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Embryology at the Universities of Lwow and Wroclaw

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ABSTRACT Embryological research at the University of Wroclaw covers hormonal control of metamorphosis, primarily invertebrate embryology and gametogenesis, vertebrate myogenesis and the developmental impact of external factors. Developmental studies at the University of Wroclaw are a continuation of those conducted at the former Jan Kazimierz (Johannes Casimirus) University in Lwow before World War II. The Wroclaw embryological school is best characterized as comparative embryology which approaches embryonic development experimentally as well as through the analysis of its natural diversity.

KEY WORDS: *embryology, Wroclaw, Lwow*

Introduction

The developmental studies at the University of Wroclaw are a continuation of those conducted before World War II at the former Jan Kazimierz (Johannes Casimirus) University in Lwow, also known as Lemberg under the Austrian rule (1772-1918) and Lviv (since 1945 in Ukraine). The Wroclaw embryological school is best characterized as comparative embryology which approaches embryonic development experimentally as well as through the analysis of its natural diversity. This approach combines the mastery of laboratory techniques (cytological, cytochemical, and, recently, immunocytochemical and molecular) with the knowledge of natural history and relationships between species under study.

As a result of the Soviet invasion of Poland on September 17, 1939, the Jan Kazimierz University fell under the Soviet administration, and then, in June 1941, was taken over by the Nazis. Many faculty members were executed and some of them imprisoned and/or deported. With Soviet annexation of Poland's eastern territories, the majority of surviving scientists moved in 1945 to Wroclaw to set up a new academic center. The zoologists continued editing their journal *Zoologica Poloniae*, which had been started in 1935 by Benedykt Fulinski, Jan Hirschler, and Gustaw Poluszynski (Fig. 1). It continues to be published at the Institute of Zoology of the University of Wroclaw - its 50th volume appeared in 2006.

Embryology in Lwow

Embryological research was well represented at the Philosophical Faculty the Jan Kazimierz Uniwersity. Jozef Nusbaum–Hilarowicz [1859-1917] studied, among other things, the development and regeneration of the nemertine worms (Nemertinea) (Nusbaum –Hilarowicz, 1916) and authored the first Polish university textbook of general embryology. Jan Hirschler [1883-1951] studied insect gametogenesis and embryology. He coined the term „fusom" for a structure filling intercellular bridges in spermatogenesis and meroistic oogenesis (Hirschler 1935, 1955) (Fig 2D), and demonstrated that this structure is comparable to parts of the mitotic spindle. Diverse kinds of fusom-type connections were subsequently analysed by Stanislaw Pilawski [1909-1976] (Pilawski, 1933) (Fig. 2A) and Janina Orska [1908–1997], Orska (1934, 1938) (Fig. 2B). Another area of Hirschler's research was the hormonal control of metamorphosis. He described the induction of metamorphosis by the organs of metamorphosed individuals placed in the larval body cavity (Hirschler, 1922). Hirschler's research on metamorphosis was continued by Kazimierz Sembrat [1902–1988], who also reviewed Hirschler's papers (Sembrat 1933). Sembrat used the selachian thyroid to experiment with the development of lizards (Sembrat and Drzewiecki, 1936) and widely employed radioiodine in his developmental experimentation (Sembrat 1958). He also studied the early stages of cleavage in mammals, such as pigs and rats, as well as the reproductive cells of the turbellarians (Sembrat 1931), polychaetes (Sembrat 1934) (Fig. 2C), coelenterates, and amphibians. He described the accumulation of yolk in the mitochondria and the distribution of Golgi vesicles and vacuome in reproductive cells. Other embryological themes were addressed by Zofia Hirschler, Stanislaw Chudoba (Chudoba, 1934), and Ludwik Monné - the latter examined spermatogenesis in gastropods and mammals (Monné, 1928, 1932). Rudolf Weigl [1883–1957], who gained most of his fame for the

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development of typhoid vaccine, covered a wide research area including developmental biology, cytology, and microbiology.

Embryology in Wroclaw

Embryological research has been continued by two laboratories of the University of Wroclaw. (1) The Laboratory of General Zoology was headed first (1946-1975) by Kazimierz Sembrat, then (1975-1994) by Boguslaw Koscielski [1926 - 1994], and since 1994 by Antoni Ogorzalek. (2) The Laboratory of Comparative Anatomy was headed first (1946 -1960) by Kazimierz W. Szarski [1904 - 1960], who studied, among other things, the development of the reproductive system in birds, then (1960–1979) by Janina Orska who was succeeded (1979–1980) by Mieczyslaw Lecyk [1923 - 1980], and finally (1980–1998) by Boguslaw Kokurewicz. In 1999 the Laboratory was renamed to Vertebrate Zoology by its new head, Andrzej Elzanowski, and has since changed its research profile.

