, within the structures of the Collegium Medicum of the Jagiellonian University, and under a changed name, the Department of Human Developmental Biology, is headed by the author of this article. Currently, the main interests of the Department concentrate on gametogenesis, gamete physiology, and didactics in medical biology with special focus on embryology and genetics for the students of medicine and related fields.

## References

- GODLEWSKI, E. JR. (1897a). Über mehrfache bipolare Mitose bei der Spermatogenese von *Helix pomatia* L. *Anz. Akad. Wissensch, Krakau*, Februar: 68-81.
- GODLEWSKI, E. JR. (1897b). Über die Umwandlung der Spermatiden in Spermatozoën bei *Helix pomatia* L. (Vorläufige Mitteilung). *Anz. Akad. Wissensch. Krakau*, November: 263-267.
- GODLEWSKI, E. JR. (1900). Über die Kernvermehrung in den quergestreiften Muskelfasern der Wirbelthiere. *Bull. Acad. Sci., Cracovie*, Avril: 1-9.
- GODLEWSKI, E. JR. (1901a). Die Entwicklung des Skelet- und Herzmuskelgewebes der Säugethiere. *Bull. Acad. Sci. Cracovie Cl. Sci. Mathem. Nat*, Octobre: 353-358.
- GODLEWSKI, E. JR. (1901b). Die Entwicklung des Sauerstoffs auf die Entwicklung von *Rana temporaria* und Versuch der quantitativen Bestimmung des Gaswechsels in den ersten Entwicklungsstadien. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 11: 585-616.
- GODLEWSKI, E. JR. (1904a). Zur Kenntnis der Regulationsvorgänge bei *Tubularia mesembryathemum*. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 18: 111-160.
- GODLEWSKI, E. JR. (1904b). Versuche über Einfluss des Nervensystems auf die Regenerationserscheinungen der Molche. *Bull. Acad. Sci. Cracovie Cl. Sci. Math. Nat*. Decembre: 492-505.
- GODLEWSKI, E. JR. (1906). Untersuchungen über die Bastardierung der Echinideen- und Crinoideenfamilie. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 20: 579-643.
- GODLEWSKI, E. JR. (1908). Plasma und Kernsubstanz in der normalen und der durch äussere Faktoren veränderten Entwicklung der Echiniden. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 26: 278-328.
- GODLEWSKI, E. JR. (1909). Des Vererbungsproblem im Lichte der Entwicklungsmechanik betrachtet. In: Roux' Vorträge und Aufsätze über Entwicklungsmechanik der Organismen. Heft IX, Engelmann, Leipzig, pp. IV + 301.
- GODLEWSKI, E. JR. (1910). Plasma und Kernsubstanz im Epithelgewebe bei der Regeneration der Amphibien (Beitrag zur Analyse der Regenerationserscheinungen). *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 30: 81-100.
- GODLEWSKI, E. JR. (1911). Studien über die Entwicklungserregung I. Kombination der heterogenen Befruchtung mit der künstlichen Parthenogenese; II. Antagonismus der Einwirkung des Spermis von verschiedenen Tierklassen. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 33: 195-245.
- GODLEWSKI, E. JR. (1918). Der Eireifungsprozess im Lichte der Untersuchung der Kernplasmarelation bei Echinodermenkeimen. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 44: 499-529.
- GODLEWSKI, E. JR. (1921). Le problème du rapport entre le plasma et le noyau au cours du développement embryonnaire. *Rev. Gen. Sci. Pures Appliquées* 32: 156-158.
- GODLEWSKI, E. JR. (1923). Die Methodik der heterogenen Bastardierung. In: V. E. Abderhaldens Handbuch der biologischen Arbeitsmethoden, Aabt. V.: Methoden zum Studium der Funktionen der einzelnen Organen im tierischen Organismus, vol. III A.: Methodik der Entwicklungsmechanik. Urban und Schwarzenberg, Berlin, pp. 617-650.
- GODLEWSKI, E. JR. (1924a). Sur l'inactivation du sperme d'Oursin par le sperme d'espèces étrangères. *C. R. Soc. Biol.* 91: 84-86.
- GODLEWSKI, E. JR. (1924b). Embryology of Vertebrates with special emphasis on Man. General Part. (in Polish) (*Embriologia zwierząt kregowych ze szczególnym uwzględnieniem człowieka*. *Czescogolna*) Ksiaznica Polska, Lwow, pp. VII+416.
- GODLEWSKI, E. JR. (1925). Problem der Entwicklungserregung. Reifung und psychologische Eigenschaften der Geschlechtselemente; Physiologie der Befruchtung, Bastardierung, Polysperme. In: A. Bethe, G. Bergmann, G. Emden, A. Ellingers. Handbuch der normalen und pathologischen Physiologie. Springer, Berlin vol. 14/1, pp. 108-155.
- GODLEWSKI, E. JR. (1928). Untersuchungen über Auslösung und Hemmung der Regeneration beim Axolotl. *Wilhelm Roux' Arch. Entwicklungsmech. Organ*. 114: 108-143.

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