Developmental research conducted at the University of Wroclaw after World War II covered hormonal control, vertebrate myogenesis, invertebrate embryology and gametogenesis, primarily of insects and turbellarians, anuran embryogeny and gametogenesis, mammalian spermatogenesis, and developmental impact of external factors.

Research in the field of hormonal control of development in fishes, urodelan and anuran amphibians, birds, and some invertebrates was conducted by Kazimierz Sembrat and coworkers (Sembrat, 1956, Sembrat, Nowakowna, Radecka, 1957, Kassner and Siuda, 1963). The main techniques used were thyreoctomy, application of methylothiouracil, and implantation or injection of homogenized endocrine glands. Main accomplishment of this research was the discovery that metamorphosis is controlled by the thyroid and endostyle.

Comparative and phylogenetic studies of the myotomal myogenesis in anurans (*Bombina variegata, Xenopus leavis, Pelobates fuscus),* urodeles (*Triturus vulgaris),* and teleosts *(Thymallus thymallus, Esox lucius*) have been performed by Leokadia Kielbowna (Kielbowna 1981) and Malgorzata Daczewska


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Fig. 1. The front cover (obverse and reverse) of the 1st issue of *Zoologica Poloniae,* printed in Lwow in 1935.

(Daczewska, 2001). Main accomplishment of this studies was a demonstration that there are at least three types of myocyte differentiation among anamniote vertebrates, and the description of the role of mesenchyme in the muscle fiber formation.

Experimental embryology of turbellarians and insects, as well as gametogenesis of insects, were studied by Boguslaw Koscielski, in part in collaboration with his wife Krystyna. Main accomplishments of this research were the discoveries of polyembryony in turbellarians (Koscielski 1976) and parasitic hymenopterans (Koscielski and Koscielska 1985), and of induced polyembryony in thysanurans (Koscielski 1993). This research continued in the studies of polyebryony in strepsipterans by Noskiewcz and Poluszynski (1935) in Lwow.

Embryogenesis and gametogenesis of *Rana esculenta* and related anurans are studied by Maria Ogielska and coworkers (Ogielska and Wagner 1993, Ogielska and Kotusz 2004), Main accomplishment of this study were the description of anomalies called "*Esculenta* developmental syndrome", mechanisms of hybrydogenesis, intrapopulational polyploidy, and ovarian development in relation to age.

Comparative studies of mammalian spermatogenesis have been performed by Jolanta Bartmanska in the insectivores, bats, and rodents (Bartmanska 1987). This research follows in the footsteps of Janina Orska, Stanislaw Pilawski and Ludwik Monné at the Jan Kazimierz University. Main accomplishment of this study was the conclusion that bat is more similar to spermatogenesis in primates than to this in rodents and insectivores.

The impact of external factors, such as temperature, ionizing radiation, and pesticides on the development of fishes, amphibians, birds and mammals was studied by Janina Orska (1956), Anna Romankowowa, Mieczyslaw Lecyk (Lecyk, 1965), Boguslaw Kokurewicz (Kokurewicz, 1970), Andrzej Witkowski, Franciszek Indyk, Aurelia Pawlowska-Indyk (Pawlowska–Indyk, 1980), Alina Konachowicz-Ostrowska, and Barbara Trela-Pikulska. Main accomplishment of these studies were the discoveries that hypothermia and hyperthermia modify both the number and the shape of vertebrae, which turned out to be relevant to the fish taxonomy as well as to fish breeding and repopulation projects.

Invertebrate oogenesis and embryogeny have been studied by Marian Paschma on oligochaetes (Paschma 1962); Boguslaw Koscielski and Leokadia Kielbowna on molluscs; BarbaraTerpilowska, Ryszard Adamski, Janusz Kubrakiewicz and Malgorzata Klimowicz on crustaceans (Kubrakiewicz and Klimowicz 1994); Janusz Kubrakiewicz on myriapods (Kubrakiewicz1991); Izabela Jedrzejowska and Zofia Badian on arachnids; Antoni Ogorzalek and Bozena Simiczyjew on the heteropteran and mecopteran insects (Simiczyjew *et al.,* 1998, Simiczyjew, 2005); and Janusz Kubrakiewicz, Marta Mazurkiewicz and Izabela Jedrzejowska on the raphidiopteran and dipteran insects (Jedrzejowska and Kubrakiewicz 2002, Mazurkiewicz and Kubrakiewicz, 1998). This research is a continuation of work by the late Jan Hirschler and Kazimierz Sembrat. Main accomplishment of these studies were the discovery of meroistic oogenesis in the oligochaetes and solitary oogenesis in the myriapods and fish lice (Branchiura, Crustacea); discovery of the asynchronic formation of cystocyte clusters in neuropterans, the discovery of the induction of follicular epithelium differentiation and vitellogenesis by the oocyte nucleus in heteropterans (Ogorzalek, 1987); and the demonstration of phylogenetic pattern in the structure and

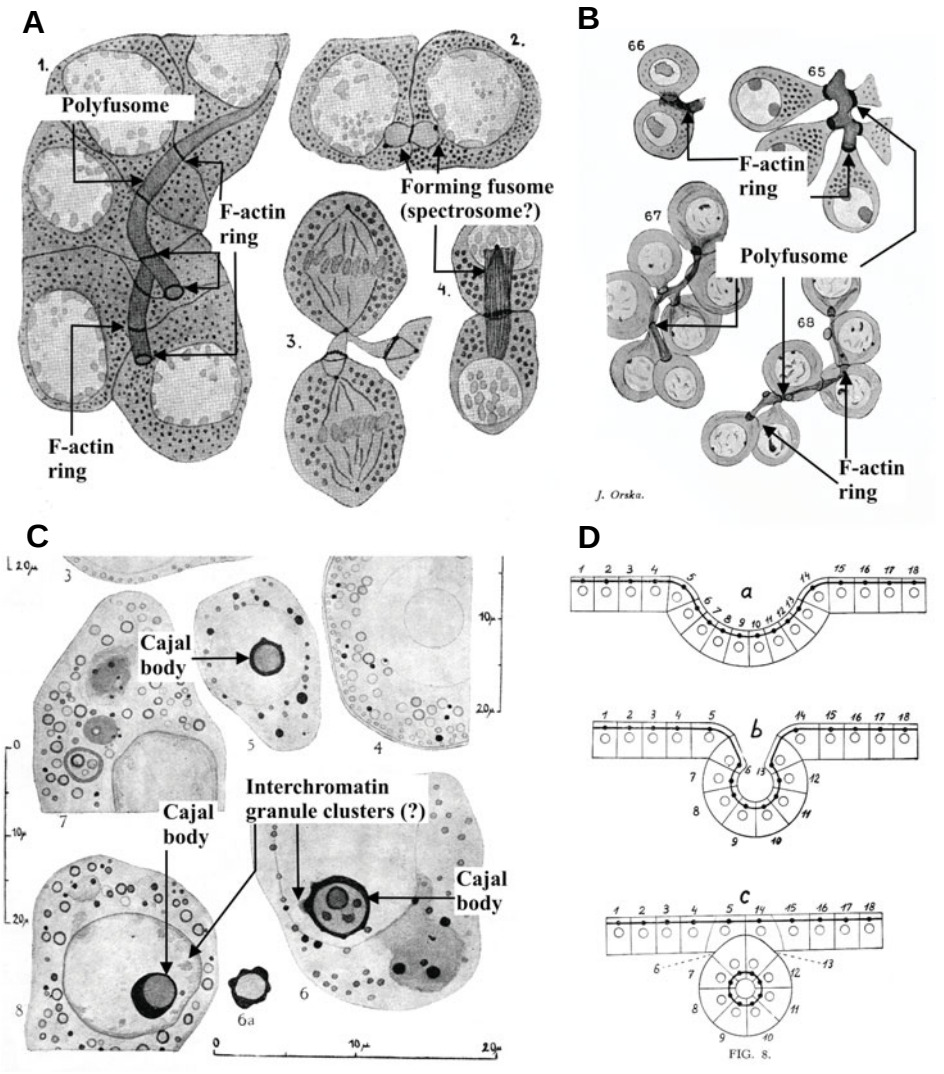

Fig. 2. Selected figures from the papers published by Polish embryologists at Lwow University before World War II. (A) *Spermatogenesis in the tiger beetle* Cicindela campestris *as shown in Plate I in Pilawski, S. (1933). Die Protoplasmastrukturen in der Käferspermatogenese* (Phyllobius glaucus *Sc.,* Cicindela campestris *L.,* Cicindela hybrida *L.* Galerucella nympheae *L) Teil II. Der Spindelrestkorper und das Centro- und Nukleofusom. Die Golgiapparat, das Vakuom un die Mitochondrien bei* Galerucella nymphae *L. Archiwum Towarzystwa Naukowego we Lwowie. 7: 1-82. Original caption: "1 - Rest bodies of cylindric type, mitochondria. 2 - Rest bodies of spherical type and mitochondria. 3 - Spermatogonia in metaphase stage, rest bodies, centrosomes and mitochondria." Current terms are shown in white rectangles.* **(B)** *Spermatogenesis in the honeybee* Apis mellifera *(formerly* Apis mellifica*) as shown in Plate 1 in Orska (1938). Les recherches cytologiques sur la spermatogenèse de l'abeille domestique (*Apis mellifica *L.). Arch. Towarzystwa Naukowego we Lwowie. 10, 1, 1 - 82. Original caption: "65 - spermatogonia connected by rest body. 66 - formation of rest bodies in telophase. 67, 68, 69 - stages of growing spermatocytes interconnected by the bundles of rest bodies." Current terms are shown in white rectangles.* **(C)** *Vitellogenesis in the Green-leaf worm* Eulalia viridis*, a phyllodocid polychaete, as illustrated in Sembrat, K., 1934, Vacuome and chondriome in the vitellogenesis of* Eulalia viridis *O. F. Muller. Kosmos, 58, 1-4, 341 - 354. Original captions: "5-6.* Eulalia viridis*, early oocytes. Dietrich-Parat Altmann. Mitochondria (some of them swelling), budding nucleoli, and the chromophil substance are to be seen. Fig. 6a shows the nucleolus of the next section through the oocyte represented in fig. 6. 7-8. Later oocytes. Dietrich-Parat, Volkonsky. Further transformation of the mitochondria into yolk spheres. Yolk elements present a mitochondrial envelope. In the cytoplasm the chromophil substance is to be seen." Current terms are shown in white rectangles.* **(D)** *Morphogenesis of the neural tube and eye lens in Amphibians as shown in Plate 8 a-c in Hirschler, J., (1955) On the cooperation of fusomes in the development of egg nurse - cell complexes in animal ovary. La Cellule, 58, 1: 67 - 87.*

function of arthropod ovaries (joint project with the Institute of Zoology of the Jagiellonian University, Krakow).

Outlook

Embryological research carried out at the Institute of Zoology of the University of Wroclaw has been changing over the last years. Some themes (such as polyembryony and hormonal control of development) were terminated while others have been expanded. At present, we conduct research on myogenesis, differentiation of egg chambers in dipterans, phylogenetic patterns in the structures of insect ovaries, induction of follicular epithelium differentiation and vitellogenesis, and amphibian development and reproduction. A selection of our results obtained in the years 2000-2005 is published in this issue of the IJDB.

Comparative studies of myotomal myogenesis of fishes, amphibians, reptiles and birds are carried out as part of the 6th European Framework Programme (MYORES) in cooperation with Clermont Ferrand of INSERM. We apply molecular markers for myocyte differentiation in *Drosophila melanogaster* (Soler *et al.,* 2004), dipnoans (*Neoceratodus forsteri*), chondrosteans (*Acipenser baeri*), and reptiles (*Lacerta agilis*) (Daczewska 2006, Kacperczyk and Daczewska 2006). We use TEM in addition to immunocytochemistry, molecular probes and *in situ* hybridization.

Research on the differentiation of egg chambers in dipterans is carried out as part of the Polonium Programme, in cooperation with INSERM, Clermont Ferrand, France. Studies of the ovaries and strategies of RNA synthesis and accumulation in the raphidopterans, mecopterans and heteropterans are primarily related to the studies on the phylogenetic patterns.

Studies using -TEM and -immunogold - methods, of modeling of the induction of follicular epithelium differentiation by the oocyte nucleus and of vitellogenesis in hemipterans are performed in cooperation with the Institute of Cytology of the Russian Academy of Sciences, Saint Petersburg. They involves tracing the distribu-

tion and activity sugar metabolism enzymes (aldolase and fructose-1,6-bisfosphatase) in ovarioles (Dziewulska and Ogorzalek 2005) and defining domains in the oocyte nucleus.

Research on amphibian development and reproduction focuses on the age-dependent development of gonads and gametogenesis. Stereological techniques are used for the examination of gonads and skeletochronology is used for determination of individual age (Rosenblut and Ogielska 2006).

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